
W8

Fraxinus excelsior-*Acer campestre*-*Mercurialis perennis* woodland

Synonymy

Oak-hazel woods Moss 1907; Damp oakwood association Moss *et al.* 1910; Ash-oakwood association Moss *et al.* 1910; Ashwood association Moss *et al.* 1910; *Quercetum roburis* Tansley 1911; *Fraxinetum excelsioris* Moss 1911; *Fraxinetum excelsioris calcar-eum* Tansley & Rankin 1911; *Quercetum roboris* Tansley 1939 *p.p.*; *Fraxinetum calcicolum* Tansley 1939; *Dryopterido dilatatae*-*Fraxinetum* Klötzli 1970 *p.p.*; *Quercu-Fraxinetum* Klötzli 1970 *p.p.*; *Hyperico-Fraxinetum* Klötzli 1970 *p.p.*; Ash-maple-hazel woodlands Rackham 1980 *p.p.*; Hornbeam-woods Rackham 1980 *p.p.*; Limewoods Rackham 1980 *p.p.*; Elmwoods Rackham 1980 *p.p.*; Ash-wych elm woodland Peterken 1981 *p.p.*; Ash-maple woodland Peterken 1981; Hazel-ash woodland Peterken 1981 *p.p.*; Ash-lime woodland Peterken 1981 *p.p.*; Hornbeam woodland Peterken 1981 *p.p.*; Suckering elm woodland Peterken 1981; Woodland plot types 1, 2, 3, 4, 5, 6, 7, 8 & 12 Bunce 1982; *Quercu-Ulmetum glabrae* Birse & Robertson 1976 *emend.* Birse 1984 *p.p.*

Constant species

Acer campestre, *Corylus avellana*, *Fraxinus excelsior*, *Mercurialis perennis*, *Rubus fruticosus* agg., *Eurhynchium praelongum*.

Rare species

Cardamine impatiens, *Daphne mezereum*, *Festuca altissima*, *Ribes alpinum*, *Primula elatior*, *P. vulgaris* × *elatior*, *Tilia platyphyllos*.

Physiognomy

Although individual kinds of *Fraxinus excelsior*-*Acer campestre*-*Mercurialis perennis* woodland are amongst our most distinctive and readily-recognisable woodland types, this community as a whole is very diverse, in both the floristics of the field layer and the composition and structure of the woody component. The patterns of variation in these separate elements are complex

enough, but they can be systematised fairly readily into sets of either different field layers or different canopy types. The real problem here is in relating the two because, though field-layer and canopy differences are by no means independent, variation in the one is not fully consonant with variation in the other, largely because of the very great influence which different silvicultural treatments have had on this kind of woodland, sometimes working with diversity related to natural factors like climate and soil, sometimes not. This makes it very difficult to devise a single satisfactory scheme for comprehending the variation included here and, with this community, more than ever, it should be remembered that the sub-communities represent a necessarily approximate summary of diversity which is complex and multi-directional. Exceptionally here, as an additional guide to variation within the community, the following general account has been sub-headed.

Major variations within the canopy

In essence, these are woodlands in which *Fraxinus excelsior*, *Acer campestre* and *Corylus avellana* provide the general diagnostic character of the woody component, though they are not always ash-maple-hazel woods in the sense of Rackham (1980) and Peterken (1981). Often, these three species do dominate in various proportions and then they frequently form the basis of some kind of coppiced underwood (though often now abandoned) but they are sometimes relegated to a minor role within coppice characterised by a local abundance of trees which are no more than occasional throughout the community as a whole, and they also occur widely here as elements of more diverse and structurally complex high forest. Some *Fraxinus* plantations, often with very little *Corylus* and *A. campestre*, or none, are also best included here on the basis of the general similarity of the vegetation.

The next most common tree throughout is oak, though there is a fairly sharp distinction among *Fraxinus*-*Acer*-*Mercurialis* woodlands as to which of the two species predominates. This is a reflection of edaphic

variation and is expressed in geographical terms because the heavier kinds of base-rich soil favoured by *Quercus robur* are predominantly to the south-east of a line from the Severn to the Humber. In this region, *Q. robur* is a very frequent constituent of these woodlands, so much so that, in early descriptive accounts, they were usually described as some kind of 'oak woodland' (e.g. Moss 1907, Moss *et al.* 1910, Tansley 1911, 1939). In fact, the abundance of oak in individual stands is very variable and often low: frequently, *Q. robur* is present only as the occasional timber trees in coppice-with-standards and, even there, it is now often overshadowed by emergent maidens of *Fraxinus* or the uncut poles of large-coppice underwood. Only rarely is it truly a dominant: in some places (as in parts of Hatfield Forest in Essex), it persists in abundance in abandoned underwood and occasionally, as with *Fraxinus*, it predominates in plantation replacements of this community. Nonetheless, though it is rather unhelpful to refer to these *Fraxinus-Acer-Mercurialis* woodlands as 'oak woods', the high frequency of *Q. robur* is the best preferential feature of the canopy in one suite of sub-communities (a–d on the table) which show a predominantly south-eastern distribution, extending to the north-west only where the soils are locally heavy and moist.

In these kinds of *Fraxinus-Acer-Mercurialis* woodland, *Q. petraea* and hybrid oaks are, generally speaking, rare. Locally in the south-east, they can make an appearance where small stands of *Fraxinus-Acer-Mercurialis* woodland mark out somewhat more base-rich conditions, as on stream-side flats, within *Quercus-Pteridium-Rubus* woodland (where *Q. petraea* is frequent) but such situations are but a minor exception. To the north and west, by contrast, *Q. petraea* and sometimes the hybrids tend to predominate, even partially replacing *Q. robur* on moister soils and becoming the usual kind of oak in the remaining sub-communities (e–g on the table) which are characteristic of more free-draining, base-rich soils over permeable limestones, very much the habitat of the *Fraxinus-Acer-Mercurialis* woodlands in this region.

But it is a very striking feature of these woodlands to the north-west that the occurrence of oak is very patchy. In some places, as along the Welsh borders, around Morecambe Bay and in the North York Moors, *Q. petraea* shows high frequency: elsewhere, as in woodlands in Derbyshire and many Yorkshire Dales, oak is relegated almost to the status of a rarity. Perhaps, here, superimposed on to the basic pattern of oak distribution in relation to soil and climate, we can see the effects of localised clearance and regeneration of these woodlands in the north-west in which oak, once removed, has failed to re-establish itself as a canopy component at the high levels of frequency which it still shows in the south-east

(Pigott 1969, Merton 1970). Not that, even there, oak regeneration is a simple matter because saplings of *Q. robur* are now generally scarce and local in coppiced stands of the community (e.g. Watt 1919, Streeter 1974, Rackham 1980). In early accounts, the great emphasis on the diagnostic value of oak often led to the north-western woodlands in which its occurrence is sporadic being classified quite separately as some kind of '*Fraxinetum*' with various types of 'oak-ash woodland' as intermediates between this and 'oak woodland' proper (e.g. Moss 1911, Tansley & Rankin 1911, Tansley 1939).

This difference in the representation of different species of oak in these woodlands is overlain by a further marked variation among the trees of the community which gives the north-western sub-communities a much clearer positive characterisation than that provided by *Q. petraea*. This involves *Ulmus glabra* and *Acer pseudoplatanus* which, generally speaking, are rare in south-eastern *Fraxinus-Acer-Mercurialis* woodlands but, towards the north-west, become very frequent and often abundant as components of high-forest or large-coppice underwood and as regenerating saplings. However, this distinction, which can convincingly be related to the wetness of the climate, does not follow quite the same geographical line as that shown by the oaks. Across the Midlands, it makes roughly the same separation along a Humber–Severn line but, further south, *Fraxinus-Acer-Mercurialis* woodlands with much *U. glabra* and *A. pseudoplatanus* occur commonly in the wet south-west peninsula and, further east, pick out locally wet sites like the north-facing coombes cut into the downland of the Home Counties. Here, then, the geographical separation between the two suites of sub-communities becomes rather blurred, though the floristic distinction on *U. glabra* and *A. pseudoplatanus* remains a good one and southern stands can usually be allocated to one or the other group without difficulty. The value of these two trees in making a major separation among these woodlands was recognised by Klötzli (1970), though his *Dryopterido-Fraxinetum* (with *U. glabra* and *A. pseudoplatanus*) and *Quercus-Fraxinetum* (generally without) do not exactly correspond with the two groups characterised here. *U. glabra* has also figured prominently in the diagnosis of distinctive western base-rich woods in Peterken's scheme (1981). In fact, of the two species, *A. pseudoplatanus* is the sharper indicator of the wetter climatic conditions, though it has often been neglected in classifications of British woodlands, perhaps because it is an introduction: it probably arrived here in late medieval times (Jones 1945). It is, however, very much at home now in the north-western *Fraxinus-Acer-Mercurialis* woodlands and shows exactly the same response to wetness of climate in Britain as it does in mainland Europe, where it is strikingly sparse in drier areas like

the Paris Basin (Pigott 1984). With the demise of *U. glabra* as Dutch Elm Disease spreads through our northern woods, it might be expected to increase its representation even further. Indeed, there already are some areas, like certain of the Durham coastal dunes, where, for some reason, *Fraxinus* and *A. pseudoplatanus* dominate to the virtual exclusion of *U. glabra*.

Other trees in the community

Of the other tree species which occur in this community, none is as generally common as those dealt with above and the patterns of occurrence, in terms of both frequency and abundance, are very variable. Some species are found occasionally throughout; others, though infrequent overall, show varying degrees of preference for different sub-communities or either of the two main suites of sub-communities. Some are characteristically solitary; others usually occur as scattered individuals but can, on occasion, be locally prominent; yet others typically occur with striking local abundance. Such variations are partly a reflection of responses to climatic and edaphic differences and partly related to the growth form of the particular trees; very often, though, they are also strongly influenced by different silvicultural treatments. Hardly any of these trees show an exclusive association with the *Fraxinus-Acer-Mercurialis* woodland as a whole; it is, rather, their occurrence here with *Fraxinus*, *Corylus* and *A. campestre* (and with the characteristic field layer of the community) that is distinctive. The community is also defined, in a negative fashion, by the absence or great infrequency of certain tree species, though some of its floristic boundaries with other kinds of woodland are rather hazy.

Among the infrequent and generally sparse associates here, the most widespread is birch. Both *Betula pendula* and *B. pubescens* occur, though the former is a little commoner overall and not so much confined to the heavier soils typical of the south-eastern sub-communities. Although both species can be coppiced, they are typically found as maiden poles which have originated from wind-blown seed that has germinated after coppicing or in natural gaps. Quite commonly, now, birch trees of about 35–40 years old can be found, perhaps related to the widespread, though sporadic, coppicing that occurred in the cold winter of 1946/7, usually without any weeding afterwards. Given sufficient light, birch can attain a grand stature here but, where woods have been well managed, the trees characteristically remain as scattered individuals, in contrast to most kinds of *Quercus-Pteridium-Rubus* woodland where birch, especially *B. pendula*, is a very frequent canopy tree and the commonest coloniser of gaps. Even here, however, drastic clearance with subsequent neglect can give birch an opportunity to attain a disproportionate temporary prominence. It has also been noted as an important

component of early seral stages in the development of *Fraxinus-Acer-Mercurialis* woodland in some places over the limestones of the north-west, as in Derbyshire, where its increase was especially noticeable after myxomatosis (Merton 1970).

Two other trees which frequently accompany birch in woodlands on less base-rich soils throughout Britain, *Ilex aquifolium* and *Sorbus aucuparia*, are, like birch, rather uncommon here, though both are a little more frequent in north-western *Fraxinus-Acer-Mercurialis* woodlands than to the south-east. *Ilex* is the commoner, occurring sometimes in the tree canopy, though more usually as scattered individuals in the understorey and its distribution in this community reflects its general avoidance of areas with a more continental climate. *Sorbus aucuparia* is generally less frequent and, among the north-western *Fraxinus-Acer-Mercurialis* woodlands, is strongly preferential to the distinctive *Teucrium* sub-community.

Much more strictly non-gregarious than these species are *Sorbus torminalis* and *Malus sylvestris*: indeed, these often occur so sparsely as to be missed if only single canopy samples, even very large ones, are taken from woods, though they often turn up if whole sites are searched. *S. torminalis* is a suckering tree which can grow to a considerable size; *M. sylvestris* is smaller, though it was rarely coppiced and can attain a venerable appearance with its sturdily-branched round crown. Feral *M. communis* can also seed into woodland of this kind. A third non-gregarious tree, the wild (though possibly introduced) pear, *Pyrus communis*, occurs much more rarely (e.g. Rackham 1975, 1980).

Similarly infrequent, though often showing a local abundance when they do occur, are *Populus tremula* and *Prunus avium*, both of which sucker to produce usually small clones. The former shows a distinct preference for the generally moister soils of the south-eastern *Fraxinus-Acer-Mercurialis* woodlands, particularly for those of the *Anemone* and *Deschampsia* sub-communities where waterlogging can continue well into late spring. *Prunus avium*, by contrast, seems to favour better-drained ground. It is not associated with any particular sub-community, but it does tend to be more obvious over wood-banks and perhaps also in more recent stands of this kind of woodland (Rackham 1980).

The remaining group of characteristic trees is rather different. These are species which, though infrequent in the community as a whole, show a distinctly preferential occurrence among the south-eastern sub-communities and which often occur there with a very marked local dominance, so much so that, in some schemes (e.g. Rackham 1980, Peterken 1981), they have been used as the diagnostic markers of quite separate kinds of woodland. This solution is not adopted here though, because

of the importance accorded to these trees elsewhere and because of their particularly complex (and different) patterns of occurrence, some special notes on each have been appended at the end of this general account. Two of these species, *Tilia cordata* and *Carpinus betulus*, are not confined to *Fraxinus-Acer-Mercurialis* woodland. They occur in a number of other communities, most notably the *Quercus-Pteridium-Rubus* woodland, the counterpart of this community on somewhat less base-rich soils and, if anything, the stands they dominate there tend to be more extensive. Both species can be found as scattered individuals, when they have sometimes formed part of a mixed-coppice crop; isolated trees of *Tilia*, in particular, also often occur as relics of a previous woodland cover. But both these trees are gregarious and both cast dense shade and they are often found here as dominants (sometimes alone, sometimes mixed) and dominants of a very uncompromising kind. Very often, the structural uniformity of this kind of *Fraxinus-Acer-Mercurialis* woodland has been further accentuated by generations of cropping for large-coppice underwood. It should be noted that *Castanea sativa*, which is often found in association with *Tilia* and *Carpinus* in *Quercus-Pteridium-Rubus* woodland is typically very rare here.

The other trees which are important as local dominants in south-eastern *Fraxinus-Acer-Mercurialis* woodlands are the invasive elms referred to the *Ulmus carpinifolia* and *procera* sections. These are very aggressive trees which are able to expand into existing tracts of woodland and into previously unwooded ground by the suckering of clonal patches. They are not confined to this community, though their expansion seems very much to be centred on it and their invasion results in the development of a rather uniform and simple physiognomy, often in association with a distinctly eutrophic kind of field layer. Much more locally, this community can be dominated by a range of other elms which seem mostly to be hybrids between *U. carpinifolia* and *U. glabra* (Rackham 1980).

Finally, among the tree associates, there are those species whose scarcity helps to define the floristic limits of the *Fraxinus-Acer-Mercurialis* woodland and these are worth mentioning because some of these boundaries can be rather imprecise, depending on the particular area and situation in which this community is encountered. The first case concerns *Fagus sylvatica* and, to a lesser extent, *Taxus baccata*, for on lighter, base-rich soils in southern Britain, these species, and especially *Fagus*, become important competitors of the major trees of this community and often relegate it to the status of a seral stage in the development of high forest dominated by beech or, more locally, yew. As defined here, the *Fraxinus-Acer-Mercurialis* woodland takes in vege-

tation which some early authors classed as successional facies of these other woodland types or as treatment-derived woodland from which *Fagus* had been systematically removed (e.g. Adamson 1921, Watt 1923, 1924, 1925, 1926, 1934a, b, Tansley 1939). Both *Fagus* and *Taxus* occur here only very infrequently, as either sparse members of the tree canopy or, especially with *Fagus*, as scattered saplings, but it is important to realise that intermediate stands can occur in which either or both of these trees increase somewhat in abundance over a field layer which can remain virtually unchanged. Although *Fagus* has been widely planted beyond its supposed natural limit in Britain and can flourish much further north on soils favoured by *Fraxinus-Acer-Mercurialis* woodland, it generally dominates there in replacements for woodlands on more acid soils and so does not often pose such sharp problems of definition as in the south. *Taxus*, likewise, is only locally dominant in the north though, in a few places, as around Morecambe Bay and in Castle Eden Dene in Durham, it may be difficult to separate stands in which it has become abundant from the surrounding vegetation of this community.

Generally much less difficult but locally a problem around flushes or on very wet plateaus with perched gleys is the interface with various kinds of *Alnus glutinosa* woodland. *Alnus* is a rare tree in the *Fraxinus-Acer-Mercurialis* woodland, occurring only as scattered individuals on wetter soils of the *Anemone* and *Deschampsia* sub-communities, where it has often been included in a coppice crop, but it can become more abundant where stands of this community include areas of permanently waterlogged ground and then it may be difficult to discern a boundary. Also, when *Fraxinus-Acer-Mercurialis* woodland on wetter ground is coppiced, the more extreme kinds of *Deschampsia* field layer which develop then may become temporarily identical to the herbaceous element of the *Alnus-Fraxinus-Lysimachia* woodland.

Shrubs of the understorey or small-coppice underwood

Because of the frequent treatment of this kind of woodland as coppice, the typical canopy/understorey structure of high forest is often absent here, especially among the south-eastern sub-communities where coppicing has been more universal. There, the typical shrubs of the community have often provided the basis of small-coppice underwood cut on a variety of rotations, though, with the widespread abandonment of such treatment, very many stands have lost a well-defined coppice physiognomy. In the north-western sub-communities, where a high-forest structure is more common, the shrubs often occur as an understorey in the strict sense, forming a frequently rather open lower tier to the woodland. In fact, in both regions now, a whole range of structures between simple coppice or coppice-with-

standards and high forest can be seen. And, superimposed on to this structural variation, there are, as with the trees, some distributional patterns among the shrubs which reflect edaphic and climatic differences between the regions.

As noted above, *Corylus avellana* is one of the most frequent woody species throughout this community and, in coppice, except where the crop consists of trees like *Tilia cordata* and *Carpinus betulus*, it is usually the most abundant component, and almost always the most prominent shrub, of the underwood. In such situations, its high frequency is natural but its great abundance is not: it reflects the ancient and widespread recognition of the general facility with which it responds to coppicing and an appreciation of the particular qualities of its young rods. The favouring of *Corylus* may also have extended to planting it in some woods to further increase its contribution to the underwood. Such a predominance is not limited to *Fraxinus-Acer-Mercurialis* woodland. It is widespread, too, in coppiced *Quercus-Pteridium-Rubus* woodland and, where uniform sylvicultural treatment has been imposed over boundaries between these two communities, an identical coppice composition and physiognomy may extend over the different field layers. Where the *Fraxinus-Acer-Mercurialis* woodland occurs as high forest, as it does more commonly to the north-west, *Corylus* remains frequent, though it is rarely so disproportionately abundant.

Apart from *Fraxinus* and *Acer campestre*, the most frequent woody companions of *Corylus*, though rarely rivalling it in cover in coppices, are the hawthorns. *Crataegus monogyna* is the more common species overall and, among the north-western sub-communities, it is the usual woodland hawthorn. *C. laevigata*, by contrast, is very much a preferential for the south-eastern sub-communities and, within this region, is much more obviously restricted to long-established stands of this community than is *C. monogyna*, which also occurs widely in younger tracts of *Fraxinus-Acer-Mercurialis* woodland, in plantation replacements of it and around its scrubby margins. When the two occur in close proximity, as they often do, their different habits and phenology can be well seen. *C. monogyna* is, strictly speaking, a small tree with a single bole, though it can be coppiced; *C. laevigata* is an untidy, multi-stemmed bush and lends itself better to cutting, under which treatment it can form stools of very considerable size (e.g. Rackham 1975). It also comes into leaf and flowers a little earlier than does *C. monogyna*. However, the two species hybridise very freely – hybrids are as common in the data as pure *laevigata* – and individual populations can show a complete range of variation between the parents (Bradshaw 1953). Both species, especially *C. laevigata*, are shade-tolerant and will persist in overgrown cop-

pice. Very big trees of *C. monogyna* can also occasionally be found growing up into the tree canopy of high forest *Fraxinus-Acer-Mercurialis* woodland.

Considerably less common than the hawthorns but occurring throughout and with patchy abundance are *Sambucus nigra* and *Prunus spinosa*. The former is very much a scrub of more eutrophic situations: it is more common and sometimes prominent where older stands of the community have been disturbed and enriched in some way and in younger woods where it is often associated with species-poor canopies of *Fraxinus* and *Crataegus monogyna* as in the *Hedera* sub-community. It is also somewhat more common in the north-western sub-communities where the free-draining soils may be naturally more eutrophic (see below). *Prunus spinosa* is less frequent than *Sambucus* but likewise rather sporadic in its occurrence: it is especially characteristic here of the more open post-coppice and ride vegetation of the *Deschampsia* sub-community where it can form dense suckering patches.

Cornus sanguinea is another associate which can attain local prominence in more open stands but it is also very much an indicator of more base-rich soil conditions, becoming more frequent where this community extends on to more calcareous superficals or on to rocky sites over the north-western limestones. *Euonymus europaeus* and *Ligustrum vulgare*, frequent companions of *Cornus* in scrub over our lowland limestones, also occur here, though less commonly than *Cornus*.

Finally here, though *Alnus glutinosa* is very uncommon, low frequencies of *Salix caprea* and, to a lesser extent, *S. cinerea*, are quite characteristic and their scattered bushes or trees are especially distinctive in early spring when the catkins appear before the canopy has come into leaf. Both species coppice very well, *S. cinerea* producing the most rapidly-growing spring of all the underwood species; when they are left, both can attain a substantial size. *Viburnum opulus*, a common associate of *S. cinerea* in fen carr, also occurs here at low frequencies and on moister soils.

Major variations in the field and ground layers

Like the woody component of this woodland, the field layer here is very variable but a good qualitative definition for the community as a whole is provided by the occurrence of *Mercurialis perennis* with mixtures of *Hyacinthoides non-scripta*, *Circaea lutetiana*, *Geum urbanum*, *Arum maculatum* and *Viola riviniana/reichenbachiana* (incompletely distinguished in the available data and difficult to separate when vegetative: Wigginton & Graham 1981, Phillips 1982). Less frequent overall, but also quite characteristic, are *Lamium galeobdolon*, *Carex sylvatica*, *Sanicula europaea*, *Adoxa moschatellina* and *Conopodium majus*. *Hedera helix* and *Brachypodium sylvaticum* occur fairly commonly, too,

though with rather more uneven frequency in the different sub-communities. Combinations of these species were recognised early as a distinctive kind of woodland field layer on fairly moist, base-rich soils in Britain (e.g. Tansley & Rankin 1911, Moss 1911, Tansley 1911, 1939) and they comprise the major group of herbs which unite the more calcicolous woodlands in the classifications of Klötzli (1970), Rackham (1980), Peterken (1981) and Bunce (1982). In this scheme, they can be found in other communities, but they always occur there either with a different canopy (as under *Fagus sylvatica* or *Taxus baccata*) or with frequent records for additional herbs which are typically scarce here (as in the upland *Fraxinus-Sorbus-Mercurialis* woodland).

Among these latter species, whose infrequency here helps distinguish the *Fraxinus-Acer-Mercurialis* woodland from its north-western upland counterpart, are ferns. No species occurs more than occasionally through the community as a whole here and most records are for *Dryopteris filix-mas* with, much less commonly, *D. borrieri*, *D. dilatata*, *Polystichum setiferum* and *Athyrium filix-femina*. Towards the north and west, there is some increase in the variety and prominence of the fern flora but there are never here the consistently high frequencies for dryopteroid ferns and *A. filix-femina* characteristic of the much wetter climate and somewhat surface-leached soils of the *Fraxinus-Sorbus-Mercurialis* woodland. This difference was noted by Klötzli (1970) in his characterisation of a north-western *Dryopterido-Fraxinetum*.

Though ferns do not provide a consistent element in the structure of the field layer here, an underscrub does, though its prominence is very variable. *Rubus fruticosus* agg. is the most frequent component, occasionally with some *Rosa canina* agg., and much more sporadically, with *Rubus idaeus*, *R. caesius*, *Ribes rubrum* and *R. uva-crispa*. Ground-growing *Lonicera periclymenum* is quite common, too, adding to the tangle. Where such an underscrub becomes prominent here with lower covers of *Mercurialis* (quite a common situation), it may be difficult to distinguish this community from the *Quercus-Pteridium-Rubus* woodland, where *Rubus fruticosus* agg., *Lonicera* and *Hyacinthoides* are all common and where silvicultural treatments can result in canopies very similar to some of those found here (as in oak-hazel, lime or hornbeam coppice). Usually, however, except in the densest shade, the presence of scattered plants of *Circaea lutetiana*, *Geum urbanum*, *Arum maculatum* and *Viola* spp., will help effect a separation. Additionally, *Pteridium aquilinum*, often very prominent in *Quercus-Pteridium-Rubus* woodland, is typically very rare here. This distinction, between what are essentially, on the one hand, dog's mercury woodlands and, on the other, bluebell woodlands has not always been maintained in

British schemes. Tansley (1939) united the two types in his broadly-defined *Quercetum roboris* and Klötzli's (1970) two major mixed deciduous woodlands also each include both types. More recent classifications which have used the dominance of such trees as *Tilia cordata* and *Carpinus betulus* (e.g. Rackham 1980, Peterken 1981) also relegate this distinction to sub-community level.

The bryophytes of the community as a whole are not especially distinctive, though they are quite commonly a prominent feature of the vegetation, especially in the winter and early spring. The most frequent species overall are *Eurhynchium praelongum*, *Brachythecium rutabulum* and *Plagiomnium undulatum* with, more occasionally throughout, *Atrichum undulatum*, *Mnium hornum*, *Eurhynchium swartzii*, *E. confertum*, *Thuidium tamariscinum*, *Hypnum cupressiforme* and *Lophocolea bidentata* s.l. Fallen and rotting timber can provide a considerably enriched bryophyte flora and, where stands occur in the more equable oceanic climate of the south-west, epiphytic species can become important.

These floristic features, then, provide a good general definition for the herbaceous element of the community as a whole, but there is a fairly sharp distinction among other field-layer species which corresponds to the major division noted among the shrubs and trees and which helps characterise more precisely the two suites of sub-communities. One group of these additional herbs follows *Quercus robur*, *Carpinus betulus*, *Tilia cordata*, the invasive elms and *Crataegus laevigata* in being more consistently associated with heavier, base-rich soils in the warmer and drier south-east. These are *Poa trivialis*, *Glechoma hederacea*, *Ajuga reptans* and *Primula vulgaris* (partly replaced in two areas in East Anglia by *P. elatior*). Among the more widespread community species, *Hyacinthoides non-scripta* and *Rosa canina* agg. also show a somewhat higher frequency here.

Except on moister soils along stream-sides or over pockets of heavy drift, all these species are distinctly less common in *Fraxinus-Acer-Mercurialis* woodlands towards the north and west. There, the increase in *Acer pseudoplatanus*, *Ulmus glabra* and, to a lesser extent, *Quercus petraea* and *Ilex aquifolium*, is matched in the field layer by consistently higher frequencies for *Urtica dioica*, *Galium aparine*, *Geranium robertianum* and *Phyllitis scolopendrium* and, among the bryophytes, *Eurhynchium striatum*, *Thamnobryum alopecurum* and, less commonly, *Ctenidium molluscum*. Among these preferences, the increase in *U. dioica* and *G. aparine* (and perhaps also in *G. robertianum*) is perhaps a reflection of the generally more rapid nutrient turnover in the usually lighter base-rich soils characteristic of the north-west. These species do occur occasionally through the south-eastern sub-communities, but they are very closely

related there to local enrichment of the soils, often resulting from human disturbance. The prominence of *Phyllitis scolopendrium*, by contrast, is a response to the milder and wetter climatic conditions towards the west of Britain. *Hedera helix*, another oceanic species, follows it somewhat in being more frequent in these sub-communities than it generally is to the south-east, but its distribution as an important field-layer species in this community is rather broader than that of *P. scolopendrium* and it also occurs in abundance across southern England under canopies which are of the south-eastern type. Its occurrence is also complicated by the fact that, with *Brachypodium sylvaticum*, it tends to become prominent in young stands of this community and in plantation replacements of it.

This major floristic distinction among the field layers is matched by a physiographic difference between the habitats characteristic of each of the suites of sub-communities. As described below, this has important implications for the kinds of vegetation that are found within each of the suites, but it also has a much more general effect on the appearance of the field layer. To the south-east, *Fraxinus-Acer-Mercurialis* woodlands are typically found over the gentle slopes and undulating plateaus developed over superficials and easily-weathered argillaceous rocks. Stands are often quite extensive (though much reduced now by clearance) and the field layer is frequently characterised by a physiognomic uniformity and gentle shifts in dominance, except where recent coppicing has introduced variation. The north-western sub-communities, on the other hand, are much more typical of the sharply-defined scenery of limestone bedrocks, with steep slopes and sometimes very intricate patterns of weathering of the exposures. Even where the field layer is floristically uniform, it can show a very complex structure, being disposed in a mosaic over the substrate surface. Such patterning can be seen in its most extreme form where *Fraxinus-Acer-Mercurialis* woodland occurs over Carboniferous Limestone pavement.

Other variations in the field and ground layers

The qualitative features described above serve to define the major floristic trends in the field layer of this community. Often, though, it is the very considerable quantitative variation among these widespread species that is the more striking here and the way in which species of fairly low overall frequency can come to dominate in field layers that seem to have little in common, one with another.

Much of this variation can be seen, in spring and summer, in terms of the differing prominence of *Mercurialis perennis* because, though this is the most characteristic herb here, its frequency and abundance are very variable. Overall, it is the commonest plant of the field layer in this community and the most frequent herba-

ceous dominant, often forming an extensive network of discrete patches or a virtually continuous carpet of coalesced clones, with sometimes upwards of 400 shoots m^{-2} (Wilson 1968, Hutchings & Barkham 1976). It is a long-lived perennial, propagating mainly by slow vegetative expansion and, though it spreads very gradually into young stands, once established it is very well adapted, in its patterns of rhizome and shoot growth, to maintaining itself as a dominant (Mukerji 1936, Wilson 1968, Hutchings & Barkham 1976). And, when it does grow well, there is every indication that it exerts a very strong influence on the composition and patterning of the field layer by virtue of the dense shade that it casts (Abeywickrama 1949, Wilson 1968, Martin 1968, Pigott 1977); it can even effect canopy regeneration by hindering the growth of tree seedlings (Wardle 1959). Its shoots emerge very early, usually from February onwards, and well in advance of most of the other possible vernal dominants here (Salisbury 1916, Wilson 1968). They can grow tall, up to almost half a metre, and quickly put out their decussate, horizontally-held leaves to form the dull green carpet that characterises these woodlands until late in the summer after which the senescing shoots finally succumb to frost and fungal infection in September and October (Wilson 1968).

In certain situations, however (and these are quite well defined ecologically), the cover of *Mercurialis* is reduced and it becomes increasingly scarce; in some kinds of woodland included in this community, it is totally absent. Minor reductions in *Mercurialis* are often marked simply by an increase in the abundance of species already present. *Hyacinthoides non-scripta* is often the most obvious of these and it commonly assumes dominance here on somewhat moister soils, where *Mercurialis* suffers from the reduced aeration (Abeywickrama 1949, Martin 1968). This can be seen within both the south-eastern and north-western kinds of *Fraxinus-Acer-Mercurialis* woodland, in the former on gentler slopes where surface water cannot easily percolate away, in the latter where colluvial soils are receiving water shed from the slopes above. Then, too, provided *Hyacinthoides* itself is not too overwhelmingly dominant (it can be), there is an increase in the cover of the other herbs and bryophytes characteristic of the community as a whole and of each of the regions. Much of this kind of quantitative variation can be contained within particular sub-communities: it is a common feature in the two mainstream kinds of *Fraxinus-Acer-Mercurialis* woodland, the *Primula-Glechoma* sub-community to the south-east and the *Geranium* sub-community to the north-west.

Sometimes, however, environmental conditions are such as to so reduce the cover of *Mercurialis*, that species which are generally scarce throughout the community as

a whole are able to assume a marked local dominance because of the lack of competition. This more marked qualitative change in the floristics of the field layer helps define some other sub-communities in each of the regions. Very often, such differences are due to very pronounced waterlogging of the soils. Among the south-eastern sub-communities, the prominence of *Anemone nemorosa* and *Ranunculus ficaria* in this kind of situation on very wet plateau soils, defines the *Anemone* sub-community. To the north-west, moist conditions on free-draining colluvial soils are marked by vegetation placed here in an *Allium ursinum* sub-community.

A reduction in *Mercurialis* cover is also a feature of soils which become ill-aerated through trampling, often associated here with coppicing, which usually takes place in winter when the soils are more susceptible to poaching. This kind of variation, often accompanied by vegetative expansion of some existing shade-tolerant species and a flush of flowering, can be seen in various kinds of *Fraxinus-Acer-Mercurialis* woodland and is often best understood as a temporary perturbation of the more stable floristic patterns of the particular sub-community that has been coppiced. Sometimes, however, coppicing (or clearance) produces a more dramatic and qualitative shift in the composition and structure of the field layer. This kind of vegetation is included here in a *Deschampsia cespitosa* sub-community among the suite of south-eastern *Fraxinus-Acer-Mercurialis* woodlands.

The remaining variation within the field layers can be accommodated in two further sub-communities. The association of frequent and often abundant *Hedera helix* with the south-eastern type of canopy noted earlier produces a very distinctive kind of woodland common in the more oceanic parts of southern Britain. The herbaceous element in this *Hedera* sub-community is often rather impoverished and, though *Mercurialis* is itself quite frequent, this sub-community also includes younger woodlands on base-rich soils from throughout the south-east.

Finally, among the *Fraxinus-Acer-Mercurialis* woodlands of the north-west, there are some very striking stands in which unusually rich and uneven-aged mixtures of trees and shrubs occur over a field layer in which the typical herbs of the region are accompanied by a variety of species reflecting an often patchy woody cover, a complex rocky topography and climatic conditions approaching those characteristic of montane parts of Britain. In general in this community, sylvicultural treatments have been so extensively applied that more natural assemblages of woodland plants survive only under much modified canopies but, in this *Teucrium scorodonia* sub-community, we perhaps have a glimpse of what certain north-western *Fraxinus-Acer-*

Mercurialis woodlands were like before widespread alteration and clearance.

Tilia cordata in *Fraxinus-Acer-Mercurialis* woodland

In this community, as in the other major kind of woodland in which it is well represented, the *Quercus-Pteridium-Rubus* woodland, *Tilia cordata* has a low overall frequency but is preferentially common and locally abundant in the south-eastern suite of sub-communities, though, even here, it shows a markedly patchy geographical distribution, being more frequent in Essex, Suffolk, Northamptonshire, Lincolnshire, the West Midlands and Somerset, and decidedly scarce south of the Thames. In general, though, it is characteristic of that part of the country where the fall in summer temperatures since the period of its great prominence at the Forest Maximum has not been so critical as to reduce it to being a relic tree, able only very sporadically to set viable seed (Pigott & Huntley 1978, 1980, 1981). This is the status which it seems to have in the north-western sub-communities of this woodland and of the *Quercus-Pteridium-Rubus* woodland, and in the most southerly stands of their upland analogues which just reach down to what seems to have been the past geographical limit of *Tilia* in northern England (Pigott & Huntley 1980). Here, *Tilia* usually persists as what are obviously very ancient stools, often isolated on more intractable topographies, around which their original woodland context has come and gone. Locating such individuals phytosociologically is difficult now: quite apart from the fact that they have outlasted clearance and regeneration, many trees occupy cliff edges with their horizontal roots beneath one kind of woodland, their vertical roots in another below, or occur in ravines with complex mosaics of habitats and field layers. Then, their association is more strictly with a site type than with a particular vegetation type, though this does not make their conservation any the less pressing: indeed, as what are probably among some of the most venerable trees in the British countryside, they are especially deserving of care.

Isolated limes can often be found further south, too, well within the range of the tree's present ability to set viable seed (Pigott & Huntley 1981). Single poles, sometimes pollarded, or stools or their clonal remnants, again often of immense size, occur commonly in stands of the south-eastern sub-communities, often on wood-banks or territorial boundaries (see maps in Rackham 1980). *Tilia* can persist in this way in those stands of *Fraxinus-Acer-Mercurialis* woodland which have a known (or strongly-suspected) history of fairly recent clearance and regeneration or which are obviously quite young plantations, as well as in those less-disturbed woodlands where it has never been common for reasons quite unrelated to treatment. However, documentary evi-

dence shows that where, among these south-eastern sub-communities, *Tilia* attains its highest frequencies and abundance, there has usually been a continuity of woodland cover and composition for a very considerable period of time. There are, though, some documented exceptions to this general rule and it does not follow, of course, that an absence of *Tilia* indicates recent origin: many *Fraxinus*-*Acer*-*Mercurialis* woodlands with a proven ancient history have no *Tilia*.

Where *Tilia* is abundant in these woodlands, it has often clearly been a coppice crop, cut for timber, wood and bast, though it seems to have been unpopular as a charcoal source because of a tendency to reignite when the stacks are opened (Pigott & Huntley 1978). Usually, now, it dominates as large coppice poles, sprung from stools which are often of great size and which sometimes have decayed centres so that rings of apparently discrete trees remain. The poles grow vigorously and straight, this last feature being especially noticeable where the tree is intermixed with the wavy-boled *Carpinus betulus*, as it quite often is, both here and in the *Quercus*-*Pteridium*-*Rubus* woodland. In abandoned coppice, *Tilia* regrowth can overtop smaller standard oaks, though in fact most stands do have some scattered *Quercus robur* and often a little *Fraxinus*. There are also occasional trees of *Acer campestre* and *Betula pendula* but underwood associates are very sparse with only rare *Corylus* or *Crataegus*.

Among the south-eastern sub-communities, *Tilia* is most often encountered and generally shows the greatest local abundance in vegetation which resembles the *Primula*-*Glechoma* and *Anemone* sub-communities. Woodlands of this kind have been classified by Rackham (1980) as lime-ash woods and were included by Peterken (1981) within his Stand type 4Ba of lowland maple-ash-lime woods. However, there is a problem in deciding whether *Tilia* is more associated with one or the other of these field layers because, wherever *Tilia* is dominant, its very dense canopy eliminates all but the most shade-tolerant of the herbaceous associates and even these often occur so sparsely that it is difficult to discern what the floristic affinities of the vegetation are. Indeed, it is sometimes hard to be sure that the vegetation does not belong to some other sub-community apart from these two, or even whether it is a *Fraxinus*-*Acer*-*Mercurialis* woodland at all. *Tilia* characteristically produces a convergent impoverishment of the field layer of whatever kind of woodland it has become prominent in and where uniform silvicultural treatment for producing crops of lime has been applied across boundaries between, say, this community and the *Quercus*-*Pteridium*-*Rubus* woodland, the poverty of the herbaceous associates means that there is often next to no sign that different vegetation types have been transformed.

In comparison with typical kinds of *Primula*-*Glechoma* and *Anemone* vegetation, only *Rubus fruticosus* agg., among the common associates, retains anything like its usual frequency here and it is often reduced to sparse trailing branches rather than forming a dense underscrub. Of the other community species, *Mercurialis perennis*, *Hyacinthoides non-scripta*, *Circaea lute-tiana*, *Geum urbanum*, *Viola* spp. and *Arum maculatum*, all show depressed frequencies under dense *Tilia* and, among the sub-community preferentials, only *Ajuga reptans* occurs more than occasionally and even this is usually found as scattered individuals. The only really positive feature of the herbaceous vegetation in these woodlands is the high frequency of certain bryophytes: although more delicate species such as *Eurhynchium praelongum*, *Brachythecium rutabulum* and *Plagiomnium undulatum* decline, there is a marked increase in the occurrence of the more robust *Mnium hornum* and, especially, *Atrichum undulatum*.

Recently-coppiced *Tilia* has not been sampled but there seems little doubt that where stands on wetter soils are cut, the characteristic plants of the *Deschampsia* sub-community could attain the temporary prominence that they show beneath other kinds of young underwood. By contrast, the low frequency of *Tilia* in the *Hedera* sub-community seems to be a real reflection of the scarcity of this tree south of a Thames-Severn line, where this kind of *Fraxinus*-*Acer*-*Mercurialis* woodland is most common. This sub-community also includes some plantations in which *Tilia* is but an infrequent survivor of an earlier woodland cover.

In those much rarer situations where *Tilia* occurs as a coppice-underwood dominant in stands of north-western *Fraxinus*-*Acer*-*Mercurialis* woodlands, a similar physiognomy to that described above can be found, though here *Quercus petraea* partially replaces *Q. robur* and there can be occasional scattered trees of *Ulmus glabra* and *Acer pseudoplatanus*. Because of the dense shade, however, the distinctive features of the north-western kind of field layer are often obscured. Where *Tilia cordata* occurs as isolated relic trees in the north-west, it is occasionally found, sometimes in association with our other native lime, *T. platyphyllos*, as in the Wye valley and in Derbyshire, in the very distinctive *Teucrium* sub-community (Pigott 1969). North-western *Fraxinus*-*Acer*-*Mercurialis* woodlands with *Tilia cordata* were included in Peterken's (1981) Stand types 4Bb western maple-ash-lime woodlands and 4C sessile oak-ash-lime woods.

***Carpinus betulus* in *Fraxinus*-*Acer*-*Mercurialis* woodland**
Like *Tilia cordata*, *Carpinus betulus* occurs commonly as a woody dominant in both this community and the *Quercus*-*Pteridium*-*Rubus* woodland and it has sometimes been used to characterise various types of 'horn-

beam woodland' which subsume parts of both these communities, as by Salisbury (1916, 1918a), in Rackham's (1980) hornbeam-ash woods and in Peterken's (1981) Stand types 9A and 9B. It has been widely planted to the north of Britain (and, in a few sites, is established in some abundance) but, in general, it is much more strictly confined to the south-east than is *Tilia*, having a clear central European distribution (Matthews 1955). Furthermore, its floristic affinities are a little clearer because, though it is, like *Tilia*, a markedly gregarious tree, it does not seem to cast such a heavy shade, so the field layer usually survives in sufficient abundance as to indicate the general nature of the vegetation. And there is no doubt that, within both the woodland communities in which it is common, *Carpinus* shows a very frequent (though not exclusive) association with vegetation in which *Anemone nemorosa* and *Ranunculus ficaria* become abundant on spring-wet soils.

As with *Tilia*, the usual woody associates where *Carpinus* is abundant in *Fraxinus-Acer-Mercurialis* woodland are *Quercus robur* and *Fraxinus*, both of which, though usually the former, can be found as standards. *Acer campestre* is generally infrequent, except where smaller *Carpinus*-dominated stands occur within more orthodox stretches of mixed canopies (as in Rackham's (1980) maple-hornbeam woodlands) and *Corylus* and *Crataegus* spp. are scarce. Structural uniformity has often been enhanced by many generations of coppicing (hornbeam has long been valued as an excellent fuel) but it has been suggested (Rackham 1980) that more extreme dominance by *Carpinus* is maintained only by a long-rotation coppice cycle. If cropping is at less than, say, fifteen years and there are no hornbeam standards to provide seed, any *Corylus*, which can fruit on a shorter cycle, may gain an advantage. Also some stools of *Carpinus* usually die after coppicing so, where hornbeam and lime grow together (quite a common occurrence), *Tilia* may increase its share of the canopy. Nowadays, with the abandonment of coppicing, *Carpinus* often grows to an impressive height, overtopping oak standards, though its stools are seldom as enormous as those of *Tilia*.

Except in the densest shade, most of the herbs and bryophytes of the south-eastern *Fraxinus-Acer-Mercurialis* woodlands retain high frequency. On somewhat drier soils *Mercurialis* or *Hyacinthoides* can be dominant in a field layer of the *Primula-Glechoma* type (equivalent to Salisbury's (1916, 1918a) *Mercurialis*, *Scilla* and *Nepeta* societies) but more often the herbaceous vegetation is that of the *Anemone* sub-community (as in Salisbury's (1916, 1918a) *Anemone* and *Ficaria* societies). Along paths and especially in more open areas, as in recently-cut panels, the *Deschampsia* sub-community can attain local prominence and post-coppice floras of

this kind can be more persistent here than beneath other kinds of underwood because *Carpinus* shows only slow early regrowth. Field layers of all these types were included in Rackham's (1980) maple-hornbeam and hornbeam-ash woods and in Peterken's (1981) Stand types 9Ab and 9Bb.

Unlike *Tilia*, which is generally a very rare coloniser in more recent spontaneous woodland, *Carpinus* is quite often found as the dominant in young extensions to older woods in which it is abundant. However, it does not seem to be an early invader but rather takes advantage of any clearance of woody pioneers and, even then, becomes prominent in the secondary canopy only slowly (Salisbury 1918b, Adamson 1932, Rackham 1980).

Invasive elms in *Fraxinus-Acer-Mercurialis* woodland

Invasion of existing woodland by suckering elms of the *Ulmus* sections *carpinifolia* and *procera* is widespread throughout lowland Britain, especially towards the south and east and most markedly of all on the heavy claylands of the Midlands and East Anglia (Rackham 1980, Peterken 1981). All available evidence suggests that the woodland types most frequently invaded are the south-eastern *Fraxinus-Acer-Mercurialis* woodlands, particularly those of the *Primula-Glechoma* sub-community, but also the wetter *Anemone* and *Deschampsia* sub-communities. These suckering elms also readily extend into neglected farmland and over abandoned settlements and such more recent woodland can have a field layer of the *Hedera* type. In certain parts of East Anglia, some other clonal, but apparently non-suckering, elms can also be encountered as dominants over these kinds of field layers (Rackham 1980). These seem to be hybrids between *U. carpinifolia* (rarely *U. procera*) and *U. glabra* but, unlike the suckering elms, these trees can also be found in association with *Tilia*, *Carpinus* and *Castanea sativa* in *Quercus-Pteridium-Rubus* woodland.

The suckering elms are aggressive trees but their invasion is characteristically local and it can be slow. Usually invasions start from established trees on wood margins, in hedges, on internal boundaries or around settlements and the expanding clones of suckers have a typically rounded outline, part-circular where the trees are invading from a wood edge, roughly circular within woods (see maps in Rackham 1975, 1980). Origin from seedlings may be a rare event but it is important in extending colonisation to new sites and in further increasing the already dismaying morphological variety that can be found between clones (e.g. Melville 1975, 1978, Rackham 1980, Richens 1983).

Although these invasive elms can fairly quickly become the tallest trees in stands of *Fraxinus-Acer-Mercurialis* woodland, where invasion is recent many of the typical floristic features persist. Mixtures of *Fraxi-*

mus, *Corylus* and *Acer campestre* with oak standards often form the context for elm-expansion and, beneath, all the characteristic south-eastern herbs can be frequent. Commonly, though, there is more *Urtica dioica* than usual and *Sambucus nigra* can be prominent in the underwood. This may be because these invasive elms spread more readily on soils which are already eutrophic (they are often very conspicuous over infilled moats and around old settlements and their gardens) or because the elm litter, with its high calcium levels (e.g. Martin & Pigott 1975), assists rapid nutrient turnover; perhaps both. However, it is not true to say (Rackham 1975, 1980) that either *Glechoma hederacea* or *Poa trivialis* are especially 'elm plants', except in so far as they are common in the kinds of wood invaded and persist under the increasing elm canopy as other herbs fade.

More advanced elm invasion of this kind also affects the existing trees and shrubs, as the oak standards and even any emergent *Fraxinus* are overtopped and shaded out as well as the underwood. Older elm clones thus often have a lot of dead wood and timber, with oak especially prominent among the latter, its killed standards being slow to fall and rot (Rackham 1975, 1980). With time, such elm woodland acquires a floristic and structural uniformity which makes it very different from the vegetation it has replaced, a point of some importance as elm invasion is one of the few major changes occurring in British woodlands at this time. Interestingly, its progress has not been markedly affected by the current epidemics of Dutch Elm Disease (*Ceratocystis ulmi*). This seems at present to attack mostly *procera* elms, the less common of the sections in woodlands, and *U. glabra* which is generally scarce in the south-east (Rackham 1980). Even where larger poles have succumbed, swarms of young suckers may persist.

Sub-communities

The seven sub-communities are described in the usual style, the four south-eastern types first, then the three north-western. In each suite, the account of the main-stream sub-community precedes the others.

***Primula vulgaris*-*Glechoma hederacea* sub-community:** Oak-hazel woods Moss 1907 *p.p.*; Damp oakwood association Moss *et al.* 1910; *Quercetum robur* Tansley 1911 *p.p.*; Ash-oakwood Association Tansley 1911 *p.p.*; *Mercurialis* and *Fragaria* societies Adamson 1912; Oak-hazel woods Salisbury 1916 *p.p.*; *Quercus robur*-*Carpinus* woods, *Mercurialis* society Salisbury 1916; *Quercus sessiliflora*-*Carpinus* woods, *Mercurialis* and *Nepeta* societies Salisbury 1918a; *Quercetum roboris*, *Scilla*, *Mercurialis* and *Primula* societies Tansley 1939; Hayley Wood zones 5 & 6 Abeywickrama 1949; *Quercus-Fraxinetum typicum* Klötzli 1970;

Ash-maple-hazel woodlands Rackham 1980 *p.p.*; Lime-ash woods Rackham 1980 *p.p.*; Maple-hornbeam woods and Hornbeam-ash woods *p.p.* Rackham 1980; Elmwoods Rackham 1980 *p.p.*; Ash-Wych elm stand type 1Bb Peterken 1981 *p.p.*; Ash-maple stand types 2A & 2B Peterken 1981 *p.p.*; Ash-lime stand type 4Ba Peterken 1981 *p.p.*; Hornbeam stand types 9Ab & 9Bb Peterken 1981 *p.p.*; Suckering elm woodland Peterken 1981; Woodland plot types 5 & 7 Bunce 1982. The three woody constants of the community, *Fraxinus*, *Corylus* and *Acer campestre*, are all frequent here, occurring in all possible combinations and very variable proportions. Very commonly, they form the basis of what has obviously been simple coppice or coppice-with-standards with variable numbers of standard timber trees, usually oak, and almost always here *Quercus robur*. Occasionally, *Fraxinus* can be found as standards or, more unusually, *A. campestre* and, rarely (as at Hatfield Forest in Essex), *Q. robur* occurs prominently in the underwood. In coppiced woodland of this kind, the composition and structure of the vegetation can still give strong clues as to the pattern of cropping for small, large or mixed coppice on various rotations in different panels. However, with the demise of coppicing, the present appearance of this kind of woodland is very varied, being strongly influenced not only by the original coppice physiognomy but also by the local environmental conditions that have affected regrowth and regeneration since the last cut.

Of the four common woody species, both *Fraxinus* and *A. campestre* are readily able to promote themselves to a tree canopy from the unchecked growth of their stools. *Fraxinus* is also the best regenerator from seed in the community as a whole: seedlings and saplings are very frequent and, provided the shade from trees and shrubs, or from *Mercurialis*, is not too intense, they can get away rapidly and form vigorous maiden poles. Emergent *Fraxinus* are thus very common here and they can shade out small standard oaks. *A. campestre* is, generally speaking, initially less abundant, springs up not quite so far and regenerates erratically from seed, so it is not so common an emergent, but it can tolerate *Fraxinus* shade and itself casts dense shade. Existing individuals can thus hold their own for a considerable time even though their proportional contribution to the canopy falls. A common pattern resulting from such interactions is for there now to be a quite well defined but uneven-topped canopy of trees, frequently extensive though usually not completely closed, made up of mixtures of any persisting oak standards, much coppice regrowth and maiden *Fraxinus* and usually smaller amounts of coppice regrowth of *A. campestre*. Less commonly, stands can be found in which *Fraxinus*, or very occasionally *A. campestre*, or rarely *Q. robur*, have

come to be sole dominants and it is possible that some of the stands with much ash and oak represent long-established plantations.

Older woodlands of this kind, whether treated as coppice or approximating more to high forest, often have occasional records for other trees: *Betula* spp., *Tilia cordata*, *Carpinus betulus*, *Sorbus torminalis* and *Malus sylvestris* occurring as scattered individuals, *Populus tremula* and *Prunus avium* in small suckering patches. Those species which can be coppiced have often been included in a mixed-coppice crop but stands in which *Tilia* or *Carpinus* predominate (forming 'lime-' or 'horn-beam-woodland') also occur here with, when the shade is not too dense, a typical *Primula-Glechoma* field layer. Elm invasion is also quite common and tracts of this sub-community can be found under *U. carpinifolia* or *U. procera*.

Except where some large-coppice tree or older elm suckers dominate or in plantation replacements for the canopy, the most obvious feature of the underwood in these woodlands is generally the persistent and often very great abundance of *Corylus*. Where the shade cast by the trees is not too dense, very large hazel bushes can themselves be the dominant in old coppice and, even where the tree canopy is closing, the bushes often grow so tall as to make stratification indistinct. But, with increasing shade, the cover of *Corylus* declines from what are really artificially high levels in coppiced versions of this woodland. The shoots are replaced more slowly and fruiting becomes less prolific; when photosynthesising at a lower rate, *Corylus* may also be less able to withstand the depredations of the *Armillaria mellea* which very commonly lives on its roots (Rackham 1980). Individual bushes begin to die and the species takes its place as one member, though usually still the most abundant, of a more open and balanced shrub cover.

Typical underwood companions of *Corylus* here are the hawthorn species and their hybrids (*Crataegus monogyna* often extending out as a prominent marginal shrub, *C. laevigata* scarcer and more obviously associated with the older more intact parts of stands), with, less commonly, *Sambucus nigra*, *Prunus spinosa*, *Salix caprea*, *S. cinerea*, *Cornus sanguinea*, *Euonymus europaeus*, *Viburnum opulus*, *V. lantana*, *Ilex aquifolium* and *Sorbus aucuparia*. Many of these would have been included with hazel in a small-coppice crop; now, with neglect, they often show a local abundance in relation to particular environmental conditions.

The particular diagnostic feature of the field layer of this sub-community as against other south-eastern types of *Fraxinus-Acer-Mercurialis* woodland is the frequent presence here of *Poa trivialis*, *Glechoma hederacea*, *Ajuga reptans* and *Primula vulgaris* (or, in wetter stands

in certain parts of East Anglia, *P. elatior*) in the general absence of *Anemone nemorosa* and *Ranunculus ficaria* or *Deschampsia cespitosa* or *Hedera helix*. All of these latter species are scarce here and never abundant within uniform stands of the *Primula-Glechoma* sub-community: small patches of *Anemone* and *Ranunculus* can mark out slight surface depressions where the ground is undulant and *Deschampsia* often spreads along the edges of paths but such areas are best regarded as fragments of other sub-communities associated with habitat heterogeneity.

Both *Poa trivialis* and, more especially under certain circumstances (see below), *Glechoma hederacea* can be quite abundant here with large patches of creeping leafy shoots. They are also both evergreen and, with the common bryophytes of the community, can give a distinctive stamp to this vegetation in late winter and early spring before either *Mercurialis* or *Hyacinthoides*, the usual vernal dominants, have begun to put up their shoots. Often, though, they occur in small amounts, together with scattered plants of *Primula vulgaris* and other species of wide occurrence throughout the community: *Circaea lutetiana*, *Geum urbanum*, *Viola* spp. and, more occasionally, *Arum maculatum*, *Carex sylvatica*, *Lamium galeobdolon* and *Sanicula europaea*. Each of these can also attain some measure of local prominence (as in the 'societies' of early descriptive accounts) but frequently they form a diverse mosaic overlain by varying amounts of *Rubus fruticosus* agg.

In spring and summer, however, the most prominent feature of the vegetation is generally the abundance of *Mercurialis*. Where its cover is high, as it tends to be in long-established woods on better-aerated soils, the associated field-layer herbs and especially the ground-growing mosses are strongly depressed in variety and abundance. Few other species seem able to survive its dense shade: the evergreen *Glechoma* and *Viola* spp. persist patchily where the cover is a little more open but, of the other associates, only *Circaea lutetiana* maintains its normal pattern of occurrence, an interesting exception since it puts up its leaves quite late. Poorer *Mercurialis*-dominated floras of this kind are often associated in this sub-community with dense coppice regrowth; sometimes there is a dominant canopy of *Fraxinus* or *Q. robur* but the understorey is frequently very well developed and often exceeds the trees in cover with *Corylus*, *Crataegus monogyna* and *Prunus spinosa* well represented. However, *Fraxinus* saplings and, more especially, seedlings are unusually sparse and regeneration of woody species from seed is probably very rare (e.g. Wardle 1959). Interestingly, *Rubus fruticosus* agg., which often spreads in undisturbed woods, is also much patchier where *Mercurialis* is overwhelmingly dominant.

Stands of this sub-community with low to moderate

(5–50%) *Mercurialis* cover show a much greater richness and diversity and three major trends can be recognised. First, where there is an increase in soil moisture, *Hyacinthoides* often takes over from *Mercurialis* as the dominant in vegetation which is otherwise little changed. *Hyacinthoides* is a common plant throughout this sub-community (indeed, the most frequent herb after *Mercurialis*) but it does not begin to become abundant until *Mercurialis* cover falls below about 30%. Often here this is where soil aeration is reduced in small hollows or on flatter plateaus where ground water cannot percolate away so readily through the usually heavy clays. A common pattern is thus for there to be small patches of dominant *Hyacinthoides* within a ground of dominant *Mercurialis* or, more strikingly, along gradients of increasing soil moisture, a belt of dominant *Mercurialis* giving way to a zone of dominant *Hyacinthoides*, a feature shown very well in Hayley Wood in Cambridgeshire (Abeywickrama 1949, Rackham 1975).

A second kind of variation is seen where *Mercurialis* declines in response to the soil compaction that results from coppicing. This automatically opens up the ground for colonisation by existing shade-tolerant species which can recover more rapidly. Among the most obvious of these here are *Glechoma* and *Lamium*, both of which can spread quickly and extensively in recently-cut panels by putting out creeping shoots from surviving, untrampled plants, and, with *Glechoma*, from seed. *Hyacinthoides* seems to show a more complex reaction (e.g. Salisbury 1924) but, with a depression in *Mercurialis* cover, it can become the temporary dominant in this sub-community in the early years after cutting. Often, though, the most striking visual change in the vegetation is the great increase in flowering in the second, sometimes the third, spring with a subsequent decline again thereafter as the canopy closes once more. Both *Glechoma* and *Lamium* can show this effect but it is the glorious show of *Hyacinthoides*, *Viola* spp. and *Primula vulgaris* that is the most renowned. On wetter soils occupied by this sub-community, which become very badly poached during coppicing, there is an increasing tendency for the post-coppice flora to show a more dramatic shift towards the *Deschampsia* sub-community but, even in drier conditions, there may be a marked and quite unpredictable variety among the adventive species which gain a temporary hold. Plants such as *Arctium minus* agg., *Epilobium angustifolium*, *Heracleum sphondylium* and *Anthriscus sylvestris* may become prominent with scattered tussocks of coarse grasses like *Dactylis glomerata* and *Holcus lanatus* or, where there is some slight surface depression of pH, *Silene dioica*, *Euphorbia amygdaloides* and *Rubus idaeus* can, with *Hyacinthoides*, *Rubus* and *Lonicera*, give a temporary feel of a *Quercus-Pteridium-Rubus* woodland. Each of these possible var-

iations may take some time to play itself out before the typical *Primula-Glechoma* flora is restored.

Finally, here, *Mercurialis* can show some depression in relation to *Hyacinthoides* where there is a reduction in the base status of the soils, as on less calcareous clays or where there is some eluviation of upper horizons with increased rainfall. Then, there tends to be a thinning of the more calcicolous element in this woodland leaving *Hyacinthoides*, *Rubus* and *Lonicera* prominent over a ground of clay-soil species like *Glechoma*, *Poa trivialis*, *Primula vulgaris*, *Viola* spp. (especially here *V. riviniana*) and *Ajuga reptans*, sometimes with a little *Oxalis acetosella* and *Dryopteris dilatata* and frequently with some *Atrichum undulatum* and *Mnium hornum*. These last four species are very characteristic of the upland *Fraxinus-Sorbus-Mercurialis* woodland but, in the south-east, this kind of *Primula-Glechoma* vegetation represents a clear transition to *Quercus-Pteridium-Rubus* woodland. It is especially characteristic of less base-rich clays in the wetter Weald where it often occurs under canopies with much *Fraxinus* and *Q. robur* with a little more *Betula* (almost always *B. pendula*) than is usual for this sub-community but it can be found, too, in very fragmentary form wherever there is local base-enrichment within tracts of *Quercus-Pteridium-Rubus* woodland, as on stream-side terraces, a feature noted by Salisbury (1916, 1918a) in his account of hornbeam-dominated stands of these kinds of woodland.

***Anemone nemorosa* sub-community:** Damp oakwood association Moss *et al.* 1910; *Quercetum roburis* Tansley 1911 *p.p.*; *Fraxinetum excelsioris*, moist sub-association Tansley 1911 *p.p.*; *Spiraea* society Adamson 1912 *p.p.*; *Quercus robur-Carpinus* woods, *Anemone* and *Ficaria* societies Salisbury 1916 *p.p.*; *Quercus sessiliflora-Carpinus* woods, *Anemone* and *Ficaria* societies Salisbury 1918a *p.p.*; *Quercetum roboris*, *Anemone* Society Tansley 1939 *p.p.*; Hayley Wood zones 2, 3 & 4 Abeywickrama 1949; *Quercus-Fraxinetum filipendulietosum* Klötzli 1970 *p.p.*; Ash-maple-hazel woods Rackham 1980 *p.p.*; Lime-ash woods Rackham 1980 *p.p.*; Maple-hornbeam woods Rackham 1980 *p.p.*; Ash-wych elm stand type 1Bb Peterken 1981 *p.p.*; Ash-maple stand types 2A & 2B Peterken 1981 *p.p.*; Ash-lime stand type 4Ba Peterken 1981 *p.p.*; Hornbeam stand types 9Ab & 9Bb Peterken 1981 *p.p.*; *Quercus-Ulmum glabrae*, Typical subassociation Birse & Robertson 1976 *emend.* Birse 1984 *p.p.* In the south-east, the tree and shrub cover here often shows the same general composition as that of the *Primula-Glechoma* sub-community and it can encompass a similar diverse range of structures in relation to coppicing and its abandonment. Indeed, where a uniform silvicultural treatment has been applied across boundaries

between the two sub-communities, the difference between the vegetation types can lie entirely in the field layer.

Overall, however, some minor differences among the woody species can be seen with certain trees and shrubs being better represented here. The most obvious involves *Carpinus betulus* which, among its occurrences in more calcicolous woods, shows a marked preference for the spring-wet soils of the *Anemone* sub-community, stands of which often form the basis of hornbeam coppice. *Populus tremula* has a similar distribution. This may have something to do with exacting moisture requirements for seedling establishment because the soils here can provide the several weeks of surface moisture from May onwards that seem to be essential for successful germination and early growth (Watt in Rackham 1980), though many clones are single-sexed and the seed therefore seldom fertile, so, once established, the tree may often behave as a vegetatively persistent relic. It is not so prominent a tree as *Carpinus*, occurring, even here, as usually small patches of suckering individuals which can be shaded out of overgrown coppice or beneath invading elm (Rackham 1975). Although its bark is very palatable, its leaves are reputed not to be and this may give it some advantage where there is heavy browsing by stock or deer (Rackham 1975, 1980). *Alnus glutinosa*, generally a rare tree in *Fraxinus-Acer-Mercurialis* woodland, may also be encountered occasionally here, as isolated trees on plateaus or at the beginning of zonations to wetter woodland around flushes. Among the shrubs, *Sambucus nigra* is a little more frequent in this sub-community, though it never rivals *Corylus* and the hawthorns, again the major understorey components here.

In general, though, the distinctive features of this vegetation are in the field layer. Many of the community associates, like *Circaea lutetiana*, *Geum urbanum*, *Viola* spp., *Arum maculatum* and *Lamium galeobdolon*, and typical south-eastern species, such as *Poa trivialis*, *Glechoma hederacea* and *Primula vulgaris* (or *P. elatior*), remain frequent here. But, in this sub-community, the usual dominance of *Mercurialis perennis* and, to a lesser extent, *Hyacinthoides non-scripta*, very commonly gives way to an abundance of *Anemone nemorosa* and *Ranunculus ficaria*. It should always be remembered, however, that the prominence of these two species is strictly a vernal event and, after June, when their last leaves have disappeared, this vegetation can be qualitatively very similar indeed to that of the *Primula-Glechoma* sub-community. *Anemone* is invariably present here, often at covers in excess of 10% and sometimes much greater; even where its abundance is low, it can be the most prominent spring plant in the often rather open field layer. *Ranunculus* is somewhat less common and generally less abundant, though it can be patchily prominent.

It also puts up its leaves, from late January, and begins to flower, from mid-February, a month or so before *Anemone*, so it may strike the early visitor as the more obvious. When both species are in bloom in April, they give this vegetation a delightful and unmistakeable aspect.

Other preferentials are few and weak. *Rumex sanguineus* occurs occasionally and there are sometimes scattered plants of *Carex pendula*, *C. remota*, *C. strigosa* and even *C. acutiformis* and these sedges may look prominent by virtue of their bulky habit.

As in the *Primula-Glechoma* sub-community, there is considerable quantitative variation here among the possible dominants. *Mercurialis* is less common than on better-aerated soils: it very often has less than 30% cover and frequently it is absent. When it is more abundant, however, *Hyacinthoides* and, more especially, *Anemone* fare badly because of the dense and early shade that it casts. As *Mercurialis* cover declines on the more anaerobic soils, *Hyacinthoides* tends to assume dominance: it is the more common of the two species overall and usually the more abundant here. Although *Anemone* becomes a little more prominent as *Hyacinthoides* takes over from *Mercurialis*, it is not until *Hyacinthoides* too has declined on the very spring-wet soils, that it really attains its greatest abundance: although *Hyacinthoides* flowers a good month after *Anemone*, it puts up its leaves a little earlier and they quickly bend over above, casting a shade (e.g. Pigott 1982). *Ranunculus ficaria*, though it is of patchier occurrence than *Anemone*, shows the same general response.

These kinds of interaction are especially well seen where there is a marked and even gradient of spring-waterlogging of the soils, as for example in moving up a gentle slope on to a plateau (as in Hayley Wood: Abeywickrama 1949, Martin 1968, Rackham 1975) where a single stand of this sub-community can show dominance by, first *Mercurialis*, then *Hyacinthoides*, then *Anemone*, with transitions between. And it is this kind of zonation which forms the framework for the increasing prominence of *Primula elatior* on spring-wet soils in the two parts of East Anglia to which it is confined. In these areas, oxlip shows a substantial geographical replacement of *P. vulgaris* in calcicolous woodlands (though not in less base-rich or more open habitats) (Christy 1897, 1922, 1924, Rackham 1975, 1980). It can occur in the *Primula-Glechoma* sub-community but it is sensitive to competition for light and rarely abundant where, as is usually the case there, higher covers of *Mercurialis* are maintained (Abeywickrama 1949, Martin 1968). Here, though, it follows *Anemone* in its behaviour, increasing, as *Mercurialis* and *Hyacinthoides* decline, to the spectacular abundance so characteristic of our wetter oxlip woods. *P. elatior* can set viable seed in Britain and seedlings can reach matur-

ity after only two years (Valentine 1947) but, unlike *P. vulgaris*, it spreads only very slowly from existing colonies, expanding mostly by vegetative extension of its clones (Rackham 1975): like *Mercurialis* and *Anemone* and, to a lesser extent, *Hyacinthoides*, it is thus a good marker of longer-established stands. It hybridises freely with *P. vulgaris* where the two species occur together but there does not seem to be any evidence to support Christy's assertion (Christy 1922, repeated in Tansley 1939) that *P. elatior* is being hybridised out of existence (Valentine 1948, 1951, Woodell 1969). Oxlip certainly has shown a marked decline in Hayley Wood but Rackham (1975) adduces firm evidence that this is due to grazing by deer and small mammals. It also often appears less prominent because the decline of coppicing means that grand displays of flowering oxlips are rare.

Where coppicing of stands of this sub-community still occurs, as in Hayley (Rackham 1975) and the Norfolk wood described by Ash & Barkham (1976), the general response among the herbaceous plants is as described for the *Primula-Glechoma* sub-community with a decrease in such *Mercurialis* as is present, a vegetative expansion of certain existing shade-tolerant perennials and a great increase in flowering, especially noticeable here in *Anemone*, *Viola* spp., *Primula vulgaris* and within its range, *P. elatior*. There is also the same variety in the invasion of adventives, first annuals and biennials, then perennials. Here, though, on these generally wetter soils, there is a much more common tendency for the field layer to shift temporarily to the *Deschampsia* sub-community with its prominent *Holcus-Juncion* and *Filipendulion* elements. This kind of post-coppice flora is described fully below.

The *Anemone* sub-community is a widespread kind of *Fraxinus-Acer-Mercurialis* woodland on the often heavy clay soils of the south-east but an essentially similar field layer occurs locally on wetter sites towards the north-west. Here *Anemone* and *Ranunculus* become prominent on more base-rich soils under somewhat different canopies. *Fraxinus* and *Corylus* and, to a lesser extent, *Acer campestre*, remain very frequent but *Quercus petraea* and hybrid oaks begin to replace *Q. robur* and *Ulmus glabra* and *Acer pseudoplatanus* become much more frequent than in the south-east. These woodlands sometimes show signs of past coppicing but often they have a high-forest structure and, though *Corylus* is very common and sometimes abundant, it usually forms, with hawthorn (always *C. monogyna* here), a rather open understorey.

As in the south-east, the field layer is dominated by various proportions of *Mercurialis*, *Hyacinthoides*, *Anemone* and *Ranunculus* with zonations often here running downslope from drier ground to wetter stream sides. Species such as *Poa trivialis*, *Glechoma hederacea* and *Primula vulgaris* are reduced somewhat in frequency and

others more characteristic of north-western *Fraxinus-Acer-Mercurialis* woods, like *Hedera helix*, *Urtica dioica* and *Galium aparine*, are a little more common. However, other north-western preferentials, like *Brachypodium sylvaticum* and *Geranium robertianum* and the distinctive bryophytes of the region, remain sparse and it seems better, on balance, to retain these stands with those of the south-east.

***Deschampsia cespitosa* sub-community:** *Quercetum roburis* Tansley 1911 p.p.; *Spiraea-Deschampsia* society Adamson 1912; Oak-hornbeam woods, marginal and path floras Salisbury 1916, 1918; *Quercetum roboris*, *Filipendula ulmaria* society Tansley 1939; Hayley Wood variants C & D Rackham 1975; Foxley Wood coppice 0–16 years Ash & Barkham 1976; Ash-maple-hazel woodlands Rackham 1980 p.p.; Maple-hornbeam woods Rackham 1980 p.p.; Hatfield Forest oakwoods Rackham 1980 p.p.; Ash-wych elm stand type 1Ba Peterken 1981 p.p.; Ash-maple stand types 2A & 2B Peterken 1981 p.p.; Hornbeam stand type 9Ab Peterken 1981 p.p.; Woodland plot type 12 Bunce 1982. The *Deschampsia* sub-community does not show any major or consistent peculiarities in the species composition of its woody component and it can be found in the south-east under canopies of the same kind and variety as those typical of the *Primula-Glechoma* and *Anemone* sub-communities. Very often though, it is associated with a more open cover of trees and shrubs than is usual among *Fraxinus-Acer-Mercurialis* woodlands. In some cases, such openness is temporary, as where this vegetation occurs as a post-coppice flora, its herbs comprising a fairly short-lived replacement for other field layers (most frequently of the *Anemone* sub-community) in the early and middle years after cutting of the underwood. Then, the woody cover can show any of the numerous floristic permutations characteristic of south-eastern *Fraxinus-Acer-Mercurialis* woodlands but with the distinctive structure of young coppice regrowth with or without standards: a low profusion of shoots springing from the cut stools, fresh growth from suckering trees and shrubs and young maiden poles left uncut or newly developed from seedlings. In the samples available from this kind of woodland, *Quercus robur* is the commonest standard with occasional *Fraxinus* and scarce *Acer campestre* and the underwood is predominantly *Corylus* and *Acer* with some hawthorn (both *Crataegus monogyna* and *C. laevigata*) and a little *Salix caprea*. Recently-cut *Tilia cordata* and *Carpinus betulus* were not sampled but it is very likely that young regrowth of these species can also occur with a *Deschampsia* field layer.

Quite often in this kind of situation, the temporarily open conditions allow quick-growing woody occasional of the community to gain a local prominence.

Suckering species such as *Populus tremula* and *Prunus spinosa* may become rapidly abundant on the moist soils here or, where the substrate is more calcareous, there may be a dense scrubby growth of *Cornus sanguinea*, *Viburnum opulus* and *Ligustrum vulgare*. Then, beneath the young spring, there often develops a thick under-scrub of *Rubus fruticosus* agg. (often *R. vestitus* on more calcareous clays), sometimes with *R. caesius* or *R. idaeus*, and much scrambling *Lonicera periclymenum*. Probably of greater long-term significance to the composition of the expanding canopy is the frequent abundance in more open areas of young *Fraxinus* saplings which, provided the canopy does not close over too quickly, can get away as maiden poles to augment the tree cover in future years. More locally, invasive elms can sucker into this vegetation. Often, however, there is a gradual re-establishment of something like the original underwood with the extinction of some smaller and more light-demanding woody species.

Very similar mixtures of trees and shrubs are found where the *Deschampsia* sub-community occurs as a more permanent vegetation cover around clearings and along rides. Here, the sub-community can form a fringe to intact stretches of *Fraxinus-Acer-Mercurialis* woodland, partly overhung by the marginal standards and underwood, and with an often untidy edge of *Prunus spinosa* and *Cornus sanguinea*, banks of trailing *Rubus* and climbing *Lonicera*, *Clematis vitalba* and *Tamus communis*.

As with the *Anemone* sub-community, the heavy, moist and often trampled soils characteristic of this vegetation can show a reduced cover of *Mercurialis* and, to a lesser extent, of *Hyacinthoides*. But, here, the most obvious feature of the field layer is the constancy, and often the great abundance, of *Deschampsia cespitosa*. In fragmentary stands, as in ill-drained hollows or along the margins of paths within tracts of the *Primula-Glechoma* or *Anemone* sub-communities, it occurs as scattered individuals, often not very vigorous and non-flowering. In the more open conditions of young coppice, clearings and rides, however, it can be truly a dominant in extensive stretches of bulky, floriferous tussocks. In coppiced woodland, such prominence is a cyclical event with the *Deschampsia* waxing and waning with the cutting rotation. Where stands of *Fraxinus-Acer-Mercurialis* woodland on moister ground are coppiced, the combination of heavy trampling and suddenly increased light seem to create ideal conditions for what can be an explosive spread of *Deschampsia* over the cleared ground (Davy & Taylor 1974a, Rackham 1975, 1980, Ash & Barkham 1976, Davy 1980). This expansion can overwhelm the slower increase in species such as *Poa trivialis*, *Glechoma hederacea* and *Lamium galeobdolon* and mask the typical flush of flowers in

plants like *Primula vulgaris*, *P. veris*, *Anemone nemorosa* and *Ranunculus ficaria*. However, with the gradual closure of the canopy, the dominance of *Deschampsia* fades so that, when it is virtually extinguished, the original field layer is restored. Such a process can take some considerable time (more than 16 years in the woodland studied by Ash & Barkham 1976) and, where short-rotation cropping is maintained on wetter ground, the *Deschampsia* sub-community may become a permanent feature, though the ground cover is often attenuated with the shade. Around continuously-maintained clearings and along rides, *Deschampsia* retains its vigour so that, of the usual field-layer associates of the community, only taller species with stem leaves, like *Circaea lutetiana* and *Geum urbanum*, persist with their usual frequency. And where clearings are replanted, the *Deschampsia* can seriously compete with the young trees (Davy 1980).

Superimposed on to this general pattern, there is, in clearings and rides and especially in young coppice with its features of disturbance and change, a further level of floristic variation which makes the vegetation of the *Deschampsia* sub-community among the most diverse of woodland floras. Overall, the shift among these additional species is towards the Holco-Juncion and Filipendulion communities with a further weedy element, but individual stands often show marked peculiarities because of the varied interactions between the colonisers and the different situations available for their establishment and spread. The weeds are the more ephemeral, varied and patchily-represented component. They can show an early prominence in the developing ground vegetation of young coppice, first annuals, then biennials, though the smaller species tend to be quickly overwhelmed there and they survive in more permanent stands of this sub-community only where disturbance along paths and in ruts continues to provide small areas of open ground. Among such plants, species of *Rumex*, *Cirsium*, *Epilobium* and *Hypericum* are often conspicuous. Some of these are able to survive a little longer as the vegetation thickens up: *Rumex sanguineus* is one and, often forming persistent clumps, *Hypericum hirsutum*, *H. perforatum*, *Epilobium hirsutum* and *E. angustifolium*, this last often marking the sites of bonfires of coppiced brushwood. *Scrophularia nodosa* is also a scarce but quite characteristic plant in this kind of vegetation. But the most striking of the longer-lived companions of *Deschampsia* here are *Juncus effusus* and, less commonly, *J. conglomeratus*. These probably germinate from buried seed (e.g. Chippindale & Milton 1934, Milton 1936, Salisbury 1964) and they can be locally very abundant, sometimes rivalling *Deschampsia* itself in their cover. It is these bulky perennials, with occasional scattered plants of *Filipendula ulmaria*, *Geum*

rivale, *Angelica sylvestris*, *Lysimachia nemorum*, *L. nummularia* and clumps (now flowering in the open conditions) of *Carex pendula*, *C. remota*, *C. sylvatica* and *C. strigosa*, that give the vegetation of the middle years of the coppice rotation and of damper rides its distinctive stamp. Very wet areas, such as rain-filled ruts and hollows, can even show an abundance of such species as *Galium palustre* or *Callitriche stagnalis*. Varied mixtures of these plants and many other occasional adventives provide a great enrichment of the flora in woods which are still regularly coppiced (e.g. Rackham 1975, Ash & Barkham 1976).

As with the *Anemone* sub-community, stands of *Fraxinus-Acer-Mercurialis* woodland with field layers rich in *Deschampsia* can be found locally towards the north-west though, as usual in this part of the country, *Ulmus glabra* and *Acer pseudoplatanus* frequently join *Fraxinus* in the canopy and such oak as is present tends to be *Q. petraea*. Coppicing is less widespread here and the sub-community usually occurs as permanent vegetation over drift-derived soils and on damp north-facing slopes. Then, it can closely resemble the *Deschampsia* sub-community of the *Alnus-Fraxinus-Lysimachia* woodland (which it can adjoin around slope-flushes) but the increased representation of *Alnus glutinosa* there and the absence of many of the more calcicolous herbs of this community will usually serve to distinguish the two vegetation types.

***Hedera helix* sub-community:** *Quercetum roburis* Tansley 1911 p.p.; Broadbalk Wilderness oak-hazel wood Brenchley & Adam 1915; *Quercetum roboris* Tansley 1939 p.p.; Hayley Triangle woodland Rackham 1975; Ash-maple-hazel woodlands Rackham 1980 p.p.; Ash-maple stand type 2C Peterken 1981 p.p.; Hazel-ash stand type 3B Peterken 1981 p.p.; Woodland plot types 4 & 6 Bunce 1982. Unlike the *Deschampsia* sub-community, this kind of woodland is almost always found with a closed cover of woody plants: there is very often a continuous canopy of trees and the understorey, too, can be very extensive, so that stands frequently have a rather dense and gloomy appearance. However, in terms of its species composition, the woody component here is less rich and variable than in other south-eastern *Fraxinus-Acer-Mercurialis* woodlands. Quite commonly, various combinations of *Fraxinus*, *Corylus* and *Acer campestre* dominate and signs of past coppicing are frequent, but neglect is almost universal with the hazel and maple stools much overgrown and the (usually *Quercus robur*) standards often overtopped by emergent maidens of *Fraxinus*. Other stands have a much simpler structure resembling high forest: here *Fraxinus* is the usual dominant (less frequently *Q. robur*) and the understorey more sparse with hawthorn (almost always here

C. monogyna) often rivalling *Corylus*, very little or no *A. campestre* and patchily abundant *Sambucus nigra*. In this kind of woodland, the trees often appear to be more or less even-aged and the canopy can have a striking uniformity, structural features strongly suggestive of fairly recent spontaneous origin or of planting. Indeed, in some cases, as on the Broadbalk Wilderness at Rothamsted (Brenchley & Adam 1915, Tansley 1939) and in the Triangle in Hayley Wood (Rackham 1975), there is well-documented evidence of the development of this sub-community by invasion and young stands progressing from hawthorn scrub can commonly be found in abandoned quarries, marl pits and neglected field corners. Occasionally, this sub-community can be dominated by suckering elms and such woodland may sometimes have been produced by the invasion of previously unwooded ground. Although individual trees of *Tilia cordata* and *Carpinus betulus* can be found in stands, this kind of *Fraxinus-Acer-Mercurialis* woodland is only rarely encountered with canopies in which these species play a major role.

Whatever the particular composition and structure of the woody component, the field layer here is distinctive in the constancy, and often considerable abundance, of *Hedera helix* growing as a ground carpet. Where it is especially extensive, *Mercurialis* and, to a lesser extent, *Hyacinthoides* tend to be sparse and often limited to the margins of sites, adjacent to established populations in existing hedgerows or tracts of older woodland: these species spread only slowly (Rackham 1975, 1980, Pigott 1977, 1984) and their scarcity in some stands of the *Hedera* sub-community can be supportive evidence of a recent origin of the woodland. Through the sub-community as a whole, however, both *Mercurialis* and *Hyacinthoides* are common, often forming a patchy cover over the *Hedera*, and all being overlain by an underscrub of *Rubus fruticosus* agg. What does seem to be important for the spread of *Hedera* is not particularly a recent origin of the woodland but an undisturbed period of canopy closure (perhaps more than 20–50 years), whether this comes about through neglect of coppicing, or uninterrupted invasion of shrubs and trees, or planting.

That, and an influence of climate, because there is no doubt that growth of *Hedera* is favoured by more oceanic conditions (e.g. Matthews 1955); ivy-dominance in the field layer, both here and in the *Fagus* analogue of this community and in its counterpart on less base-rich soils, the *Quercus-Pteridium-Rubus* woodland, is very much a feature of the south-west. In this region, the general similarity of ivy-dominated field layers of each of these woodland types can give rise to some confusion, though there are usually sufficient other floristic features about the vegetation to effect a

separation between them. *Fagus*-dominance is usually obvious enough to distinguish *Fagus-Mercurialis* woodlands with much *Hedera*, though younger stands where *Fagus* is only just beginning to take over from *Fraxinus* and *Quercus robur* may present more of a problem. Separating the *Hedera* sub-communities of *Fraxinus-Acer-Mercurialis* woodland and *Quercus-Pteridium-Rubus* woodland can be much more difficult, especially where the canopy consists of planted *Q. robur*, as it can in both these communities, and where there has been insufficient opportunity for *Mercurialis* to invade and give some indication of the affinities of the field layer. But this is a reflection of the very real fact that younger plantations of oak on both less and more base-rich soils tend to have a rather similar herbaceous vegetation.

With the abundance of the carpet of *Hedera* here, many of the typical associates of south-eastern *Fraxinus-Acer-Mercurialis* woodlands show a depressed frequency and abundance. *Geum urbanum* and *Circaea lutetiana*, with their taller leafy stems, hold up quite well throughout but *Poa trivialis*, *Glechoma hederacea*, *Primula vulgaris* and *Ajuga reptans* are generally much scarcer than in the *Primula-Glechoma* and *Anemone* sub-communities and very much restricted to areas where the ivy is not too thick on the ground and where it is not replaced by either *Mercurialis* or *Hyacinthoides* as the field-layer dominant. Bryophytes, too, are much sparser than usual with even the common species like *Eurhynchium praelongum*, *Brachythecium rutabulum* and *Plagiommium undulatum* reduced in frequency and cover.

Other species of note are few but *Brachypodium sylvaticum* is much more generally frequent in this kind of woodland than in other south-eastern sub-communities and *Sanicula europaea*, though not common, can be locally very prominent. Both these species are animal-dispersed: *Brachypodium* has rough-awned fruits and those of *Sanicula* are densely clothed with hooks, features which aid their quick spread by transport on fur, feather (*Sanicula*) or trousers. Another bird-dispersed plant which can occasionally be found – its fruits are eaten and its seeds defaecated – is *Iris foetidissima*, but this is an Oceanic Southern species (Matthews 1955) and its local abundance here is strongly related to the more equable climate of the south-west. Like *Hedera*, it is a feature, too, of certain kinds of more base-rich *Fagus* woodlands in this region.

***Geranium robertianum* sub-community:** *Fraxinetum excelsioris*, drier sub-association Moss 1911; *Fraxinetum excelsioris calcareum* Tansley & Rankin 1911; *Fraxinetum calcicolum*, dry soil society Tansley 1939; Ash-oak wood Tansley 1939 *p.p.*; *Dryopterido-Fraxinetum phyllitidetosum* Klötzli 1970 *p.p.*; Ash-wych elm

stand types 1Aa & 1D Peterken 1981 *p.p.*; Hazel-ash stand type 3C Peterken 1981 *p.p.*; Ash-lime stand types 4Bb & 4C Peterken 1981 *p.p.*; Woodland plot types 1, 2, 8 & 12 Bunce 1982; *Quercus-Ulmetum glabrae*, Typical subassociation Birse & Robertson 1976 *emend.* Birse 1984 *p.p.* In this central type of north-western *Fraxinus-Acer-Mercurialis* woodland, both *Corylus* and, much more obviously in moving towards the limit of its British range, *Acer campestre* play a less prominent role than towards the south-east and these are not usually ash-maple-hazel woods in the sense of Rackham (1980) or Peterken (1981). The continuing importance of *Fraxinus* led early workers to class this vegetation as some kind of '*Fraxinetum*' but, though ash often predominates and is sometimes the only tree, the most obvious distinctive feature of the canopy in this sub-community is the great frequency, alongside *Fraxinus*, of *Acer pseudoplatanus* and *Ulmus glabra*. Occasionally, these species occur in various combinations as a large-coppice underwood, but coppicing is not as universal as among the south-eastern sub-communities and more often they are co-dominants in a high-forest canopy. The other striking difference here is the marked patchiness of oak and, when it does occur, it is usually *Quercus petraea* or hybrids rather than *Q. robur*. As noted earlier, this uneven representation of oak may be the result of extensive felling of these woodlands in the past, because in many areas (like the Yorkshire and Derbyshire Dales), stands of this sub-community have every appearance of being more or less even-aged spontaneous woodland of not very great antiquity (Pigott 1960, 1969, Merton 1970). Some tracts may have been planted.

No other tree here attains anything like the frequency of *Fraxinus*, *Ulmus* or *Acer pseudoplatanus* but a number of additional species occur, as in the south-east, as scattered occasionals. The most widespread of these is birch and, on the generally free-draining soils characteristically occupied by this sub-community, it is almost always *Betula pendula*. In certain situations, its abundance can show a local increase: it can be prominent, for example, in younger stands as a coloniser alongside *Fraxinus* and *Crataegus monogyna* (e.g. Merton 1970) and, in areas of complex geological and edaphic variation, it can pick out somewhat less base-rich substrates, a feature well shown over the Oolite sequence in the dales of the North York Moors where a belt of birch marks out a transition to more acidophilous woodland over calcareous grit interbedded with limestones.

Other species occurring less frequently are *Fagus sylvatica* (a tree beyond its natural limit over much of the range of this sub-community but occasionally seen in stands in south Wales and spreading in from planted trees further north), *Taxus baccata* (locally prominent in

some areas, as around Morecambe Bay, and occurring as isolated specimens on cliffs elsewhere), *Prunus avium*, *Sorbus aria* and, in more southerly stands, *S. torminalis*. *Tilia cordata* and *Carpinus betulus* are sometimes found but usually as isolated trees, those of *Tilia* especially often being of very obvious antiquity: only rarely do these species show that marked local abundance in large-coppice underwood which is so characteristic of their occurrence in the south-east. Invasion by suckering *carpinifolia* or *procera* elms is rare. Species of *Larix* or *Pinus* have sometimes been planted into stands which are used for amenity purposes or have invaded from nearby conifer plantations.

Shrubs and smaller trees occur most commonly here as part of a distinct high-forest understorey and, though this can be quite dense in younger stands or in gaps, in mature woodland of this kind it is characteristically rather open. *Corylus* in particular, though it has sometimes obviously been coppiced, does not in general have that disproportionate abundance so typical of most south-eastern *Fraxinus-Acer-Mercurialis* woodlands. Indeed, it is often rivalled or even exceeded in cover by hawthorn which here is almost always *Crataegus monogyna*. This is especially abundant in younger stands but, even in mature woodland, individual hawthorns may be very conspicuous because they can grow to substantial size and contribute to the tree canopy. The same is true of *Acer campestre*, less frequent here than either *Corylus* or *Crataegus*, and also of *Ilex aquifolium* which, in response to the milder winter climate of this more oceanic region, shows a slight but distinct increase in frequency here compared with the south-eastern sub-communities. Usually, however, all these species occur in a well-defined lower tier beneath the tree canopy.

Two other features of the understorey are noticeable. The first is the high frequency of *Sambucus nigra* which is almost as common throughout as *Corylus*, a striking contrast to the south-east where it is very much an indicator of local disturbance and enrichment. Its abundance is still very variable, though in certain situations it becomes the most prominent shrub. Second, there is often a great abundance of saplings because, though oak regenerates as badly here as in the south-east, *Fraxinus*, *Ulmus* and *Acer pseudoplatanus* are all very well represented by young trees of all ages, except where shade from the canopy of field-layer plants like *Mercurialis*, *Urtica dioica*, *Phyllitis scolopendrium* or *Rubus* is too dense to allow seedlings to get away (e.g. Wardle 1959). Gaps quickly become filled by cores of young ash and sycamore (*Ulmus* seems less speedy a coloniser) and all three species can readily spread out around ungrazed margins of stands.

Finally, among the woody species, there are occasional records for *Salix caprea*, *S. cinerea*, *Prunus spinosa*,

Euonymus europaeus, *Malus sylvestris* and, less commonly, *Populus tremula*.

The field layer here shares with those of the south-eastern sub-communities frequent records for *Mercurialis*, *Geum urbanum*, *Circaea lutetiana*, *Rubus fruticosus* agg. and, occurring less commonly, *Arum maculatum* and *Dryopteris filix-mas*. *Hyacinthoides* remains quite frequent but it is noticeably less common on the generally free-draining soils here and only rarely assumes dominance. Much more obviously reduced in frequency is that group of species so characteristic of the heavy clay soils of south-eastern *Fraxinus-Acer-Mercurialis* woodlands: *Poa trivialis*, *Glechoma hederacea*, *Primula vulgaris*, *Ajugareptans*, *Viola* spp. and, to a lesser extent, *Carex sylvatica* and *Lamium galeobdolon*. In the north-west, all these species tend to be restricted to locally-occurring stands of the *Anemone* and *Deschampsia* sub-communities or to flush surrounds carrying the *Alnus-Fraxinus-Lysimachia* woodland.

By contrast, there is a marked increase in the representation of species which, in the south-east, occur only locally, if at all. The commonest of these are *Urtica dioica* and *Galium aparine*, the high frequency of which, as with *Sambucus*, perhaps reflects the more rapid nutrient turnover that occurs in these better-aerated soils. *Geranium robertianum* and *Brachypodium sylvaticum*, two other readily-dispersed species, are also of widespread occurrence here. Then, with the milder climatic conditions, there is often an abundance of ground-growing *Hedera helix*. This feature can be seen too in the *Hedera* sub-community of the south-west but, here, *Hedera* is often accompanied by the oceanic fern *Phyllitis scolopendrium*, a very good marker of all the north-western kinds of *Fraxinus-Acer-Mercurialis* woodland. Although the early spring emergence of *Mercurialis* still gives this vegetation a distinct vernal aspect, it is often the winter-green character of the field layer that strikes the regular visitor most, with the carpet of ivy and the prominent sprays of *Phyllitis* fronds which persist until March or later, until the new growth emerges (Page 1982). Other ferns which can contribute to the lush appearance of the field layer, especially where ravines or large crevices further increase the shelter, are *Polystichum setiferum* (often strikingly gregarious), *P. aculeatum* (more local and typically solitary) and (much rarer but occurring under miniaturised versions of this woodland in Carboniferous Limestone grikes in the Yorkshire Dales), *P. lonchitis* and *Dryopteris villarii* (Gilbert 1970). Smaller crevices can provide a niche for *Asplenium trichomanes*, *A. viride*, *A. ruta-muraria* and *Cystopteris fragilis*. Note, however, that a high frequency of ferns like *Dryopteris filix-mas*, *D. dilatata* and *Athyrium filix-femina* is not characteristic here: this is one feature which helps separate the north-western

Fraxinus-Acer-Mercurialis woodlands from their upland counterpart, the *Fraxinus-Sorbus-Mercurialis* woodland.

The luxuriant quality of the vegetation is also frequently enhanced by an extensive and diverse bryophyte cover: bryophytes, mostly fairly bulky mosses, are more varied and abundant here than in the south-east, sometimes forming a virtually continuous vivid green carpet over the soil or rocky substrate. As well as the community species *Eurhynchium praelongum*, *Brachythecium rutabulum* and *Plagiomnium undulatum*, *Eurhynchium striatum* and *Thamnobryum alopecurum* become preferentially frequent in the north-west and there are occasional records, too, for *Ctenidium molluscum*, *Eurhynchium swartzii*, *Fissidens taxifolius*, *F. bryoides*, *Mnium hornum*, *Atrichum undulatum*, *Thuidium tamariscinum*, *Cirriphyllum piliferum*, *Rhytidiadelphus triquetrus*, *Plagiomnium rostratum* and *Rhizomnium punctatum*. In especially sheltered spots like ravines or rock clefts, even greater enrichment of the bryophyte flora can be found (e.g. Proctor 1960).

As in the south-eastern *Fraxinus-Acer-Mercurialis* woodlands there is considerable quantitative variation in the representation of these characteristic species. Once again, this is often most obviously seen in terms of the abundance of *Mercurialis*, though the resulting vegetation patterns are expressed in rather a different way over the commonly sharp valley-side topography typically occupied by this sub-community. Overall, *Mercurialis* is the commonest dominant here and it can maintain a high cover even over rocky and very sharply draining scree slopes from which *Hyacinthoides* is totally excluded and where such species as *Geum urbanum* and *Circaea lutetiana* are diminished not by direct competition with the *Mercurialis* but by the dry conditions. In this kind of woodland, *Brachypodium sylvaticum* is often the most frequent companion of *Mercurialis*; here and there can be scattered tussocks of *Arrhenatherum elatius*, especially where the cover of shrubs and trees thins out somewhat. Where *Mercurialis* maintains its cover in less extreme conditions, many of the herbaceous associates are diminished by the dense shade that it casts and seedlings and small saplings of trees become much less common. As in the south-east, the richest and most varied field layers tend to be associated with situations where, for one reason or another, *Mercurialis* itself is reduced in abundance. Most often, here, this occurs where the soil becomes naturally moister, rather than badly aerated because of the trampling that accompanies coppicing. Such conditions can be found where this sub-community extends on to less permeable calcareous bedrocks like shales or clays or occurs over heavy-textured superficials, or where there is flushing around springs, in slope-foot colluvium or on alluvial flats.

There, reduction in *Mercurialis* and an increase in other species may mark the beginning of a transition to the *Anemone* or *Deschampsia* sub-communities over ill-drained ground, or to the *Allium* sub-community over very moist but free-draining soils.

However, there is a further quite common kind of quantitative variation within this sub-community that seems to be related to the trophic state of the soils and which is marked most obviously by differences in the abundance of *Urtica dioica* and, to a lesser extent, *Galium aparine*. These species occur throughout this kind of vegetation, though usually at low cover, and Pigott & Taylor (1964) have shown that, though *Urtica* readily germinates on a wide range of soils occupied by this sub-community, it only makes good subsequent growth where supplies of all minerals, including phosphate, are high. Such conditions can be found here, as in the south-east, where there is local disturbance, dumping of waste or burning but they are quite often met in the habitat of this kind of woodland on the deep and largely stone-free colluvium which accumulates at the bottom of slopes. In such situations, dominance in the field layer frequently passes to *Urtica* with a consequent reduction in the abundance of *Mercurialis*, a feature well shown in Pigott & Taylor's (1964) transects from the Derbyshire Dales. *Geranium robertianum* tends to follow *Urtica* and *Galium*, perhaps because it, too, is more nutrient-demanding: on rocky soils, it often shows a marked reddening that betokens deficiency of phosphate or nitrogen. And, among the shrubs, *Sambucus nigra* often increases its cover in this kind of vegetation. However, other species in the field layer may become more abundant here because colluvial soils are also generally moister than those on the valley sides above.

***Allium ursinum* sub-community:** *Fraxinetum excelsioris*, moist sub-association Moss 1911 p.p.; *Fraxinetum calcicolum*, *Allium ursinum* society Tansley 1939; Ash-oak wood, *Allium ursinum* society Tansley 1939; Ash-wych elm stand types 1Aa & 1Ab Peterken 1981; *Quercus-Ulmetum glabrae*, *Allium ursinum* subassociation Birse & Robertson 1976 emend. Birse 1984 p.p. This sub-community maintains all the general features of the woody component of typical north-western *Fraxinus-Acer-Mercurialis* woodlands: a mixed canopy of *Fraxinus*, *Ulmus* and *Acer pseudoplatanus*, with or without oak, and an understorey with *Corylus*, *Crataegus monogyna*, *Sambucus nigra*, *Acer campestre* and abundant saplings of the leading trees. On the deeper, moister soils which this kind of woodland occupies, growth of these woody species is often vigorous and majestic trees here can contrast with poorer specimens in stands of the *Geranium* sub-community over more rocky substrates. Where these two sub-communities occur contiguously,

there can be some sorting of trees between the two kinds of woodland with *Ulmus*, *Acer pseudoplatanus* and, if locally represented, oak being much more obvious and well grown in the *Allium* sub-community and *Fraxinus* leading in the *Geranium* sub-community on the drier slopes above. This kind of contrast was noted in early accounts of the Mendip woodlands (e.g. Moss 1907, Hope-Simpson & Willis 1955).

However, the really distinctive feature of this sub-community is the prominence of *Allium ursinum* in the field layer. This species can be found occasionally in pockets of moister soil within stands of the *Geranium* sub-community but here it is preferentially frequent and commonly the vernal dominant, often carpeting the ground from March to July with an even cover of its shiny leaves and providing a spectacular sight when flowering between April and June. *Mercurialis*, though, remains very frequent and *Hyacinthoides*, though less common, can be patchily abundant. On occasion, either or both of these can share dominance with *Allium* in the spring and, on these moister soils, there may also be occasional scattered plants of *Anemone nemorosa* or *Ranunculus ficaria*. When the leaves of *Allium* have died down in mid-summer, the more persistent shoots of *Mercurialis* can become for some time the most obvious feature of the field layer. Indeed, at this time of year, there may be little to separate this vegetation from more luxuriant stands of the *Geranium* sub-community: there is often a patchy carpet of *Hedera* and scattered individuals of *Urtica*, *Galium aparine*, *Geranium robertianum*, *Phyllitis scolopendrium*, *Geum urbanum*, *Circaea luteotiana* and *Arum maculatum* are common. In other stands, the flaccid, pale green remains of the *Allium* foliage finally disappear to leave only the fruiting stems and a remnant smell of garlic hanging over an expanse of bare ground or an extensive cover of bryophytes on the exposed soil.

***Teucrium scorodonia* sub-community:** *Fraxinetum excelsioris*, dry stony sub-association Moss 1911 *p.p.*; *Fraxinetum calcicolum* Tansley 1939 *p.p.*; Uneven-aged limestone woodland Pigott 1969; Ash-wych elm stand type 1D Peterken 1981 *p.p.*; Hazel-ash stand type 3C Peterken 1981 *p.p.*; Ash-lime stand type 4C Peterken 1981 *p.p.* This highly distinctive kind of woodland shares many floristic features with the *Geranium* and *Allium* sub-communities but it is richer and more varied in its composition and has a structural complexity to its woody component that is lacking from many north-western *Fraxinus-Acer-Mercurialis* woodlands. *Fraxinus*, *Ulmus* and *Acer pseudoplatanus* all remain frequent here, though the last two, and particularly *Acer*, play a less prominent role in the canopy than is usual. Furthermore, although *Fraxinus* is frequently

the most abundant tree, it is often accompanied here by a variety of other species that are generally of restricted occurrence in the region. First, oak (both *Quercus petraea* and *Q. robur* have been recorded) is a little commoner than is the rule; more accurately, in areas where oak is generally absent from *Fraxinus-Acer-Mercurialis* woodlands, such trees as do survive are more often in stands of this sub-community, rather than in (even adjacent) tracts of the *Geranium* or *Allium* sub-communities. Then, there may be some *Taxus baccata*, occurring as scattered trees or, in some stands, as in Matlock Dale in Derbyshire (Pigott 1969), forming a distinct lower tier to the canopy. *Fagus sylvatica* can occur too, though its representation differs according to the locality. To the north, as in the Derbyshire Dales, it is typically very rare, even though it has been widely planted throughout the region and often occurs close by; in the Wye valley, by contrast, this kind of woodland occurs within the supposed natural limit of *Fagus* and occasional trees, sometimes of grand size, can be found. Finally among these larger species, both our native limes, *Tilia cordata* and the much rarer *T. platyphyllos* can occur, together with apparently natural hybrids between them; indeed, in Derbyshire, trees of intermediate character are more common than the parents (Pigott 1969). Although trees of different ages occur in this locality, some individuals are clearly very old, with massive stools rooted into crevices or maintaining a hold, as bent and spreading specimens, on talus which has shifted beneath and around them (Pigott 1969, Merton 1970). *T. cordata*, as noted earlier, is not limited in Britain to *Fraxinus-Acer-Mercurialis* woodland, but *T. platyphyllos* almost always is and, within this community, is very characteristic of these rocky stands of the *Teucrium* sub-community. In some localities, where populations approach pure *cordata* or *platyphyllos*, the somewhat different ecological preferences of the two species can be seen, as in Kingley Wood at Ilam in Derbyshire, where the former occurs over less base-rich soils (Pigott 1969).

In some stands, all these species occur together as co-dominants in a mixed canopy; in others, there is a patchy mosaic with different trees (notably *Fraxinus*, *Taxus* and *Tilia*) showing local prominence here and there. Signs of coppicing can sometimes be seen (e.g. Merton 1970, Ratcliffe 1977) but typically the structure is that of high forest with an uneven and complicated age structure (Pigott 1960, 1969, Merton 1970). Together with the fact that this kind of woodland often occurs over the very uneven topography of talus slopes and rocky bluffs and cliffs, this means that the canopy is characteristically rather open and uneven-topped. Frequently, there is a complete gradation between the leading maidens, younger trees, smaller trees and shrubs and saplings,

and the cover can be punctuated or fringed by stretches of more scrubby growth.

Among the smaller woody species, *Corylus*, *Crataegus* (always here *C. monogyna*) and *Acer campestre* are all well represented, though hawthorn does not usually have the prominence that it often shows in the *Geranium* and *Allium* sub-communities. *Sambucus nigra*, too, is noticeably less common and abundant here than in many north-western *Fraxinus-Acer-Mercurialis* woodlands. *Ilex aquifolium* occurs occasionally and there are sometimes scattered individuals of *Prunus spinosa*, *Malus sylvestris*, *Euonymus europaeus*, *Salix caprea* and *S. cinerea*. Again, however, what is most noticeable about the understorey is the additional occurrence of species which, when they do occur in the *Geranium* sub-community, are, like the preferential trees, usually found only as isolated individuals, often clinging to cliffs. Here, by contrast, there are frequent records for *Cornus sanguinea*, *Viburnum opulus*, *Rhamnus catharticus* and *Sorbus aucuparia*, with *Prunus padus* a little less common. All of these can occur scattered in an open understorey or in thicker scrubby patches beneath gaps and around the margins of stands.

A further feature of interest here is the occurrence of various of the rarer Sorbi. *Sorbus torminalis* can sometimes be found as a tall tree, but there are also records for the bushier *S. anglica* and a number of the disjunct polyploid apomicts of the *S. aria* group: *S. rupicola* and, in the Wye valley, *S. porrigentifformis* and *S. eminens* (Pigott 1969, Ratcliffe 1977).

The field layer of this sub-community also has its own peculiarities, though its general relationships to north-western *Fraxinus-Acer-Mercurialis* woodlands are fairly clear. Thus, there are frequent records for *Mercurialis perennis*, *Rubus fruticosus* agg., *Circaea lutetiana*, *Geum urbanum* and some of *Hyacinthoides*, *Urtica*, *Galium aparine*, *Geranium robertianum*, *Hedera helix* and *Phyllitis scolopendrium*, and a general absence of those plants more associated with the heavy clay soils of the south-east. Although substrate heterogeneity can allow species like *Deschampsia cespitosa*, *Filipendula ulmaria*, *Angelica sylvestris*, *Allium ursinum* and *Anemone nemorosa* to flourish locally in pockets of deeper soil or on damper ledges, the overall feel of the vegetation is of a drier kind of *Geranium* sub-community field layer, though with some notable additions. Typically, however, there is no consistent pattern of dominance because one important factor in the increased richness of the herbaceous component here is the patchy shade cast by the characteristically discontinuous canopy. The usual appearance of the field layer is thus of a diverse mosaic of vegetation distributed over less well lit areas interspersed with scrubby glades. Plants like *Brachypodium sylvaticum* and *Arrhenatherum elatius*, which become abundant in

drier open areas in the *Geranium* sub-community, are more common here and often joined by *Teucrium scorodonia*, *Melica uniflora*, the rarer *M. nutans*, *Campanula latifolia* and *Myosotis sylvatica*. Although not a constant feature, a further very distinctive associate in this kind of woodland is *Convallaria majalis*, a plant not confined in Britain to calcicolous woods but one which seems to perform better than *Mercurialis* on drier, more unstable limestone screes and which can be quite abundant here, even in areas of deeper shade (Pigott 1969, Merton 1970). Where the canopy thins out more markedly to a shrub-dominated cover, fragments of vegetation more characteristic of sunny, calcicolous scrub may be encountered with species like *Geranium sanguineum*, *Rosa villosa*, *R. pimpinellifolia* and national rarities such as *Polygonatum odoratum*, *Carex digitata* and *Epipactis atrorubens*. Other plants of restricted distribution which can be found here are *Daphne mezereum* (as well as the more widespread *D. laureola*) and, in deeper shade, *Cardamine impatiens*. Stands of this sub-community also include some of the southern-most stations of *Rubus saxatilis* (like *Melica nutans*, a Northern Montane species) and the oceanic fern *Polystichum aculeatum* is sometimes encountered in moister, shaded crevices.

On the drier, often well illuminated, substrates here, the typical bryophytes of the north-western *Fraxinus-Acer-Mercurialis* woodlands are rather poorly represented, apart from the community species *Eurhynchium praelongum* and *Plagiomnium undulatum*. However, in more open areas there is often a considerable enrichment of the ground cover by species characteristic of rocky, calcicolous grassland and there *Ctenidium molluscum*, *Homalothecium lutescens*, *Thuidium tamariscinum* and *Tortella tortuosa* can all be recorded.

Although stands of the *Geranium* sub-community sometimes approach the richness of this kind of woodland in one or another respect, the peculiar variety of this flora is seen in all its fullness in only a few localities. Stands can be extensive but it is a noticeable feature of this vegetation that regeneration appears very slow. Although the canopy typically comprises uneven-aged trees, younger saplings are very much less obvious than in other north-western *Fraxinus-Acer-Mercurialis* woodlands. For one thing, *Ulmus* and *Acer pseudoplatanus* are less common here and, though young *Fraxinus* often occur, oak regenerates badly and only in exceptionally warm summers does *Tilia cordata* set viable seed in these areas (Pigott 1969, Pigott & Huntley 1981), though *T. platyphyllos* fruits more regularly. *Cornus sanguinea*, too approaching the north-western limit of its range here, and *Prunus padus*, predominantly a northern species in which fruit development is favoured by cool, wet conditions (Jarvis 1960), also rarely reproduce sexually

in Derbyshire, though both sucker freely (Pigott 1969). Some of the characteristic field-layer species, like *Convallaria*, *Melica nutans* and *Rubus saxatilis*, though they fruit, also seem to rely predominantly on vegetative spread (Pigott 1969). For all its variety and luxuriance therefore, this type of woodland appears to be remnant vegetation of quite a fragile kind and to have survived largely because of the intractable character of the topography.

Habitat

The *Fraxinus-Acer-Mercurialis* woodland is typically a community of calcareous mull soils in the relatively warm and dry lowlands of southern Britain. Over much of its range, it probably represents the climax forest type of more base-rich soils, though almost universally its structure and floristics have been affected by silvicultural treatment. In some cases, stands occupy sites known to have been continuously wooded for very considerable periods of time but the community also includes vegetation of relatively recent spontaneous or planted origin.

This woodland occurs on soils derived from a wide variety of more calcareous parent materials, being most common over sedimentary limestones, shales and clays and superficial deposits like glacial drift. Over such substrates, it is confined to those parts of the country where the annual rainfall is less than 1000 mm (*Climatological Atlas* 1952, Chandler & Gregory 1976) and where there are fewer than 160 wet days yr^{-1} (Ratcliffe 1968). In such areas, these materials weather to produce soils in which leaching is generally limited to superficial depletion of calcium carbonate and mobilisation of clay minerals. Thus, though surface pH of the soils under the community can be reduced to quite low values (down to about 4.5 or even less), base-rich conditions are usually maintained below and there is often much exchangeable calcium in the lower horizons (e.g. Hodge & Seale 1966, Martin & Pigott 1975). Where the influence of the parent material is more dominant, the profiles can be base-rich and calcareous throughout, with surface pH between 6 and 7 or more. However, except in very rocky or heavily-waterlogged situations, these are usually mull soils with an active invertebrate fauna rich in lumbricid worms. Typically, the litter, made up predominantly here of the leaves of plants with softer and more palatable foliage, is incorporated very quickly; even by mid-winter, the ground between the evergreen herbs and bryophytes is often quite bare, apart from the more resistant leaves of oak and twigs. Sometimes, transitional moder conditions are encountered but surface mor is rare.

These general edaphic features are reflected in the vegetation by the strong representation here of woodland plants tolerant of more base-rich conditions. A

more strictly calcicolous element is not always the most obvious feature though: its prominence is often muted by the abundance of plants characteristic of mull soils and variation in factors other than the base-status of the soil commonly produces floristic differences which mask its presence. Nonetheless, among British woodlands, this community (together with its analogues dominated by *Fagus* and *Taxus*) represents one extreme of variation in relation to pH. The frequent presence of *Fraxinus* and *Acer campestre* with plants like *Mercurialis*, *Geum urbanum*, *Circaea lutetiana*, *Viola reichenbachiana*, *Arum maculatum* and *Sanicula europaea* is unique to this kind of woodland and helps define edaphically-related boundaries between the community and other woodland types. Thus, though some of these plants continue northwards over more calcareous substrates which occur beyond the range of the *Fraxinus-Acer-Mercurialis* woodland, the higher rainfall there means that they are accompanied by plants indicative of more marked surface eluviation, such as *Dryopteris dilatata* and *Athyrium filix-femina*. These are species which, generally speaking, are rare here and which help separate this community from its northern analogue, the *Fraxinus-Sorbus-Mercurialis* woodland. Towards the drier south, too, the boundary between the *Fraxinus-Acer-Mercurialis* woodland and its closest relative, the *Quercus-Pteridium-Rubus* woodland, is essentially an edaphic one. Although this community also has frequent records for plants tolerant of a wide range of soil pH (e.g. *Quercus robur*, *Corylus*, *Crataegus* spp., *Hyacinthoides* and *Rubus*), more calcicolous plants fade out there with the shift to moder and mor soils of lower pH derived from non-calcareous bedrocks and superficals.

As well as helping define the general limits of the *Fraxinus-Acer-Mercurialis* woodland, edaphic variation plays a major role in influencing floristic differences between and within the two suites of sub-communities here and contributes to their striking geographical association with either the north-west or the south-east. In the latter part of the country, this kind of woodland is relatively rare on more free-draining soils developed over pervious calcareous deposits like the Chalk and Jurassic limestones. Here, *Fagus* and, more locally, *Taxus* are important competitors with *Quercus robur* and, to a lesser extent, *Fraxinus*, and usually come to dominate over rather similar field layers. Much more commonly in the south-east, the *Fraxinus-Acer-Mercurialis* woodland occurs over softer argillaceous rocks, such as the Jurassic, Cretaceous and Tertiary clays which underlie the basins and vales, and fine-textured superficals, like the Chalky Boulder Clay that is very widely distributed over the east Midlands and East Anglian plateaus. The soils derived from such materials typically have a clay or clay-loam texture and their chief

characteristic is their general impermeability to excess rain which results in seasonal surface-water gleying (e.g. Hey & Perrin 1960, Hodge & Seale 1966, Martin & Pigott 1975, Curtiss *et al.* 1976, Fordham & Green 1980). Although the rainfall here is relatively low (less than 600 mm yr⁻¹ over much of the area), the fine texture of the sub-surface horizons impairs the drainage so that, as winter advances, the upper layers of the soil become very wet, the clays swelling and closing the pores, and, in extreme cases, there can even be a thin patchy cover of standing water on the surface. In spring, the soils dry and, during early summer, shrink and crack above, sometimes to a distinctive coarse blocky structure, and let in air which re-oxidises iron and manganese compounds producing the characteristic red-brown/grey mottling of the B and C horizons (e.g. Hodge & Seale 1966, Martin & Pigott 1975). The degree of impermeability and the extent of gleying vary so that profiles can range from incipiently gleyed typical brown soils right through to stagnogleys (though some of these soils, like the Hanslope Series, which is very widespread in East Anglia, are now classed as pelosols because of the predominance of clay in the profile: Avery 1980, Soil Survey 1983). Although there is very little hard evidence, it is likely that such soils are rather poor in major nutrients (e.g. Martin & Pigott 1975), a condition accentuated in many cases by generations of cropping for underwood and timber, with no fertilisation apart from that derived from litter decay and the occasional bonfire. Both trophic state and pH are probably reduced as the tendency to gleying increases, perhaps because of poorer incorporation of litter by reduced earthworm populations (Martin & Pigott 1975, Rackham 1975).

It is where the *Fraxinus-Acer-Mercurialis* woodland occurs on soils such as these, that it is characterised by the frequent presence of *Quercus robur* and, in the field layer, of such plants as *Primula vulgaris* (or *P. elatior* in parts of East Anglia), *Poa trivialis*, *Glechoma hederacea*, *Ajuga reptans* and *Viola* spp. and by the preferentially common occurrence of *Hyacinthoides*, all of them plants tolerant, to varying degrees, of heavier and moister soils. Also here, more eutrophic species like *Urtica* and *Galium aparine* are generally rather local, occurring mostly where there is some obvious enrichment over old settlements and bonfires, along wood margins affected by fertiliser drift from adjacent farmland or beneath invasive elms with their calcium-rich litter (Martin & Pigott 1975).

Furthermore, among these south-eastern kinds of *Fraxinus-Acer-Mercurialis* woodland, there is every indication that many of the floristic differences between the *Primula-Glechoma* and *Anemone* sub-communities and, to a lesser extent, the *Deschampsia* sub-community, are related to the extent and duration of the soil waterlogging. The *Primula-Glechoma* sub-community is the

central type and it is very widely distributed throughout the region on more base-rich brown soils with a less marked tendency to gleying. It even extends a little on to more permeable mull rendzinas over the southern Chalk and on to better-drained brown soils derived from generally less calcareous parent materials like Clay-with-Flints. For the most part, however, it occurs over deposits like the Weald, Oxford and London Clays, provided these do not remain waterlogged well into the spring. Often, this is where a natural slope (even a very slight slope) allows quicker run-off of surface water such that the soils are gleyed only in the lower part of the profile.

Where similarly-structured soils derived from the same parent materials remain wetter longer, as they do in surface hollows and on flatter plateaus, there is an increasing tendency for the *Anemone* sub-community to take over on soils that are gleyed right up to the base of the A horizon. Quite commonly, such patterns can be seen as zonations within the same wood, as at Hayley, where they have been very neatly related, by both observation and field laboratory experiments, to an increasing gradient of waterlogging (Abeywickrama 1949, Martin 1968, Martin & Pigott 1975, Rackham 1975). In fact, the switch between what are defined here as the *Primula-Glechoma* and *Anemone* sub-communities is often a rather gradual one and it seems to be based on the decreasing sensitivity of the major species involved to the ferrous ions which accumulate in the reduced atmosphere of gleyed soils (Martin 1968). Thus, as the most susceptible plants, first *Mercurialis*, then *Hyacinthoides*, lose their vigour over more markedly gleyed soils, others which are more tolerant, like *Anemone*, *Primula vulgaris* and, in East Anglian woods like Hayley, *P. elatior*, are able to assume dominance in striking patterns of zoned vegetation. In some places, the zonation continues to the *Deschampsia* sub-community over soils which are free from waterlogging for only a short period in the summer months. *D. cespitosa* was the species most tolerant of ferrous ions among those examined by Martin (1968), although its prominence in many stands of the *Deschampsia* sub-community is clearly related to the distinctive combination of reduced aeration due to trampling and the increased light that follows clearance or coppicing on heavy soils. In some of these species at least, tolerance of waterlogging appears to be due to an ability to export oxygen from aerenchymatous roots and so produce a protective oxidised rhizosphere (Martin 1968).

The increased soil moisture marked by these changes in the field layer also influences woody species in these sub-communities, and *Populus tremula* and, to a more obvious extent, *Carpinus betulus* both tend to increase over strongly-gleyed profiles. Seedlings of *Fraxinus* are also often very numerous here, though much of this

response may be due to the extensive patchwork of more open ground characteristic of the wetter soils. *Alnus* can also become a little more frequent but, though the *Deschampsia* field layer is very similar to that found in some kinds of *Alnus-Fraxinus-Lysimachia* woodland, *Alnus* itself is probably limited here by the fact that, in summer, the soils can bake very hard.

Both the *Anemone* and *Deschampsia* sub-communities can occur to the north-west over pockets of less permeable parent materials like glacial drift or where there is some gleying by ground waters along stream sides and around slope flushes. For the most part, though, more base-rich soils occur in this region over pervious bedrocks like the Carboniferous Limestone (in the Mendips, Wales, Derbyshire, the Pennines and around Morecambe Bay), Jurassic limestones (in the North York Moors), Magnesian Limestone (in Yorkshire and Durham) and the Chalk (mainly in the Yorkshire Wolds). Even with the higher rainfall in these areas (750–1000 mm yr⁻¹ with around 140–160 wet days yr⁻¹: *Climatological Atlas* 1952, Ratcliffe 1968), the soils derived from such deposits remain generally calcareous and of high base-status, particularly on the frequent steep slopes which are generally drift-free and often unstable and actively weathering. More importantly, though these soils can be quite moist, especially on north-facing slopes or where there is some accumulation of colluvium receiving downwash, they are, in contrast to those of the south-east, free-draining. The *Fraxinus-Acer-Mercurialis* woodland is thus most often found here over rendzinas and, in extreme cases, scrubby versions of the community can extend on to very fragmentary protorendzinas between talus fragments, in cliff crevices or, over Carboniferous Limestone, in pavement grikes. On such soils, the clay-soil species so characteristic of the south-eastern sub-communities occur very sparsely and *Hyacinthoides* becomes generally much less common. By contrast, plants like *Brachypodium sylvaticum* and *Geranium robertianum*, which readily colonise free-draining substrates, increase in frequency. Quite obvious here, too, is the much more widespread occurrence of *Sambucus nigra*, *Urtica dioica* and *Galium aparine*, perhaps indicating a faster nutrient turnover in these well-aerated calcareous soils. The frequent stoniness of the profiles often means that this more eutrophic character is not fully expressed because the amount of nutrient per unit area is reduced (Pigott & Taylor 1964) but it becomes very apparent in the *Geranium* sub-community where deeper stone-free colluvium has accumulated. Often, too, such slope-foot soils are moister and here the north-western kind of *Fraxinus-Acer-Mercurialis* woodland extends on to mull rendzinas and brown calcareous earths in the striking vegetation of the *Allium* sub-community.

Although much of the floristic character of this community and its various sub-divisions can be related to edaphic interactions between different parent materials and climates across the country, both rainfall and temperature also have some more direct effects on the vegetation. These influences are various, complex and often imperfectly understood but, in general, they tend to confirm the soil-related patterns of variation and the way in which the two suites of sub-communities are associated with distinct regions. First, the distribution of the community as a whole corresponds roughly with the limits of the more Continental influence in the British flora. By and large, the *Fraxinus-Acer-Mercurialis* woodland is restricted to those parts of the country with a mean annual maximum temperature in excess of 26 °C (Conolly & Dahl 1970) and the presence here of a number of species with Continental or Continental Southern distributions in Europe helps separate this community from the more northerly *Fraxinus-Sorbus-Mercurialis* woodland. Thus, plants such as *Acer campestre*, *Carpinus betulus*, *Cornus sanguinea*, *Euonymus europaeus*, *Rhamnus catharticus*, *Sorbus torminalis*, *Tilia cordata*, *T. platyphyllos*, *Viburnum lantana*, *Clematis vitalba*, *Tamus communis*, *Arum maculatum*, *Daphne laureola* and *Lamium galeobdolon* are all of very sporadic occurrence beyond the northern bounds of the *Fraxinus-Acer-Mercurialis* woodland, though some of them, of course, occur widely in other kinds of woodland within their ranges. However, the extreme limits of these species are often of rather complicated configuration. *Acer campestre*, for example, and a number of the other trees and shrubs listed above, tend to have a gap in their distribution in the central Pennines (where this community is common) and to reappear with renewed frequency around Morecambe Bay. Then, some, like *Tilia cordata* and *Sorbus torminalis*, are much more frequent along the western side of the northern fringe of the *Fraxinus-Acer-Mercurialis* woodland than to the east, a slanted limit which runs in reverse direction to that of the community as a whole (Pigott & Huntley 1978). The reasons for these variations are probably varied and not necessarily of climatic origin: *A. campestre* is generally a hedgerow tree towards its north-west limit and many of the *Fraxinus-Acer-Mercurialis* woodlands in the central Pennines are of fairly recent spontaneous origin, so human interference may well have eaten away at more coherent past boundaries. Even where distributions can be generally related to climatic variation, the work of Pigott & Huntley (1978, 1980, 1981) on *T. cordata* has shown just how intricate the control can be. To set fertile seed, this tree requires three to four consecutive days during its flowering period when the mean daily maximum air temperature exceeds 19 °C so as to allow sufficient time for the pollen tubes to extend right to the ovular micropyle. At the

present time, such conditions are only regularly met roughly south-east of the Humber–Severn line: in this area, seedlings can often be found and the tree maintains itself as widespread populations, often with great local abundance. Further north, however, where the climate is generally cooler and somewhat less predictable, fertilisation occurs only sporadically in exceptionally warm summers (like those of 1976 and 1984). Also, flowering is two weeks or so later than towards the south (late July to early August as opposed to early July) and the onset of cooler autumn temperatures allows less time for complete development of the seed, even when fertilisation has occurred. Added to this, some at least of the often very old and isolated trees in the north seem to show ovular sterility and self-incompatibility (Pigott & Huntley 1981). Beyond the area in which it is actively reproducing at the present time, *T. cordata* thus seems to persist largely because the great longevity of its individuals plus very occasional sexual regeneration has ensured its survival from the time in the Forest Maximum when conditions were much more widely suitable for the production of viable seed. The rough coincidence of its overall range with that of the community can thus be related to long-past climatic conditions; its preferential frequency in the south-eastern sub-communities reflects the present climatic regime. Other species (like *Cornus sanguinea*, for example, which does not readily set viable seed towards the north: Pigott 1969) may well show this kind of relationship.

A second more direct effect of climate on the floristics of this woodland can be seen in the somewhat more oceanic character of the north-western sub-communities. In fact, the influence of the more equable climate of the western parts of Britain can already be seen towards the south where the frequency of *Hedera helix* as a ground carpet increases greatly in moving from the heartland of the *Primula-Glechoma* sub-community towards the south-west. Here, the *Hedera* sub-community becomes very common, even in longer-established woodlands where the abundance of ivy is not due largely to the uninterrupted development of dense canopy shade as in young scrub and plantations and abandoned coppice. In this kind of *Fraxinus-Acer-Mercurialis* woodland, the south-eastern type of canopy, with frequent *Quercus robur* and little *Ulmus glabra* or *Acer pseudoplatanus*, is maintained, though most of the clay-soil herbs are uncommon: this may be because they are suppressed by the thick ivy cover. Another oceanic species, *Iris foetidissima*, is an uncommon but very characteristic associate of *Hedera* in some stands in the south-west.

Hedera continues as an important component of the field layer in most *Fraxinus-Acer-Mercurialis* woodlands in the north-west, though, throughout the sub-

communities typical of this region, a much better preferential indicator of the oceanic conditions is *Phyllitis scolopendrium*. This fern is much commoner in Britain in those areas with a more continuously humid climate, freedom from frequent frost and a long growing season (Page 1982). It is generally much scarcer towards the south-east, though its local occurrences (as in cool and moist, north-facing coombes in the North Downs) help define far-flung stands of the largely north-western *Geranium* sub-community. *Polystichum setiferum*, though far less frequent than *Phyllitis*, has a similar distribution among these woodlands. Interestingly, all the forementioned plants are evergreen or winter-green and, together with the more abundant bryophytes of the north-western *Fraxinus-Acer-Mercurialis* woodlands, may carry out the bulk of their photosynthetic activity in the relatively mild winter months when the canopy is bare of leaves. Finally, among this group, there is *Ilex aquifolium*, also evergreen but probably slightly more frequent among the north-western sub-communities because of its sensitivity to low winter temperatures (Iversen 1944, Peterken & Lloyd 1967, Pigott 1970b).

Third, and last among these kinds of climatic influence, there is the marked association with the north-western sub-communities of *Ulmus glabra* and *Acer pseudoplatanus*, both as frequent and abundant canopy components and as often prolific saplings. Neither of these trees is confined to this community (though the former is a fairly good preferential) but, in all the woodland types in which they occur, they attain constancies in excess of III only where the annual rainfall is fairly high: the fit between the distribution of samples of such woodland types and areas with rainfall in excess of 762 mm (30") yr^{-1} is especially good for *Acer* (Rodwell in Pigott 1984). Though the fact that this tree is essentially a species of damp ravine woodland is a commonplace in Europe, the reasons for its behaviour, and for the similar pattern in *U. glabra*, are unclear. However, the diagnostic value of these species here is very obvious and a recognition of the climatic response in *Acer* needs to temper statements about its value as an indicator of human interference: within the region where many ancient stands of this woodland survive, it may not be able to perform well for quite natural reasons. As with the geographical influence of a more oceanic climate, it should be noted that areas of higher rainfall extend across the extreme southern part of England to take in some of the western Chalklands and the downland of the Home Counties, so outlying stands of largely north-western sub-communities can be found here; indeed, in this region, the coincidental occurrence of abundant *Phyllitis* under sycamore-rich canopies is a very striking local feature.

Climate and soils, then, are of prime importance in

determining the general character of the *Fraxinus-Acer-Mercurialis* woodland and much of the floristic variation within it; and they play a major role in governing its overall distribution and the range of its two suites of sub-communities. Very often, though, their controlling influence is overlain by the effects of silvicultural treatments. In general terms, treatments have operated within the constraints which the natural factors impose, though they have not always worked in the same direction. In some cases, as with selection for *Carpinus* as a large-coppice underwood crop on moister soils, treatment has accentuated variation related to, in this instance, edaphic conditions. In other cases, as with the reduction in the abundance of *Quercus robur* to occasional standards in many kinds of coppice in the south-east, treatment has worked against a natural trend, blurring floristic patterns. Also, very commonly, treatments have affected species of broad tolerance of different soils and climates (like *Corylus*) which have now come to vary quite independently of such factors or to show spurious associations with certain environmental conditions because of simple accidents of selection.

The net result of such effects is that variation in the woody component of the community has been dislocated to some extent from differences in the herbaceous element. This can be seen very clearly where the same field and ground layers occur under very different canopies derived by diverse manipulations of the same basic assortment of trees and shrubs. The *Primula-Glechoma* herbs and bryophytes, for example, can be found beneath coppiced underwood of *Corylus*, *Acer campestre* or *Fraxinus*, or various combinations of these, with or without an admixture of other shrubs and small-coppice trees and with or without varying numbers of standards, usually *Quercus robur*, occasionally *Fraxinus*, rarely *Acer campestre*; under large-coppice underwood of *Carpinus* or (provided it is not too dense) *Tilia cordata*, or various mixtures of these, again with or without standards; beneath invasive suckering elms; in semi-natural high forest with signs of only sporadic removal of timber or coppice-wood; and in older plantations, mainly of *Quercus robur* or *Fraxinus* (Figure 19). Conversely, where similar treatment has been applied to stands of different sub-communities, it has often evened out any natural variation among the woody species so that virtually identical canopies survive over different field and ground layers; this is a common occurrence with the *Primula-Glechoma* and *Anemone* sub-communities.

Of the various styles of treatment, it is coppicing that has left the most striking legacy in surviving stands of the *Fraxinus-Acer-Mercurialis* woodland, especially among the sub-communities of the south-east. Here, these kinds of woodland have been the major source of

coppice-wood and timber over more base-rich soils, probably for many centuries. Here, too, the coppicing tradition survived longer, though only a small proportion of stands are now actively worked (Peterken 1972, 1981, Rackham 1976, 1980) so the effects of treatment are usually seen these days filtered through long periods of neglect. As in other woodland communities, the impact of coppicing in a given stand is a complex function of the nature of the existing vegetation, local traditions of management and market forces worked out through systems of underwood and timber extraction on a variety of rotations with additional manipulations like cleaning, planting, layering and promotion. The diligent work of Peterken (1974, 1977, 1981; see also Peterken & Harding 1975) and Rackham (1967, 1971, 1975, 1976, 1980) has shown just how multifarious and complex are the local manifestations of such practices on the surviving vegetation, but how powerful a tool an understanding of treatment can be in giving a historical perspective on this community, especially when it is combined with the use of archaeological and documentary evidence. Many older stands of the *Fraxinus-Acer-Mercurialis* woodland constitute an irreplaceable record of past land use and its effects on the vegetation.

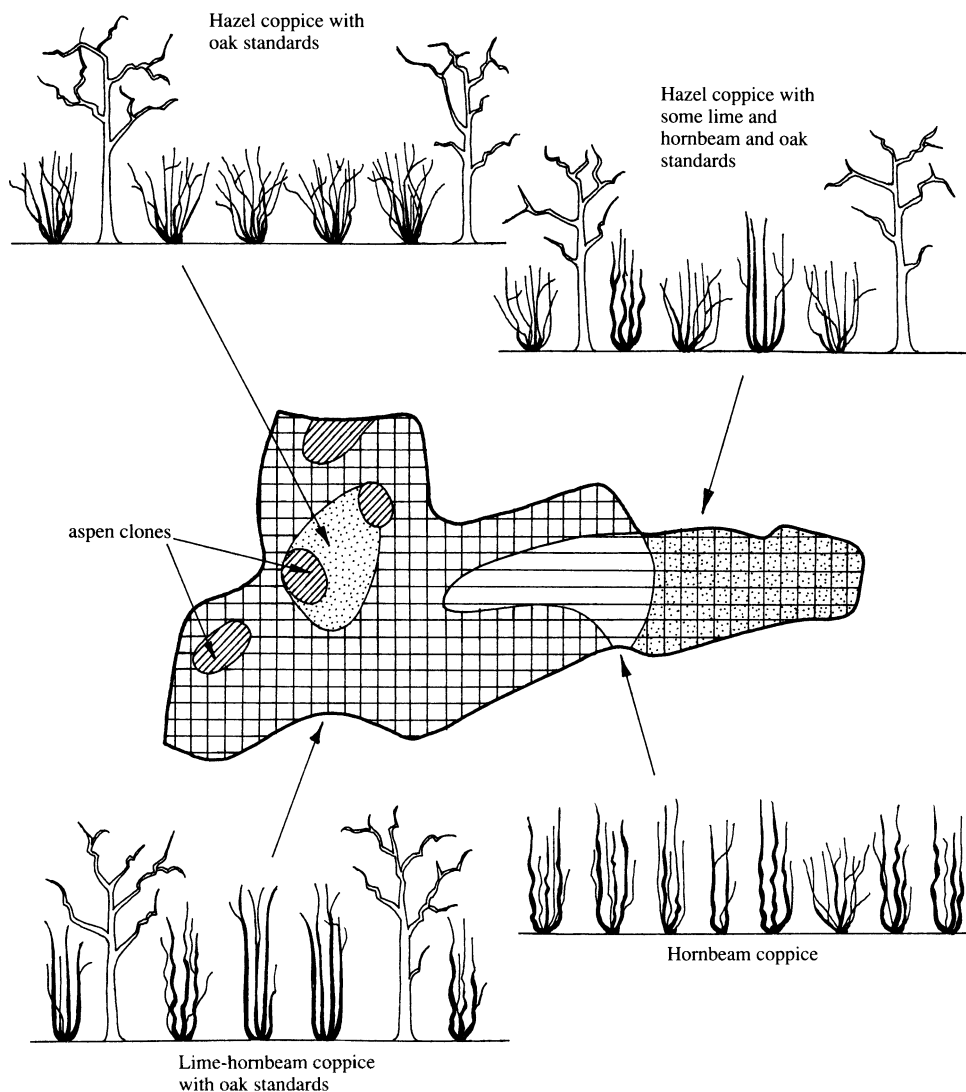
Although coppicing has been responsible for the development of great floristic and physiognomic contrasts between the woody cover of different stands of this community, within stands it is, in the long run, a conservative kind of treatment. At any one site, its major impact is to be seen in response to the periodic perturbations that accompany each cut: a sudden increase and steady decline in the exposure of the ground to the unshaded climatic environment during each rotation (Salisbury 1924, Rackham 1975, 1980, Ash & Barkham 1976, Peterken 1981) together with the trampling and disturbance associated with the cropping and removal of underwood and occasional timber. Although the shrubs and trees may show some slight differences in the proportions of the species represented as regrowth occurs, it is the cyclical changes in the field layer that are more obvious. As in all coppiced woodland communities, these patterns can be very varied, but some general features can be recognised. First, there is often a quick decline and slow recovery of *Mercurialis*, in response to the consolidation of the ground with trampling and consequent development of adverse anaerobic conditions, especially marked when the winter and spring of the cut are wet and the soil becomes badly poached (e.g. Pigott 1977). *Mercurialis* can decline, too, when the increased exposure of the soil to higher surface temperatures induces droughting in the summer after the cut (Martin 1968, Ash & Barkham 1976). Either way, any reduction in this, the commonest field-layer dominant here and a strong competitor to other herbs, opens up

more ground for subsequent prominence of the existing field-layer associates and the spread of any adventives.

Among the former, the characteristic post-coppice flowering can be seen in great splendour in this community with its various mixtures of *Hyacinthoides*, *Primula vulgaris*, *P. elatior*, *Anemone*, *Ranunculus ficaria*, *Viola* spp., *Glechoma* and *Lamium*. Individual plants can increase greatly in vigour producing larger rosettes or spreading carpets and seedlings may appear in profusion. Other characteristic species in the community may be able to make more obvious temporary capital on areas of open ground. *Rubus* often increases with the prolonged summer light and, on lighter soils, *Sanicula*

europaea, *Brachypodium sylvaticum* and *Geranium robertianum* may appear in profusion; these latter species are often abundant in coppiced versions of the north-western sub-communities. To the south-east, it is often the spread of *Deschampsia cespitosa* which marks the combination of increased light and trampling associated with coppicing and, on moister ground, there may be sufficient shift in the vegetation as to mark the development of the *Deschampsia* sub-community. Such changes may outlast the repetition of the coppice cycle, especially where bulkier perennials of this woodland (like *Deschampsia* and *Filipendula ulmaria*) become well-established in between-times. Often, though, the characteristic herbs of the particular sub-community being coppiced settle down once more into an assortment which may show quantitative changes but which preserves the general qualitative features of the original

Figure 19. Variation in canopy and underwood in *Fraxinus-Acer-Mercurialis* woodland at House Copse, Rusper in Sussex.



field layer. *Mercurialis* recovers and adds its own canopy to that of the regrowing shrubs and trees, the more shade-sensitive associates thin out and, if the next cut is long delayed, a ground carpet of ivy may spread and lead to the development of the *Hedera* sub-community.

Superimposed on these variations in the existing herbaceous flora of these woodlands, there is often a temporary abundance of adventive species in the more open conditions after the coppice cut. A clear sequence of life-forms is usually obvious, with annuals, then biennials, then perennials attaining prominence in turn, but the particular species represented vary greatly according to local edaphic and climatic conditions and the supply of propagules. Again, it is among the more frequently coppiced south-eastern sub-communities that this element has been best described (e.g. Salisbury 1916, 1918a, 1924, Rackham 1975, 1980, Ash & Barkham 1976, Peterken 1981). Some of these adventives, like the *Juncus* spp., appear to originate from buried seed (Rackham 1975, Peterken 1981, Brown & Oosterhuis 1981); many others colonise from permanently open rides and clearings, neighbouring hedgerows or field margins. Some favour moister soils, like the Junci, *Epilobium hirsutum* or *Cirsium palustre*; even semi-aquatic species can appear in patches of standing surface water. Others spread on drier ground and some species, like *Urtica dioica* and *Epilobium angustifolium*, mark out areas of local enrichment, like the sites of brushwood bonfires. Provided there is uninterrupted re-establishment of the canopy, few, if any, of these species last into the later stages of longer rotations, though clumped perennials can be quite persistent and may become a permanent feature where cutting is very frequent. Within whole woods, of course, where there is rotational cropping, medleys of these species represented in compartments at different stages of the cycle can become an enduring source of enrichment to the site.

However, even where extensive old coppiced stands of the *Fraxinus-Acer-Mercurialis* woodland survive, such temporal and spatial variety is usually a thing of the past. There are quite widespread signs of a last cut around the time of the Second World War or in the cold winter of 1946/7, a few woodlands are still cropped commercially or for research purposes and there is a renewed interest in the practice of woodmanship; in general, though, the picture now is one of long neglect.

Other stands give some clues as to how the community responds to different kinds of treatment. Some have obviously been clear-felled in the relatively recent past. This is a more drastic treatment than coppicing though, if there is opportunity for undisturbed regrowth and attention to the spread of woody adventives (notably birch), something like the original canopy composition (not structure) may re-establish itself over an essentially unchanged field layer. Monks' Wood in Cambridges-

hire, for example, was extensively cleared in the First World War but has substantially recovered (Hooper 1973, Ratcliffe 1977, Rackham 1980). Modest inter-planting, too, provided the characteristic hardwoods are used, need not destroy the floristic richness and diversity of existing stands, though it alters the age structure and genetic diversity of the canopy.

The survival of the essential features of the community is much more problematical where clear-felling is combined with replanting. Some existing stands of *Fraxinus-Acer-Mercurialis* woodland are certainly plantations, derived either by re-forestation or planting on soils which would naturally carry this community. In such woodland, the canopy is usually of *Quercus robur* and/or *Fraxinus* and it bears obvious signs of its origin in the ordered rows of even-aged trees of similar morphology. Younger stands of this kind are often of the *Hedera* sub-community with its rather dull field layer but, where there has been time for slow-spreading herbs to immigrate from the margins or spread from surviving patches, something like the richness of the field layers of the *Primula-Glechoma* or *Anemone* sub-communities (in the south-east) or the *Geranium* sub-community (to the north-west) can slowly be attained. We do not know how long such a process takes, though recorded rates of spread of *Mercurialis*, *Hyacinthoides*, *Anemone* and *Primula elatior* are of the order of only a few metres per century (Rackham 1975, Pigott 1984).

Where existing stands of the *Fraxinus-Acer-Mercurialis* woodland are felled and replanted, the crucial factors in maintaining field-layer diversity are probably an avoidance of damage to the existing herbs, the maintenance of or quick progression to a fairly light canopy and the continuance of a mull humus regime. Although ornamenting with occasional larch or pine is quite common, this community will stand only very dilatory coniferisation. Clear-felling, scrub-bashing, herbicide treatment and replanting with softwoods spell a quick and irreparable end. Sadly, this has been the fate of many stands.

Against this extensive loss must be placed an increase in the extent of *Fraxinus-Acer-Mercurialis* woodlands by relatively recent invasion of neglected farmland and disused chalk pits and quarries. As in plantation stands, the trees in such situations are often more or less even-aged (or grouped in pronounced age-classes where colonisation has been in waves), but the woody cover is often more varied and, even after many years, it may preserve elements of the early scrub (like large old hawthorns). Again, the *Hedera* sub-community is very characteristic of the dense woodland that often develops in such situations, though more open stands on heavier soils may show the *Deschampsia* sub-community or, on lighter soils, the *Geranium* sub-community. In the early stages, more slow-spreading herbs are usually limited to the margins. However, such younger *Fraxinus-Acer-*

Mercurialis woodlands are well worthy of study: sites such as the Hayley Wood Triangle (Rackham 1975) and Geescroft Wilderness at Rothamsted (Brenchley & Adam 1915, Tansley 1939, Pigott 1977) provide ready-made opportunities for monitoring the development of high-forest canopies and the establishment of the full richness of the field-layer flora here. In some areas, like the Yorkshire Dales, younger stands probably comprise the bulk of the woodland cover and, where old chalk pits and quarries lie close to urban areas, they offer vegetation robust enough for heavy amenity and educational use.

Zonation and succession

Most commonly, zonations between different kinds of *Fraxinus-Acer-Mercurialis* woodland and from this community to other woodland types are under the primary influence of soil variation. Treatment differences can accentuate or confuse such patterns and also produce direct effects of their own. Agricultural improvement has often truncated zonations and created a wide variety of artificially sharp transitions to herbaceous vegetation.

Over wooded tracts of suitably base-rich soils, the most widespread zonations between different sub-communities here are related to variations in soil moisture. On the heavy, impermeable clays which form the typical substrate for the community in much of the south and east, such variations are often directly dependent on the extent of surface-water gleying, itself a function of slope. Slope differences are often very slight over the clay superfcials characteristic of many stands of *Fraxinus-Acer-Mercurialis* woodland in East Anglia and the east Midlands, but quite sufficient to induce a shift from the *Primula-Glechoma* sub-community to the *Anemone* sub-community wherever there are flatter plateaus on which water becomes perched or shallow hollows into which it runs. As in the patterns described above from Hayley Wood, there is often a superimposed zonation of dominance within these sub-communities, as the major species succumb in turn to the increased waterlogging (Abeywickrama 1949, Martin 1968, Martin & Pigott 1975, Rackham 1975). Quite frequently, too, the zonation continues to the *Deschampsia* sub-community on even more waterlogged soils. This kind of woodland can be found in wet hollows within stands of the *Anemone* sub-community but it also often forms a transition around flushes and springs to some type of alder woodland. Flushes in this kind of situation often carry the *Alnus-Fraxinus-Lysimachia* woodland but, where there is pronounced ground-water gleying and some accumulation of fen peat below spring-heads, the *Alnus-Carex* woodland can terminate the sequence. Repeated patterns of this kind are very characteristic of the more calcareous strata of the Wealden and Atherfield Clays in

Surrey and Kent, where series of springs emerge at the base of the overlying Lower Greensand. Where streams with some alluvial deposition flow through *Fraxinus-Acer-Mercurialis* woodlands, the *Deschampsia* sub-community can give way to the more eutrophic *Alnus-Urtica* woodland on the flats.

Flush-surround and stream-side zonations of this type are also quite frequent to the north and west, where *Fraxinus-Acer-Mercurialis* woodlands can sometimes be found on more calcareous shales of the Carboniferous and Oolite sequences or over superfcials. Typically, though, the substrates of the community in this region are more free-draining limestones and the *Primula-Glechoma* sub-community is absent. More usually, here, there is a rather sharp transition from any stands of the *Anemone* or *Deschampsia* sub-communities to the *Geranium* sub-community on rendzina soils over steeply-sloping surrounding ground. On this more rugged topography of the north and west, however, aspect can confuse this basic pattern because, on cooler and wetter north-facing slopes, the *Anemone* and *Deschampsia* sub-communities can sometimes extend on to quite steep ground, forming patches within tracts of the *Geranium* sub-community (or the rarer *Teucrium* sub-community) over pockets of moister soil. Such patterns are well seen in some of the Derbyshire Dales and in the Mendips, where opposite faces of the valleys and gorges can present a sharp contrast in the extent of the different sub-communities. Finally, on the steeper slopes in this region, downwash is often important and a very typical pattern here is for the *Geranium* sub-community to give way to the *Allium* sub-community wherever there is an accumulation of deep, moist and free-draining colluvium.

Although all kinds of the *Fraxinus-Acer-Mercurialis* woodland are characteristic of more base-rich soils, individual woodland sites in which the community is represented often span geological transitions to less calcareous rocks or superfcials. Then, zonations to less calcicolous woodland can be found, usually to the *Quercus-Pteridium-Rubus* woodland, which is the counterpart of this community throughout its range on brown earth soils of moderate to low base-status. Where there are sharp bedrock differences, as where limestones or calcareous shales or clays are interbedded with arenaceous deposits, a common feature of the Carboniferous, Jurassic and Cretaceous sequences, the corresponding vegetational boundaries can be quite clear. However, it is important to remember that some of the leading species in the *Fraxinus-Acer-Mercurialis* woodland continue to be prominent in the *Quercus-Pteridium-Rubus* woodland and can therefore run across such junctions with no change in their abundance. Among the woody species, for example, *Quercus robur*, *Carpinus betulus*, *Tilia cordata*, *Corylus* and *Crataegus monogyna*

and, in the north-west, *Acer pseudoplatanus*, can all occur commonly in both communities; and, among the field-layer plants, *Hyacinthoides*, *Rubus fruticosus* agg. and, on moister soils, *Anemone* and *Ranunculus ficaria* can likewise be found in both. Usually, however, these transitions from one community to the other are marked by an obvious fading in the prominence of *Fraxinus*, *Acer campestre* (and, in the north-west, *Ulmus glabra*), *Mercurialis*, *Geum urbanum*, *Circaea lutetiana*, *Arum maculatum* and *Viola reichenbachiana* and by an increase, at least where the soils are not waterlogged, in *Pteridium*. In the south-east, the transitions commonly involve a switch from the *Primula-Glechoma*, *Anemone* or *Hedera* sub-communities of the *Fraxinus-Acer-Mercurialis* woodland to the Typical, *Anemone* or *Hedera* sub-communities of the *Quercus-Pteridium-Rubus* woodland respectively, depending on such factors as the amount of soil moisture and light. To the north-west, analogous transitions are usually from the *Geranium* sub-community of the *Fraxinus-Acer-Mercurialis* woodland to the *Holcus mollis* sub-community of the *Quercus-Pteridium-Rubus* woodland.

Over superficial deposits where there can be very diffuse or disorderly variations in calcium carbonate content and base-status, transitions may be much harder to discern or understand. Sometimes, sandier patches are marked by obvious islands of the *Quercus-Pteridium-Rubus* woodland within tracts of the *Fraxinus-Acer-Mercurialis* woodland, as at Gamlingay in Cambridgeshire (Adamson 1912) and many other East Anglian woods (Rackham 1980). In other cases, there may be no more than the haziest impression that one kind of woodland is trying to 'break through' the other with scattered *Mercurialis* and *Pteridium* intermixed over soils of intermediate quality.

There are situations, too, where variations in the base-status of the soils within woodlands are related, not to geological differences, but to flushing with calcium-rich waters. Where streams flow through stands of the *Quercus-Pteridium-Rubus* woodland, for example, the better drained of the alluvial flats often carry fragments of the *Fraxinus-Acer-Mercurialis* woodland, sometimes little more than small patches of *Mercurialis* inside every loop of the stream with an occasional scattered *Fraxinus*. These were a marked feature of the *Carpinus*-dominated woodlands described from Hertfordshire by Salisbury (1916, 1918a) but the phenomenon is very widespread.

Very commonly, and especially in the south-east, these kinds of soil-related zonations within stands of the community and to other types of woodland are overlain by treatment-derived patterns of variation. Sometimes, treatments have reinforced elements of natural zonations by selecting for trees or shrubs favouring particular soil conditions and accentuating their association with a certain field layer (as with *Carpinus* in the

Anemone sub-community). Usually, however, treatments have been applied with no reference to the disposition of soils of different moisture content or base-status, so that coppice compartments or patterns derived from timber extraction or replanting are superimposed independently over the natural transitions. This means that woods often show fairly clear soil-related variations within the field layer and equally clear but artificial and quite differently-disposed differences in the cover of underwood and timber.

As described above, different styles of treatment can affect the field-layer composition and physiognomy in the various sub-communities in different ways, but much of this variation can be seen as temporary (often cyclical) disruptions which do not, in the long term, modify the soil-related patterns. By and large, then, zonations persist while treatment-derived mosaics come and go within their components and across their boundaries. But there are some exceptions to this general rule. First, where trampling and increased light are combined, as they are when tracts are coppiced or clear-felled and allowed to regenerate (or planted with the usual hardwoods of the community), the parcel or compartment is often clearly marked out by a stretch of the *Deschampsia* sub-community which interrupts the natural zonation. Where short-cycle rotations are maintained on soils approaching the wet state of those normally occupied by this vegetation, the stand may persist. And, where trampling and high light levels are maintained permanently along paths and rides, there can be similar sudden switches to the *Deschampsia* sub-community, winding in narrow strips through the wood or marking out regular compartments in a grid.

Second, there can be abrupt transitions to the rather species-poor and gloomy vegetation of the *Hedera* sub-community at the boundaries of tracts where regrowth has been left unhindered for more than 20–50 years or so as in long-neglected coppice parcels or in planted compartments at the pole stage. Often, too, newer additions to older woods, originating from planting or by spontaneous invasion, show a sharp switch to the *Hedera* sub-community at the original boundary, or a little way beyond it if there has been time for invasion of the more slow-spreading herbs (as in the Hayley Triangle: Rackham 1975).

Third, at those few localities to the north and west where the *Teucrium* sub-community survives, the boundaries between it and the more widespread *Geranium* sub-community seem to mark a treatment-related distinction between older woodland that has escaped gross interference and younger woodland derived by a mixture of planting and natural regeneration on open ground over the past few centuries (Pigott 1960, 1969, Merton 1970). As noted earlier, such boundaries are often compounded with a topographic and edaphic

transition to less intractable ground where treatment has been easier to execute and colonisation speedier.

Finally, here, topographic alterations to the woodland environment associated with silvicultural treatments have sometimes modified soil conditions themselves and produced artificial edaphic zonations. Woodbanks, for example, are often better-drained than their surrounds and can provide, in the south-east, a belt of the *Primula-Glechoma* sub-community terminating (at the wood boundary) or interrupting (within woods) a stretch of the *Anemone* or *Deschampsia* sub-community. Where older stands of the *Fraxinus-Acer-Mercurialis* woodland have been cleared and replanted, ancient banks can provide narrow strips of richer field-layer vegetation with *Mercurialis*, *Hyacinthoides* and *Primula vulgaris*, often with interesting relic boundary specimens of *Tilia cordata* or *Carpinus*, surviving within tracts of the *Hedera* sub-community and providing nuclei from which the herbs can subsequently spread. Woodbanks are often too substantial to have been totally destroyed when compartments have been turned over to agricultural use in the past, but ploughing has often evened out natural surface undulations, so any new woodland developing on such sites shows much less variation in the ground topography and soil water content. Quite frequently, though, ploughing has created patterns of its own, notably ridge-and-furrow and, where woodland has been long established over abandoned farmland, the field-layer herbs can sort themselves over the drier ridges and wetter furrows such that stripes of the *Primula-Glechoma* and *Anemone* sub-communities alternate one with the other.

Almost always now, stands of the *Fraxinus-Acer-Mercurialis* woodland in the south-east, whether they comprise whole woods or the marginal parts of more varied sites, have artificially sharp boundaries. Where older woodlands survive intact, the boundaries may be very old, but, even in such cases, stands are invariably very closely hemmed in by intensive agricultural land. Many stands, of course, have been reduced in extent: here the boundaries are younger but generally equally abrupt. The usual picture now is of isolated fragments, often fringed by a narrow band of the shrubs and climbers of the community or by a belt of stabilised *Crataegus-Hedera* scrub with *Rubus-Holcus* underscrub below and a basal zone of the *Arrhenatheretum*, then a sharp transition to an arable crop (the usual pattern over much of East Anglia) or intensive pasture (as in wetter areas like parts of the Midlands). Where zonations are very tight, elements of all these vegetation types may be compressed into a confused mixture that can defy classification.

To the north and west, the pattern is a little different. The losses here have also been extensive though, in many places, they have been to commercial forestry, not to

agriculture. But, where stands do persist or have developed more recently within stretches of agricultural land, their boundaries are frequently not so sharply defined from the surrounding vegetation. Very often this is pasture of a less improved kind and under less intensive management than in the south-east. Where grazing (it is usually by sheep or mixtures of sheep and cattle) is lighter or more sporadic, stands can develop quite an extensive fringe of *Crataegus-Hedera* scrub or mixtures of young *Fraxinus*, *Betula* spp., *Acer pseudoplatanus* and *Ulmus glabra*. A typical picture in many parts of the Yorkshire and Derbyshire Dales is for patchworks of stands of the *Geranium* sub-community of different ages to be disposed over Carboniferous Limestone scree slopes with intervening stretches of open calcicolous grassland, either the more northerly types of the *Festuca-Avenula* grassland or *Sesleria*-dominated swards (e.g. Merton 1970).

Where complex surface topography hinders grazing, rather specialised mosaics with herbaceous vegetation can be found. Over Carboniferous Limestone pavements, for example, fragmentary miniaturised stands of the *Fraxinus-Acer-Mercurialis* woodland are frequently found in the deeper, shaded grikes, the canopies of the trees and shrubs browsed and wind-pruned at the level of the pavement surface and the herbs of the community disposed over grike-bottom soil and on small ledges and in crevices. Fern-dominated vegetation often occurs intermixed with the woodland and, where the clefts give way to shallower solution hollows in the more accessible and exposed clint surfaces, the mosaics include developing stands of *Sesleria-Galium* grassland.

The quite common existence of younger stands of the community to the north-west has meant that it has been possible there to monitor its seral development or make deductions about succession from spatial patterns (e.g. Scurfield 1959, Okali 1966, Merton 1970). In the south-east, evidence is more fragmentary: opportunities provided by some early studies, mostly on abandoned farmland, (e.g. Adamson 1912, 1921, Brenchley & Adam 1915, Salisbury 1918b, Tansley & Adamson 1925) have largely been lost and neglected open ground is now very rare. The most that can be done here is to collate existing results (e.g. Tansley 1939), add such continuing observations on these sites as there have been (Pigott 1977), set these in the context of the ecology of the mature stands of the community (e.g. Rackham 1980, Peterken 1981) and make some educated guesses. And, also, consider the conclusions in the light of more detailed work on successional development of related communities like the *Fagus-Mercurialis* and *Taxus* woodlands (e.g. Watt 1923, 1925, 1926, 1934a, b).

This latter is of some considerable importance because it seems clear that, within the natural British range of *Fagus*, the starting point for the development of

climax *Fraxinus-Acer-Mercurialis* woodland is not usually bare limestone or shallow rendzina soils with calcicolous grasslands. *Quercus robur* is, in any case, at some disadvantage against *Fraxinus* in the more excessively draining of these situations but, more importantly, neither of these trees can ultimately compete with *Fagus*, especially in areas like the Chilterns where the climate is drier. *Fraxinus-Acer-Mercurialis* woodland certainly can develop over deeper rendzinas carrying swards like those of the *Festuca-Avenula* grassland (or its less heavily grazed derivatives dominated by *Bromus erectus* or *Brachypodium pinnatum*) and perhaps even from more fragmentary soils over Chalk spoil in quarries and pits (e.g. Tansley 1922, Tansley & Adamson 1925, Hope-Simpson 1940b, 1941b, Wells 1969, 1973). But, even where rainfall is higher, as in the North and South Downs, it appears to be often a seral stage in the eventual development of beech forest (Watt 1925, 1934a, b). Much more locally, *Taxus* can overtake young *Fraxinus*-dominated stands of the community and come to dominate in yew forest (Watt 1926).

Much more likely precursors of the *Fraxinus-Acer-Mercurialis* woodland in the south-east are the more calcicolous forms of mesotrophic grasslands developed over deeper, moister base-rich soils derived from argillaceous bedrocks, like calcareous clays and shales, and calcareous superficials. Here, *Quercus robur* is very much at home and can maintain its important role amongst the mixtures of more calcicolous trees and shrubs that eventually come to dominate. However, because the vast majority of these soils have been under cultivation (or existing woodland) for very long periods of time, we do not know what the natural course of succession might be. Where the community has arisen secondarily on abandoned farmland, quite diverse lines of development have been seen to converge into young stands of the community. On old arable land with loamy brown earths, early mixtures of weeds have been seen to progress to some kind of *Arrhenatheretum*, then scrub, then woodland (as on Broadbalk Wilderness: Brenchley & Adam 1915, Tansley 1939); on heavier clay soils (as in Geescroft Wilderness: Brenchley & Adam 1915, Tansley 1939, Pigott 1977), *Holcus-Deschampsia* grassland has gained a dominant hold and a slower invasion of shrubs and trees has been observed; within abandoned pasture, the more vigorous of the existing grasses have grown rank as woody species have colonised to form 'tumble-down' scrub and then woodland (e.g. Adamson 1912).

From what we know of the ecology of existing stands of these precursors and of the *Fraxinus-Acer-Mercurialis* woodland itself, the limits defining the possible development of the community are almost certainly edaphic and, though they are quite wide, these seem to be fairly well defined. On better-drained soils, base-status is likely to be the controlling factor, so the most

obvious precursors will be the *Centaurea* and *Pastinaca* sub-communities of the *Arrhenatheretum*, the *Avenula pubescens* grassland or, where old pasture runs down, the more calcicolous forms of the *Centaureo-Cynosuretum* and the *Lolio-Cynosuretum*. Less base-rich soils with other sub-communities of these mesotrophic grasslands are likely to develop eventually into the *Quercus-Pteridium-Rubus* woodland. With increasing soil moisture, the *Holcus-Deschampsia* grassland, and perhaps also certain kinds of *Holco-Juncetum*, mark the probable limits of invasion: where waterlogging becomes more extreme, *Salix cinerea* and *Alnus* begin to assume importance as invaders and succession moves to wetter kinds of woodland.

The major trees of the south-eastern types of *Fraxinus-Acer-Mercurialis* woodland can invade these communities directly, provided there is no undue restriction on colonisation in general by the growth of very rank grasses (like *Deschampsia*): even *Quercus robur* which now regenerates badly within existing stands of woodland has no difficulty in appearing within old pasture. However, very frequently, there is a preliminary stage of scrub development before the woodland proper, especially where existing grassland is being colonised. In this scrub, *Crataegus monogyna* is almost invariably a major component and early stages in succession usually converge into the *Crataegus-Hedera* scrub, through which the trees of the community eventually emerge.

The appearance of a stand of the south-eastern kind of *Fraxinus-Acer-Mercurialis* woodland with all its diagnostic woody species (*Fraxinus*, *Q. robur*, *Acer campestre*, *Corylus* and *Crataegus*) does not necessarily take very long: the early studies were dealing with tracts which had already attained this degree of maturity after only 50 years or so. However, it probably takes very much longer for the other woody associates to appear in the kinds of mixtures that are widespread in the south-east with *Tilia cordata*, *Carpinus*, *Sorbus torminalis* and *Crataegus laevigata*. And, some of the most characteristic herbs of the community are very slow to colonise: young stands are often clearly of the *Hedera* or, over moister soils, the *Deschampsia* sub-community. Even after 90 years, the Geescroft woodland had acquired little more than a marginal fringe of *Mercurialis* (Pigott 1977) and Rackham (1975) estimated that it would take at least another 150 years for the Hayley Triangle (already 50 years old) to acquire something like the herbaceous flora of the older parts of the wood.

To the north-west, the *Fraxinus-Acer-Mercurialis* woodland can also probably develop from mesotrophic swards over more heavy-textured calcareous soils, though, with the higher rainfall here, there is an increased tendency for succession in moister situations to move towards its upland counterpart, the *Fraxinus-Sorbus-Mercurialis* woodland (as in higher-altitude dale

heads) or the *Alnus-Fraxinus-Lysimachia* woodland (where there is pronounced local flushing). More frequently in this region, which is largely outside the natural range of *Fagus*, the *Fraxinus-Acer-Mercurialis* woodland is the culmination of the invasion of bare limestones and shallow, free-draining rendzinas. Its usual precursors are therefore calcicolous grasslands, either the *Dicranum* sub-community of the *Festuca-Avenula* grassland (in the Mendips, Derbyshire and Durham), the *Sesleria-Scabiosa* grassland (in Durham) or the *Sesleria-Galium* grassland (in the Yorkshire Dales and around Morecambe Bay).

Usually, it is grazing which mediates the succession on more accessible slopes here. These often have a somewhat more intact and deeper soil cover, derived by long weathering or from colluvium, glacial drift or loess and, in such situations, *Crataegus* is again an important early invader, sometimes thickening up to form dense *Crataegus-Hedera* scrub before being overtaken by colonising trees (Scurfield 1959, Pigott 1969, Merton 1970). Over more broken slopes with scattered outcrops and fine talus intermixed with downwash, *Corylus* can colonise quickly and, on warmer slopes, it is often accompanied by *Cornus sanguinea*, *Rhamnus*, *Euonymus* and *Rosa* spp. (in the so-called 'retrogressive scrub' of Moss 1913: see Merton 1970). It is this kind of scrub which seems to persist as the understorey in the more open stands of the *Teucrium* sub-community (Pigott 1969).

Very often, however, and especially on coarser, and even mobile, talus, *Fraxinus* invades very open herbaceous vegetation in the early stages and, with little or no grazing, it can quickly overtake *Crataegus* or *Corylus* and establish the basis of a canopy of *Fraxinus-Acer-Mercurialis* woodland. Very commonly, too, it is accompanied or sometimes largely replaced by *Acer pseudoplatanus*: although this tree is often found associated with disturbed sites (like mine spoil or failed plantations: Merton 1970), its prominence in successions in the region is closely related to the wetness of climate and soil. How well it competes with *Fraxinus* is unclear: Okali (1966) suggested that it was less tolerant than *Fraxinus* of sub-optimal conditions, though availability of seed-parents may have been an important factor in the development of the local variation in the relative abundance of these trees that can be seen now (Merton 1970). Clearly, though, both species and, more locally, birch (usually *Betula pendula* on the drier soils), have behaved almost like woody weeds in the speedy and diverse successions that have given rise to many stands of the *Geranium* sub-community.

Although Merton (1970) reported the presence in scrub of certain herbaceous species usually associated with older stands of north-western *Fraxinus-Acer-Mercurialis* woodlands (*Convallaria majalis* for example), there is again little doubt that it takes some time for

developing stands to acquire the full range of canopy and field-layer species. *Ulmus glabra* is usually slower to colonise than *Fraxinus* and *Acer pseudoplatanus* and, towards the north-west, *A. campestre* is approaching the limit of its range. *Quercus*, too, has been notably unsuccessful in gaining a place in younger stands. The herbaceous component in the early stages also often has a strong representation of the grassland or open scree species with *Arrhenatherum elatius*, *Brachypodium sylvaticum* and *Geranium robertianum* prominent. The complexity found in the *Teucrium* sub-community may take many generations to develop and some of its typical species (like *Tilia cordata*) now regenerate very infrequently.

Distribution

The *Fraxinus-Acer-Mercurialis* woodland is widespread over more base-rich soils in lowland Britain, becoming progressively sparser in moving to the smaller exposures of calcareous rocks and superficials in the cooler and wetter climate of the north-western uplands where it is replaced by the *Fraxinus-Sorbus-Mercurialis* woodland. The sub-communities show a well-defined geographical division. To the south-east, the central type is the *Primula-Glechoma* sub-community which is especially well represented in the east Midlands, East Anglia and the Weald. On moving to the more oceanic south-west, there is an increasing tendency for this to be replaced by the *Hedera* sub-community, though this kind of woodland can also be found throughout the region in younger stands. The *Anemone* and *Deschampsia* sub-communities are also commoner on the generally heavy soils of the south-east but they can occur locally, where edaphic conditions permit, to the north-west. Usually, however, in this region, the community is represented by the *Geranium* sub-community which is especially characteristic of the Yorkshire and Derbyshire Dales, the Welsh Marches and scattered sites further south wherever there is locally high rainfall. The *Allium* sub-community follows essentially the same pattern. The *Teucrium* sub-community is much rarer, having been recorded only in parts of the Wye valley and Derbyshire with more fragmentary stands in the Yorkshire Dales.

Affinities

The *Fraxinus-Acer-Mercurialis* woodland brings together vegetation types which, in early descriptive accounts and in Klötzli's (1970) phytosociological treatment, were separated into 'damp oakwood' (e.g. Moss *et al.* 1910, Tansley 1911, 1939), the major woodland of heavier base-rich soils in the drier south-east and included within Klötzli's *Quercus-Fraxinetum*, and 'ash-wood' (e.g. Moss *et al.* 1910, Moss 1911, Tansley & Rankin 1911, Tansley 1939), its counterpart on the more free-draining calcareous soils in the wetter north-west,

constituting the core of Klötzli's *Dryopterido-Fraxinetum*. This floristic distinction is still visible here in the recognition of two suites of sub-communities but the general similarities between their constituents are a powerful argument for retaining them within a single community characteristic of our relatively warm and dry lowlands. In this scheme, then, the major distinction among British calcicolous mixed deciduous woodlands is between this community as a whole and the more obviously sub-montane *Fraxinus-Sorbus-Mercurialis* woodland, a vegetation type not prominent in early accounts and one subsumed by Klötzli (1970) in his *Dryopterido-Fraxinetum* as the *Blechnum* sub-community. In geographical terms, the dividing line has thus been pushed somewhat further to the north and west, corresponding here with a rough lowland/upland distinction along the 1000 mm isohyet and at the extreme limit of continental influence in our woodland flora.

The community includes only more calcicolous woody vegetation and does not subsume, under a general dominance of *Quercus robur* or mixtures of this species with *Carpinus* or *Tilia cordata*, field layers in which *Mercurialis* and its associates give way to *Rubus* and *Pteridium* with a vernal dominance of *Hyacinthoides*. Here, such vegetation is considered as a different kind of woodland altogether, the *Quercus-Pteridium-Rubus* woodland. In this respect, the treatment returns to the earliest British accounts (Moss *et al.* 1910, Tansley 1911) and does not follow the later tradition, enshrined in Tansley (1939), of recognising a single, compendious 'oakwood' with a very wide range of field-layer societies. There is a very clear floristic basis for this kind of separation between 'mercury' and 'bluebell' woodlands in Britain: the distinction is visible among some important woody species as well as herbs and it corresponds to a major edaphic contrast which is repeated in both lowlands and uplands. Klötzli (1970), at least in the lowlands, draws the edaphic bounds of his *Quercus-Fraxinetum* somewhat more broadly than here, taking in vegetation which is considered as part of the *Quercus-Pteridium-Rubus* woodland. Rackham (1980) and Peterken (1981) too, though they have a narrower view of 'oakwood' than Tansley (1939), take in both 'mercury' and 'bluebell' woodlands within their communities dominated by *Carpinus* and *Tilia*.

With such schemes as those of Rackham (1980) and Peterken (1981), there are other difficulties of comparison because of the weight they give to treatment-derived variations among the trees and shrubs. Here, such differences have not been used as a basis for making major sub-divisions within this community (or any other), but regarded as constituting a finer tier of variation within a framework related primarily to climate and soils. The sub-communities of the *Fraxinus-Acer-Mercurialis* woodland thus cross-cut distinctions

made in these other classifications on the basis of dominance in canopy or underwood by such species as *Fraxinus*, *Acer campestre*, *Corylus*, *Tilia cordata*, *Carpinus* and *Ulmus glabra*. But the two approaches are not irreconcilable: groups of stands within sub-communities could, for example, be recognised as variants with different woody dominants. The reverse procedure, using sub-community species to characterise variants within Rackham woodland communities or Peterken stand types, produces a much more cumbersome result and obscures what are here taken to be the major lines of natural variation. Correspondence between the sub-communities recognised here and the woodland types diagnosed in the other recent classification, by Bunce (1982), is unfortunately patchy. Roughly speaking, the *Fraxinus-Acer-Mercurialis* woodland is equivalent to the first quarter of Bunce's hierarchy but half of the sub-communities have no clear counterpart.

Although the kinds of woodland included in this community have clear equivalents on the Continent, it is not easy to set them in a European context because many of them lie beyond the natural limits of *Fagus* and *Carpinus*, the two trees which have tended to control the phytosociological perspective on north temperate forests on neutral to base-rich soils. In the south-east, where both these species can occur, relationships are clearer. The consensus would be that, here, the community is obviously part of the alliance Carpinion which comprises oak-hornbeam forests typical of those parts of Europe with only relatively low annual rainfall and moderately high summer temperatures (Neuhäusl 1977, Ellenberg 1978). In north-west Europe, in a zone which Noirfalise (1968) saw as encompassing northern France, Belgium, the southern Netherlands and south-eastern England, such oak-hornbeam woods occur widely on soils too wet for *Fagus* to thrive or where beech-dominance is prevented by treatment, exactly the behaviour described by Watt (1923, 1924, 1925, 1934a, b). Much of the *Fraxinus-Acer-Mercurialis* woodland could thus be taken in as a calcicolous portion of a community like the *Endymio-Carpinetum* (Noirfalise 1968, 1969; see also Noirfalise & Sougnez 1963) or, in the older terminology, *Querceto-Carpinetum* (e.g. Lemée 1937, Dethioux 1955) or *Quercetum atlanticum* (LeBrun *et al.* 1949). However, as argued above, there is a strong case, at least in Britain, for maintaining a sharp distinction between more and less calcicolous woodlands, so a better solution would be to regard the *Fraxinus-Acer-Mercurialis* woodland as a quite separate Carpinion community from such as these, which are more closely equivalent to the *Quercus-Pteridium-Rubus* woodland. One would then have a pair of British Carpinion communities, exactly parallel to those dominated by *Fagus*. The *Fraxinus-Acer-Mercurialis* woodland would thus be the British equivalent of Belgian and

Dutch communities like the *Fraxino-Ulmetum* (LeBrun *et al.* 1955) or the *Fraxineto-Ulmetum* (Westhoff & den Held 1969).

Whether the phytosociological affiliations of the north-western sub-communities are as clear is a moot point. Here, we are well beyond the natural limits of *Fagus* and *Carpinus*, though both trees grow well when planted within *Fraxinus-Acer-Mercurialis* woodland in this region. Oak is of low frequency but this is probably treatment-related and, though *Quercus petraea* is the commoner species, this tree is well represented in continental Carpinion woodlands on more free-draining substrates. Furthermore, *Acer pseudoplatanus* and *Ulmus glabra*, the best woody preferentials in the north-west, are common in mainstream Carpinion woods in wetter parts of north-west Europe: indeed, Noirfalise (1968) regarded the abundance of the former as a good distinguishing feature of his *Endymio-Carpinetum*. Dis-

tinct phytosociological equivalents of these north-western sub-communities have been described from damp ravines in Europe (e.g. the *Scolopendrieto-Fraxinetum* of Schwickerath 1944, Vanden Berghen 1953, Durin *et al.* 1968, and the *Acereto-Fraxinetum* of Le Brun *et al.* 1949) and their relationships with the Carpinion stressed. Birse (1984) also placed his Scottish *Quercus-Ulmetum* in the Carpinion. Klötzli (1970), on the other hand, saw the distinctive character of these woodlands, with their abundance of *Acer pseudoplatanus*, occasional presence of *Tilia platyphyllos* and abundance of evergreen ferns, as arguing for a place among the montane ravine woodlands of the Tilio-Acerion. Shimwell (1968*b*) recommended the erection of a new alliance within the Fagetalia, the Fraxino-Brachypodion, to contain the bulk of the north-western *Fraxinus-Acer-Mercurialis* woodlands he described from Derbyshire.

Floristic table W8

| | a | b | c | d | e | f | g | 8 |
|----------------------------|-----------|-----------|-----------|-----------|-----------|------------|-----------|------------|
| <i>Fraxinus excelsior</i> | IV (1–10) | IV (1–7) | IV (1–9) | V (2–10) | V (1–10) | III (2–8) | V (2–10) | IV (1–10) |
| <i>Acer campestre</i> | II (1–7) | I (2–5) | II (1–4) | II (1–8) | I (3–6) | II (4–6) | I (2–6) | II (1–8) |
| <i>Salix caprea</i> | I (2–7) | I (1–3) | I (2) | I (1–4) | I (1–5) | I (7) | I (1–3) | I (1–7) |
| <i>Fagus sylvatica</i> | I (1–3) | I (4–7) | | I (3–6) | I (1–8) | I (6–7) | I (2–4) | I (1–8) |
| <i>Taxus baccata</i> | I (4) | I (1–3) | | I (1–7) | I (3–4) | | I (4) | I (1–7) |
| <i>Larix</i> spp. | I (3–8) | I (4) | I (3) | I (2–4) | I (1–4) | | | I (1–8) |
| <i>Quercus</i> hybrids | I (2–9) | I (4–6) | I (6–7) | | I (2–6) | I (4–6) | | I (2–9) |
| <i>Ilex aquifolium</i> | I (1–2) | | | I (2–3) | I (1–4) | | I (2–8) | I (1–8) |
| <i>Salix cinerea</i> | I (3–5) | | | I (3) | I (1–3) | | I (1–3) | I (1–5) |
| <i>Sorbus aria</i> | | | | I (1–4) | I (1) | I (4) | | I (1–4) |
| <i>Betula pubescens</i> | I (3–6) | | I (1–4) | I (3–4) | I (1) | | | I (1–6) |
| <i>Malus sylvestris</i> | I (1–3) | | | | I (1) | | I (1–3) | I (1–3) |
| <i>Prunus avium</i> | I (1) | I (1–5) | | | | I (4) | | I (1–5) |
| <i>Sorbus aucuparia</i> | I (3) | | | | I (2–5) | | | I (2–5) |
| <i>Alnus glutinosa</i> | | I (1–4) | I (2–3) | | | | | I (1–4) |
| <i>Quercus robur</i> | IV (1–10) | III (1–8) | III (1–7) | IV (2–10) | I (1–7) | I (5–8) | I (1–5) | III (1–10) |
| <i>Carpinus betulus</i> | II (1–10) | II (5–7) | | I (2–8) | I (1) | | | I (1–10) |
| <i>Betula pendula</i> | II (1–10) | I (1–5) | I (3) | I (1–4) | I (1–6) | | | I (1–10) |
| <i>Tilia cordata</i> | II (1–10) | I (1) | | I (1–2) | I (3) | | I (4–6) | I (1–10) |
| <i>Ulmus carpiniifolia</i> | II (3–10) | I (8–9) | | I (4) | | | | I (3–10) |
| <i>Populus tremula</i> | I (3–8) | I (5) | I (3–7) | I (4) | | | | I (3–8) |
| <i>Ulmus procera</i> | I (2–6) | | | I (7) | | | | I (2–7) |
| <i>Ulmus</i> spp. | I (4–10) | | I (5) | | | | | I (4–10) |
| <i>Castanea sativa</i> | I (3–4) | I (6) | | | | | | I (3–6) |
| <i>Sorbus torminalis</i> | I (1–3) | | | | | | | I (1–3) |
| <i>Acer pseudoplatanus</i> | I (2–5) | II (1–10) | II (1–6) | I (4–8) | IV (2–10) | III (4–10) | III (1–8) | II (1–10) |
| <i>Ulmus glabra</i> | | II (4–7) | II (1–5) | I (4) | IV (1–10) | III (5–7) | III (1–7) | II (1–10) |
| <i>Quercus petraea</i> | I (1–8) | I (2–9) | I (1–5) | I (2–9) | II (2–8) | I (4) | I (1–6) | I (1–9) |
| <i>Tilia platyphyllos</i> | | | | | | | II (4–8) | I (4–8) |
| <i>Corylus avellana</i> | V (2–10) | IV (1–9) | V (4–9) | V (2–10) | III (1–9) | IV (2–9) | V (2–8) | V (1–10) |
| <i>Crataegus monogyna</i> | III (1–7) | IV (1–5) | III (4–7) | V (2–7) | IV (1–7) | III (1–4) | IV (1–6) | III (1–7) |

Floristic table W8 (cont.)

| | a | b | c |
|------------------------------------|-----------|------------|-----------|
| <i>Acer campestre</i> | II (1–6) | I (3) | III (2–5) |
| <i>Fraxinus excelsior</i> sapling | II (1–8) | II (1–3) | IV (2–6) |
| <i>Sambucus nigra</i> | I (1–5) | II (1–7) | |
| <i>Cornus sanguinea</i> | II (2–8) | I (3) | II (2–4) |
| <i>Prunus spinosa</i> | I (1–8) | I (1–4) | II (2–5) |
| <i>Euonymus europaeus</i> | I (2–3) | | I (2) |
| <i>Fagus sylvatica</i> sapling | I (1–10) | I (1–4) | |
| <i>Malus sylvestris</i> | I (1–2) | | I (1–2) |
| <i>Taxus baccata</i> sapling | | | |
| <i>Crataegus laevigata</i> | I (3–6) | I (3) | I (3–4) |
| <i>Quercus robur</i> sapling | I (2–3) | | I (2–3) |
| <i>Viburnum lantana</i> | I (4) | I (3) | |
| <i>Crataegus hybrids</i> | I (3–5) | I (2) | |
| <i>Carpinus betulus</i> | I (2–10) | I (3–10) | |
| <i>Betula pendula</i> sapling | I (2–6) | I (2) | |
| <i>Castanea sativa</i> sapling | I (3) | I (3–4) | |
| <i>Ulmus carpinifolia</i> suckers | I (3–7) | | |
| <i>Ulmus</i> spp. suckers | I (3–9) | | |
| <i>Acer pseudoplatanus</i> sapling | I (1–4) | II (1–5) | II (1–5) |
| <i>Ilex aquifolium</i> | I (3–4) | I (6) | I (4) |
| <i>Ulmus glabra</i> sapling | | II (1–5) | II (1–4) |
| <i>Viburnum opulus</i> | I (2–4) | I (1–3) | I (2–4) |
| <i>Sorbus aucuparia</i> | | I (1–2) | |
| <i>Rhamnus catharticus</i> | | | |
| <i>Prunus padus</i> | | I (1) | |
| <i>Mercurialis perennis</i> | IV (1–10) | III (1–10) | II (2–6) |
| <i>Eurhynchium praelongum</i> | IV (1–9) | IV (1–7) | III (3–6) |
| <i>Rubus fruticosus</i> agg. | IV (1–10) | III (2–8) | V (3–8) |
| <i>Poa trivialis</i> | III (1–9) | II (1–8) | II (3–5) |
| <i>Glechoma hederacea</i> | III (2–8) | II (1–4) | I (3–4) |

| d | e | f | g | 8 |
|-----------|-----------|-----------|-----------|-----------|
| III (1-7) | III (1-6) | II (2-4) | III (1-5) | III (1-7) |
| II (2-6) | III (1-5) | I (3) | III (1-5) | III (1-8) |
| II (1-7) | III (1-6) | II (1-5) | II (1-6) | II (1-7) |
| I (2-4) | I (2-3) | I (3) | III (1-6) | II (1-8) |
| I (2-5) | I (1-6) | I (1) | I (2-3) | I (1-8) |
| I (1-5) | I (1-5) | I (3) | I (1-3) | I (1-5) |
| I (3) | I (1-4) | I (1) | | I (1-10) |
| I (1-3) | I (1) | | | I (1-3) |
| I (1) | I (1) | | I (1-4) | I (1-4) |
| I (5) | | | | I (3-6) |
| I (3) | | | | I (2-3) |
| I (1-8) | I (1-4) | | | I (1-8) |
| I (3) | | | | I (2-5) |
| I (3) | | | | I (2-10) |
| | | | | I (2-6) |
| | | | | I (3-4) |
| | | | | I (3-7) |
| | | | | I (3-9) |
| I (2-6) | III (1-5) | II (2-4) | I (1-2) | II (1-6) |
| I (1-3) | II (1-4) | II (1-4) | II (1-8) | II (1-8) |
| I (3-4) | II (1-6) | II (1-4) | | I (1-6) |
| I (2-5) | I (1-2) | | III (1-4) | I (1-5) |
| | I (1-3) | | III (1-6) | I (1-6) |
| | | | III (1-6) | I (1-6) |
| | | | II (1-5) | I (1-5) |
| V (2-10) | IV (1-10) | V (4-9) | V (4-10) | V (1-10) |
| II (1-8) | IV (1-8) | V (4-7) | V (1-6) | IV (1-9) |
| IV (2-9) | III (1-9) | III (1-6) | II (2-4) | IV (1-10) |
| I (1-7) | I (1-5) | | I (1-3) | II (1-9) |
| I (2-6) | I (1-5) | | I (1-4) | II (1-8) |

| | | | | | | | | |
|--|-----------|----------|----------|-----------|------------|-----------|-----------|------------|
| <i>Primula vulgaris</i> | III (1–4) | II (3–5) | I (3) | I (2–6) | I (1–4) | I (1) | I (1–2) | II (1–6) |
| <i>Viola riviniana/reichenbachiana</i> | II (2–6) | II (2–5) | II (4–6) | II (1–7) | I (1–5) | | II (1–4) | II (1–7) |
| <i>Ajuga reptans</i> | II (1–6) | II (2–3) | II (2–3) | I (2–5) | I (3) | | | I (1–6) |
| <i>Primula elatior</i> | I (2–7) | I (4–5) | I (3) | I (4) | | | | I (2–7) |
| <i>Primula vulgaris</i> × <i>elatior</i> | I (5) | I (5) | | | | | | I (5) |
| <i>Anemone nemorosa</i> | I (2–6) | V (1–9) | I (4) | I (1–5) | I (1–8) | II (1–4) | I (1–3) | I (1–8) |
| <i>Ranunculus ficaria</i> | I (1–5) | IV (1–7) | | I (2–5) | I (1–6) | II (2–4) | | I (1–6) |
| <i>Lamium galeobdolon</i> | I (1–6) | II (1–4) | I (1–6) | I (1–6) | I (1–6) | I (2–4) | I (1–5) | I (1–6) |
| <i>Rumex sanguineus</i> | I (1–4) | II (2–3) | | I (1–3) | I (1–4) | | | I (1–4) |
| <i>Deschampsia cespitosa</i> | I (1–4) | I (1–4) | V (4–9) | I (1–4) | I (2–7) | I (4) | II (2–7) | I (1–9) |
| <i>Filipendula ulmaria</i> | I (1–4) | I (5) | II (3–7) | I (4) | I (2–5) | I (3) | II (1–3) | I (1–7) |
| <i>Potentilla sterilis</i> | I (1–4) | I (1–2) | II (3–4) | I (3) | I (1–3) | | I (1–4) | I (1–4) |
| <i>Lysimachia nemorum</i> | I (1–3) | I (2–3) | II (1–2) | | | | | I (1–3) |
| <i>Juncus effusus</i> | | | II (1–5) | | | | | I (1–5) |
| <i>Hedera helix</i> | II (2–9) | II (1–7) | II (4–6) | IV (2–10) | III (1–10) | III (2–8) | II (2–5) | III (1–10) |
| <i>Urtica dioica</i> | II (1–8) | II (1–7) | | I (1–5) | III (1–9) | III (1–4) | III (1–6) | II (1–9) |
| <i>Galium aparine</i> | I (1–7) | II (1–7) | I (4) | I (2–5) | III (1–6) | III (2–5) | II (1–4) | II (1–7) |
| <i>Geranium robertianum</i> | I (1–4) | I (3) | | I (1–7) | III (1–7) | II (2–3) | II (1–3) | II (1–7) |
| <i>Eurhynchium striatum</i> | I (1–6) | I (1–6) | | I (3–7) | III (1–7) | II (3–5) | II (2–5) | II (1–7) |
| <i>Thamnobryum alopecurum</i> | I (1–8) | I (3–4) | I (5–6) | I (1–6) | II (1–7) | II (4–6) | I (1–4) | I (1–8) |
| <i>Phyllitis scolopendrium</i> | | | | I (1–8) | II (1–5) | II (1–4) | I (3) | I (1–8) |
| <i>Ctenidium molluscum</i> | | | | | I (1–7) | I (3) | I (1–5) | I (1–7) |
| <i>Allium ursinum</i> | I (3–4) | I (2–5) | I (4) | I (3) | II (1–4) | V (6–10) | I (1–2) | I (1–10) |
| <i>Brachypodium sylvaticum</i> | II (2–8) | I (4–5) | II (3–4) | III (2–7) | II (1–8) | I (1) | IV (1–6) | II (1–8) |
| <i>Teucrium scorodonia</i> | | I (3) | | I (4) | I (2–4) | | IV (1–4) | I (1–4) |
| <i>Melica uniflora</i> | I (2–6) | I (2–4) | I (5) | I (2–5) | I (2–7) | | III (2–4) | I (2–6) |
| <i>Arrhenatherum elatius</i> | | | | | I (1–5) | I (3) | III (1–4) | I (1–5) |
| <i>Campanula latifolia</i> | | I (2) | | | I (1–2) | | II (1–4) | I (1–4) |
| <i>Polystichum aculeatum</i> | I (2–4) | | | | I (1–6) | | II (1–4) | I (1–6) |
| <i>Myosotis sylvatica</i> | | | | | I (1–3) | | II (1–3) | I (1–3) |
| <i>Plagiothecium denticulatum</i> | | | | | I (5) | | II (1–5) | I (1–5) |
| <i>Convallaria majalis</i> | | | | | I (1–3) | | II (1–7) | I (1–7) |

Floristic table W8 (cont.)

| | a | b | c | d | e | f | g | 8 |
|------------------------------------|-----------|-----------|-----------|------------|-----------|----------|-----------|------------|
| <i>Melica nutans</i> | | | | | | | II (1–7) | I (1–7) |
| <i>Rubus saxatilis</i> | | | | | | | II (2–3) | I (2–3) |
| <i>Rosa villosa</i> | | | | | | | I (1–2) | I (1–2) |
| <i>Hyacinthoides non-scripta</i> | III (2–9) | IV (1–9) | III (2–4) | III (3–10) | II (1–9) | II (2–6) | II (1–3) | III (1–10) |
| <i>Brachythecium rutabulum</i> | III (1–8) | II (1–8) | III (3–6) | II (2–5) | III (1–9) | V (2–8) | I (2) | III (1–9) |
| <i>Plagiomnium undulatum</i> | III (2–7) | III (1–6) | II (2–4) | I (1–4) | III (1–5) | II (2–4) | III (1–5) | III (1–7) |
| <i>Circaea lutetiana</i> | III (2–5) | I (1–5) | III (2–4) | II (2–4) | II (1–7) | II (3–6) | III (1–6) | III (1–7) |
| <i>Geum urbanum</i> | III (1–6) | I (1–4) | II (3–5) | II (1–4) | II (1–7) | I (2) | III (2–5) | II (1–7) |
| <i>Fissidens taxifolius</i> | II (1–4) | I (1–3) | III (2–4) | I (2–5) | II (1–4) | II (1–3) | | II (1–5) |
| <i>Arum maculatum</i> | II (1–6) | II (1–4) | I (3) | II (1–7) | II (1–5) | II (2–4) | I (1–3) | II (1–7) |
| <i>Atrichum undulatum</i> | II (2–6) | I (1–4) | II (3–4) | I (4) | I (1–4) | I (1–3) | II (2–4) | II (1–6) |
| <i>Mnium hornum</i> | II (1–7) | II (1–6) | I (2–3) | I (4) | I (1–5) | | II (1–5) | II (1–7) |
| <i>Fraxinus excelsior</i> seedling | II (1–3) | I (1–3) | II (2–4) | II (1–4) | II (1–4) | I (1–2) | I (2) | II (1–4) |
| <i>Dryopteris filix-mas</i> | II (1–4) | II (1–4) | | I (1–4) | II (1–5) | I (5) | II (1–4) | II (1–5) |
| <i>Rosa canina</i> agg. | II (2–6) | I (1–4) | II (3–6) | II (1–6) | I (1–4) | | I (1–4) | II (1–6) |
| <i>Lonicera periclymenum</i> | II (1–6) | II (1–6) | II (2–6) | I (1–5) | I (1–4) | I (2) | | II (1–6) |
| <i>Thuidium tamariscinum</i> | II (2–7) | I (1) | II (3–7) | I (2–4) | I (1–7) | I (3) | I (2–3) | I (1–7) |
| <i>Carex sylvatica</i> | II (1–4) | I (4) | I (1–3) | I (2–5) | I (1–3) | | II (1–4) | I (1–5) |
| <i>Tamus communis</i> | I (2–4) | I (3) | II (2–4) | II (1–4) | I (1–3) | | II (1–4) | I (1–4) |
| <i>Eurhynchium swartzii</i> | I (2–3) | II (1–5) | | I (4–7) | II (1–5) | II (1–4) | | I (1–7) |
| <i>Silene dioica</i> | I (1–5) | I (1–4) | I (3) | I (1–5) | II (1–7) | I (1) | I (1–2) | I (1–7) |
| <i>Lophocolea bidentata</i> s.l. | I (1–4) | I (1) | I (4) | | I (1–4) | | II (1–4) | I (1–4) |
| <i>Ligustrum vulgare</i> | I (1–8) | I (2) | I (1–3) | I (1–4) | I (2–4) | | I (1–6) | I (1–8) |
| <i>Sanicula europaea</i> | I (1–3) | I (3–4) | | I (2–5) | I (1–4) | | I (1–4) | I (1–5) |
| <i>Angelica sylvestris</i> | I (1–3) | I (2) | I (1–3) | I (4) | I (1) | I (1) | I (1–2) | I (1–4) |
| <i>Stachys sylvatica</i> | I (2–5) | I (1–3) | I (3) | I (1–4) | I (1–5) | I (2) | I (1–2) | I (1–5) |
| <i>Dryopteris borrieri</i> | I (4) | I (1) | I (1) | I (1–4) | I (1–4) | I (1) | I (2–3) | I (1–4) |
| <i>Poa nemoralis</i> | I (1–6) | I (3) | I (3–4) | I (2–4) | I (1–4) | | I (1–4) | I (1–6) |
| <i>Festuca gigantea</i> | I (1–4) | I (1–3) | I (2–4) | I (1–6) | I (1–4) | | I (1) | I (1–6) |
| <i>Bromus ramosus</i> | I (1–3) | I (4) | I (4) | I (1–4) | I (1–4) | | I (1–3) | I (1–4) |
| <i>Veronica chamaedrys</i> | I (1–3) | I (2–3) | I (3) | I (1–3) | I (1–3) | | I (3) | I (1–3) |
| <i>Euphorbia amygdaloides</i> | I (1–4) | I (3) | I (3) | I (1–5) | I (1–2) | I (1) | | I (1–5) |

| | | | |
|--------------------------------------|---------|---------|---------|
| <i>Amblystegium serpens</i> | I (1–3) | I (1) | I (3) |
| <i>Hypnum cupressiforme</i> | I (1–4) | | I (3) |
| <i>Taraxacum officinale</i> agg. | I (1) | I (1) | I (1–4) |
| <i>Pteridium aquilinum</i> | I (1–5) | I (2–5) | I (3) |
| <i>Ranunculus repens</i> | I (1–3) | I (1) | I (2–3) |
| <i>Holcus lanatus</i> | I (3–4) | I (2–3) | I (3–4) |
| <i>Oxalis acetosella</i> | I (1–7) | I (2–3) | I (2) |
| <i>Athyrium filix-femina</i> | I (4–5) | I (2) | |
| <i>Dactylis glomerata</i> | I (2–3) | I (1–4) | |
| <i>Galium odoratum</i> | I (2–4) | I (1–6) | |
| <i>Adoxa moschatellina</i> | I (3) | I (7) | |
| <i>Fragaria vesca</i> | I (2–4) | | I (3) |
| <i>Conopodium majus</i> | I (1–4) | I (1–6) | |
| <i>Acer pseudoplatanus</i> seedling | I (1–2) | I (1–4) | |
| <i>Dryopteris dilatata</i> | I (1–4) | I (1–5) | |
| <i>Heracleum sphondylium</i> | I (2–3) | I (1–3) | |
| <i>Stellaria holostea</i> | I (2–3) | I (3–4) | |
| <i>Isoetes myosuroides</i> | I (2) | I (1–3) | |
| <i>Eurhynchium confertum</i> | I (2–6) | I (2) | |
| <i>Moehringia trinervia</i> | I (1–4) | I (1) | I (4) |
| <i>Plagiochila asplenoides</i> major | I (2) | I (1) | I (4) |
| <i>Clematis vitalba</i> | I (1–4) | I (3) | |
| <i>Listera ovata</i> | I (1–3) | I (3–4) | |
| <i>Anthriscus sylvestris</i> | I (2–3) | I (2) | |
| <i>Polystichum setiferum</i> | I (4) | I (1–4) | |
| <i>Crataegus monogyna</i> seedling | I (1–3) | | I (1–2) |
| <i>Luzula sylvatica</i> | I (1–4) | I (1–7) | I (2–4) |
| <i>Prunella vulgaris</i> | I (2–5) | | I (3) |
| <i>Vicia sepium</i> | I (2–3) | | I (3) |
| <i>Arctium minus</i> agg. | I (2–3) | | I (3) |
| <i>Rubus idaeus</i> | I (3–6) | I (1) | |
| <i>Cardamine flexuosa</i> | I (2–5) | I (2) | |
| <i>Holcus mollis</i> | I (3–6) | I (1–7) | |
| <i>Campanula trachelium</i> | I (1) | I (1) | |
| <i>Milium effusum</i> | I (3–6) | I (1–5) | |
| <i>Veronica montana</i> | I (3–4) | I (1–6) | |

| | | | | |
|---------|---------|---------|---------|---------|
| I (2) | I (1-5) | I (3) | | I (1-5) |
| I (1) | I (1-3) | I (1-3) | I (1-4) | I (1-4) |
| I (1-4) | I (1-3) | | | I (1-4) |
| I (3-5) | I (1-4) | | | I (1-5) |
| I (3) | I (1) | | | I (1-3) |
| I (2) | | | I (1-6) | I (1-6) |
| | I (1-3) | I (2) | | I (1-7) |
| I (5) | I (1-5) | | I (2-3) | I (1-5) |
| I (1) | I (1-5) | | I (1-3) | I (1-5) |
| I (6-7) | I (1-6) | | I (2-4) | I (1-7) |
| I (4-5) | I (1-5) | | I (3) | I (1-5) |
| I (2-4) | I (1-2) | | I (2-4) | I (1-4) |
| I (1-5) | I (1-3) | I (1-3) | | I (1-5) |
| I (1-4) | I (1-3) | I (2) | | I (1-4) |
| I (1-3) | I (1-4) | I (1-3) | | I (1-4) |
| I (1-3) | I (1-6) | I (1-2) | | I (1-6) |
| I (3-4) | I (1-5) | I (3) | | I (1-5) |
| | I (1-4) | I (1-4) | I (1-3) | I (1-4) |
| | I (1-4) | I (2-4) | I (1-2) | I (1-6) |
| | I (1-4) | | I (2-4) | I (1-4) |
| | I (1-4) | | I (1-4) | I (1-4) |
| I (1-8) | I (1-4) | | | I (1-8) |
| I (2) | I (2-5) | | | I (1-5) |
| I (3-4) | I (3-4) | | | I (2-4) |
| I (3) | I (1-8) | | | I (1-8) |
| I (1-4) | I (1-3) | | | I (1-4) |
| | I (5) | | | I (1-4) |
| | I (1-2) | | I (1-3) | I (1-5) |
| | I (1-2) | | I (1) | I (1-3) |
| | I (1-2) | | I (1-3) | I (1-3) |
| | I (1-4) | | I (1-2) | I (1-6) |
| | I (1) | | I (1-2) | I (1-5) |
| | I (1-4) | | I (2-6) | I (1-6) |
| | I (1-2) | | I (1-3) | I (1-3) |
| | I (1-5) | | I (1-3) | I (1-6) |
| I (1-4) | | I (3) | | I (1-6) |

Floristic table W8 (cont.)

| | a | b | c |
|--------------------------------------|---------|---------|---------|
| <i>Plagiothecium sylvaticum</i> | I (1–4) | I (1) | |
| <i>Plagiomnium affine</i> | I (2–3) | | |
| <i>Ribes uva-crispa</i> | | | |
| <i>Cirriphyllum piliferum</i> | | I (1) | |
| <i>Rhytidiadelphus loreus</i> | | I (2) | |
| <i>Ranunculus auricomus</i> | I (3) | | |
| <i>Alliaria petiolata</i> | I (1–3) | | |
| <i>Iris foetidissima</i> | I (1–3) | | |
| <i>Orchis mascula</i> | I (2–3) | I (1) | |
| <i>Polygonatum multiflorum</i> | I (1–3) | I (4) | |
| <i>Digitalis purpurea</i> | I (2–4) | | I (4) |
| <i>Fagus sylvatica</i> seedling | | I (1–3) | |
| <i>Chrysosplenium oppositifolium</i> | | I (1) | |
| <i>Acer campestre</i> seedling | | | I (3) |
| <i>Daphne laureola</i> | | | |
| <i>Epilobium angustifolium</i> | I (1–4) | | |
| <i>Plagiomnium rostratum</i> | I (3) | | |
| <i>Climacium dendroides</i> | I (4–5) | | |
| <i>Epilobium montanum</i> | | I (1) | |
| <i>Lapsana communis</i> | | I (1) | |
| <i>Carex remota</i> | I (1–4) | | I (4) |
| <i>Platanthera chlorantha</i> | I (1) | | I (1) |
| <i>Rumex crispus</i> | I (3–4) | | |
| <i>Plagiochila asplenoides</i> | I (3–4) | | |
| <i>Lophocolea heterophylla</i> | I (1–4) | | |
| <i>Dicranella heteromalla</i> | I (2–3) | | |
| <i>Hypericum hirsutum</i> | | | I (3) |
| <i>Rubus caesius</i> | | | I (1–3) |
| <i>Ilex aquifolium</i> seedling | | | |
| <i>Corylus avellana</i> seedling | | | |
| <i>Polypodium vulgare</i> | | | |
| <i>Viola odorata</i> | | | |
| <i>Ribes rubrum</i> | | | |

| d | e | f | g | h |
|---------|---------|---------|---------|---------|
| | I (1-3) | I (1) | | I (1-4) |
| | I (2) | I (2) | I (2-3) | I (2-3) |
| I (1-2) | I (1-3) | I (1) | I (1) | I (1-3) |
| | I (1-6) | I (1) | I (2) | I (1-6) |
| | I (1-4) | I (1-5) | I (1-2) | I (1-5) |
| I (2-3) | | I (3) | | I (2-3) |
| I (1-2) | | I (1) | | I (1-3) |
| I (4-6) | I (1-4) | | | I (1-6) |
| | I (2-3) | | | I (1-3) |
| | I (1-4) | | | I (1-4) |
| | I (1-5) | | | I (1-5) |
| I (1) | I (1-3) | | | I (1-3) |
| I (4) | I (1-5) | | | I (1-5) |
| I (1-4) | I (1-2) | | | I (1-4) |
| I (2-4) | I (1-2) | | I (1) | I (1-4) |
| | I (2-7) | | I (3) | I (1-7) |
| | I (1-2) | | I (1-2) | I (1-3) |
| | I (3) | | I (1-4) | I (1-5) |
| | I (1-3) | | I (1-2) | I (1-3) |
| | I (1-3) | | I (1-2) | I (1-3) |
| | | | | I (1-4) |
| | | | | I (1) |
| I (3) | | | | I (3-4) |
| | I (1-3) | | | I (1-4) |
| | I (1) | | | I (1-4) |
| | | | I (1-2) | I (1-3) |
| | | | I (1-2) | I (1-3) |
| | | | I (1-3) | I (1-3) |
| I (1-3) | I (1-2) | | | I (1-3) |
| I (1) | I (1) | | | I (1) |
| I (1-2) | I (1) | | | I (1-2) |
| I (1-4) | I (1-4) | | | I (1-4) |
| | I (1-3) | I (2) | | I (1-3) |

| | | | | | | | | |
|-----------------------------------|-------------|-------------|-------------|-------------|-------------|--------------|--------------|-------------|
| <i>Rhizomnium punctatum</i> | | | | | I (1–3) | | I (1–2) | I (1–3) |
| <i>Ranunculus acris</i> | | | | | I (1–3) | | I (1) | I (1–3) |
| <i>Rhytidiadelphus triquetrus</i> | | | | | I (1–4) | | I (1–4) | I (1–4) |
| <i>Fissidens bryoides</i> | | | | | I (1) | | I (1) | I (1) |
| <i>Mycelis muralis</i> | | | | | I (1–2) | | I (1–2) | I (1–2) |
| <i>Pellia epiphylla</i> | | | | | I (1–4) | | I (2–3) | I (1–4) |
| <i>Daphne mezereum</i> | | | | | I (1) | | I (1) | I (1) |
| <i>Narcissus pseudonarcissus</i> | | | | | | I (4) | I (3) | I (3–4) |
| Number of samples | 128 | 79 | 12 | 67 | 81 | 27 | 35 | 429 |
| Number of species/sample | 24 (5–48) | 26 (12–35) | 24 (17–43) | 20 (7–53) | 27 (6–53) | 27 (16–37) | 29 (19–64) | 25 (5–64) |
| Tree height (m) | 15 (8–26) | 19 (9–35) | 16 (12–20) | 19 (8–32) | 18 (8–32) | 19 (15–20) | 13 (8–15) | 17 (8–35) |
| Tree cover (%) | 79 (10–100) | 85 (10–100) | 53 (10–90) | 89 (30–100) | 83 (15–100) | 84 (70–100) | 92 (40–100) | 83 (10–100) |
| Shrub height (m) | 5 (1–12) | 3 (1–7) | 5 (2–8) | 5 (1–10) | 3 (1–12) | 3 (1–4) | 3 (3–4) | 4 (1–12) |
| Shrub cover (%) | 63 (1–100) | 37 (1–100) | 65 (10–100) | 46 (1–100) | 33 (0–90) | 23 (0–100) | 54 (10–100) | 48 (0–100) |
| Herb height (cm) | 36 (3–140) | 32 (15–70) | 44 (15–80) | 33 (10–100) | 42 (10–150) | 29 (10–45) | no data | 36 (3–150) |
| Herb cover (%) | 81 (1–100) | 92 (5–100) | 90 (50–100) | 87 (5–100) | 96 (30–100) | 94 (65–100) | 93 (70–100) | 87 (1–100) |
| Ground height (mm) | 18 (10–50) | 19 (5–50) | 15 (5–40) | 14 (10–30) | 19 (5–80) | 16 (10–30) | no data | 17 (5–80) |
| Ground cover (%) | 29 (0–100) | 21 (0–100) | 24 (0–95) | 13 (0–100) | 34 (1–95) | 35 (5–85) | 38 (10–80) | 27 (0–100) |
| Altitude (m) | 91 (15–203) | 85 (10–250) | 71 (30–120) | 98 (5–230) | 115 (8–240) | 100 (40–235) | 224 (60–290) | 105 (5–290) |
| Slope (°) | 2 (0–45) | 10 (0–30) | 0 (0–4) | 4 (0–30) | 25 (0–85) | 18 (5–50) | 40 (10–45) | 11 (0–85) |

a *Primula vulgaris*-*Glechoma hederacea* sub-community

b *Anemone nemorosa* sub-community

c *Deschampsia cespitosa* sub-community

d *Hedera helix* sub-community

e *Geranium robertianum* sub-community

f *Allium ursinum* sub-community

g *Teucrium scorodonia* sub-community

8 *Fraxinus excelsior*-*Acer campestre*-*Mercurialis perennis* woodland (total)

