
W10

Quercus robur-*Pteridium aquilinum*-*Rubus fruticosus* woodland

Synonymy

Damp oakwood association Moss *et al.* 1910 *p.p.*; *Quercetum roboris* Tansley 1911 *p.p.*; *Quercetum arenosum roboris et sessiliflorae* Tansley 1911 *p.p.*; *Quercetum sessiliflorae* Moss 1911, 1913, *p.p.*; *Quercus robur*-*Carpinus* woodland Salisbury 1916 *p.p.*; *Quercus sessiliflorae*-*Carpinus* woodland Salisbury 1918a *p.p.*; *Quercetum roboris* Tansley 1939 *p.p.*; *Quercetum petraeae sessiliflorae* Tansley 1939 *p.p.*; Ash-maple-hazel woods Rackham 1980 *p.p.*; Hornbeam-woods Rackham 1980 *p.p.*; Limewoods Rackham 1980 *p.p.*; Oakwoods Rackham 1980 *p.p.*; Birch-woods Rackham 1980 *p.p.*; Chestnut-woods Rackham 1980 *p.p.*; Hazel-ash woodland Peterken 1981 *p.p.*; Ash-lime woodland Peterken 1981 *p.p.*; Oak-lime woodland Peterken 1981 *p.p.*; Birch-oak woodland Peterken 1981 *p.p.*; Hornbeam woodland Peterken 1981 *p.p.*; Woodland plot types 9, 17, 19, 20 & 24 Bunce 1982; *Lonicero-Quercetum* (Birse & Robertson 1976) Birse 1984 *p.p.*; *Quercus-Betuletum* Klötzli 1970 *p.p.*; *Blechno-Quercetum fraxinetosum* Klötzli 1970 *p.p.*

Constant species

Quercus robur, *Lonicera periclymenum*, *Pteridium aquilinum*, *Rubus fruticosus* agg.

Physiognomy

The *Quercus robur*-*Pteridium aquilinum*-*Rubus fruticosus* woodland, like its counterpart on more base-rich soils, the *Fraxinus-Acer-Mercurialis* woodland, is a variable community in which floristic differences related to climate and soil are overlain by treatment-derived variation in the canopy and underwood. Here, though, the resultant combinations of these patterns are not so numerous or complex and the overall definition of the community is a little more straightforward.

Essentially, these are oakwoods, though in a narrower sense in which that term was applied in early British studies (e.g. Moss *et al.* 1910, Tansley 1911, 1939). Oak

is the most characteristic tree here and, though its cover has been very widely modified by treatment, it remains far and away the commonest tree throughout and is the only woody constant. Quite often, it is very abundant, dominating in semi-natural high-forest canopies and, where the community has been worked as coppice (a frequent, though now largely discontinued, practice), it is invariably the standard. It can also sometimes be found as a component of the underwood itself and the community includes, too, oak plantations whose general floristic character clearly places them here.

Of the two species of oak, *Quercus robur* is very much the commoner throughout, being especially characteristic of this kind of woodland over most of the lowland south-eastern part of the range of the community. Towards the west and north, it is partly replaced by *Q. petraea* and a perplexing range of hybrids between the two, which add to the already considerable amount of variation within each species (Jones 1959, 1968, Cousens 1965, Wigston 1974). But this general geographic distinction, which reflects a shift of the community on to more free-draining soils to the north-west, is not a hard and fast one and there are some prominent enclaves in the lowland zone where *Q. petraea* is the usual oak in these woodlands, most notably in south-east Essex, parts of Hertfordshire and Sherwood in Nottinghamshire: this replacement does not always show a clear edaphic correlation (Jones 1959, Gardiner 1974). The picture is further complicated by the bias, of long standing until recent times, towards *Q. robur* as the preferred oak for planting (Gardiner 1974, Penistan 1974) which might explain some of the more unexpected occurrences of this tree in northerly stands. Whatever the origin of this geographical patterning among the oaks, it is not accompanied here by any other absolutely exclusive floristic features. The prominence of *Q. petraea* to the north-west helps define the *Acer-Oxalis* sub-community and local abundance to the south-east is sometimes associated with the presence of other trees such as *Carpinus betulus* (in Essex and Hertfordshire) or

Castanea sativa (in Essex) but there is no sound basis for using the species of oak to make sub-divisions within the community (cf. Peterken 1981).

The next most common tree throughout is birch, almost always here *Betula pendula*. This is often a very prominent species in younger stands of the community developing by colonisation of open ground on neglected commons and in field corners, but it is also the most frequent and initially successful invader of gaps, recently-cut coppice and clear-felled areas in established tracts of this woodland and has attained increased patchy abundance with the decline in traditional kinds of management. It often marks, for example, areas where post-coppice cleaning was neglected after the cuts of the 1940s. Where oak is dominant in the surrounding woodland in such situations, its own poor regeneration may leave successive generations of birch in occupation as locally-established groves. However, though this tree has undoubtedly spread in recent years, it also occurs very often here as an integral low-cover component of mature high-forest canopies, turning over at a more rapid rate than the other tree species, but apparently maintaining its contribution continually and attaining a grand stature that can belie its reputation as simply a forest weed. In some stands of the community, birch has also been included within a coppice crop (Rackham 1980). The prominence of birch here was recognised by Klötzli (1970) in his definition of a lowland *Quercus-Betuletum* and by Peterken's (1981) diagnosis of many of these woodlands as belonging to his birch-oak stand types (parts of 6C and 6D). There is also some small overlap between this community and the birchwoods of Rackham (1980).

The shift in emphasis towards the pre-eminence of oak and birch here is also marked by the great scarcity in the community of *Acer campestre* and the restricted occurrence of *Fraxinus excelsior*. *Fraxinus* is only occasional in this kind of woodland as a whole and distinctly patchy towards the south-east. Here, it can attain local prominence, sometimes on quite acidic, though probably fairly fertile, soils, as in Rackham's (1980) 'pure ashwoods' in East Anglia and some of Peterken's (1981) 3A oak-hazel-ashwoods and it figures, too, in some *Castanea sativa*-dominated woodlands of this community and in plantations. But only in the *Acer-Oxalis* sub-community of the wetter north-west does it attain the kind of frequency that is commonplace through the *Fraxinus-Acer-Mercurialis* woodland and, even then, it is usually of low abundance. *Acer pseudoplatanus* shows the same general pattern of distribution, effectively marking out areas of higher rainfall and being prominent in the drier south-east more as a local invader of gaps and cleared areas (though often a very successful invader) than as a consistent component of this woodland. To the north-west, by contrast, it is very much at

home here, occurring along with *Fraxinus* and the oaks in well-established high-forest canopies and with a full complement of the community herbs. It has also been treated in this region as a coppice crop, supplying wood for bobbins for the textile industry. A third tree, *Ulmus glabra*, follows *Fraxinus* and *A. pseudoplatanus* geographically, though it is less frequent here, even in the north-west, than it is in the *Fraxinus-Acer-Mercurialis* woodland and decidedly rare in south-eastern stands of the community.

Three other trees are of major importance in certain kinds of *Quercus-Pteridium-Rubus* woodland, occurring quite widely in the warmer and drier south-east as infrequent companions to oak and birch but also being found in this region with very marked local prominence. *Tilia cordata* and *Carpinus betulus* are not exclusive to this community: they occur in other kinds of woodland, notably the *Fraxinus-Acer-Mercurialis* woodland, though the stands in which they dominate here tend to be larger. As elsewhere, the naturally gregarious tendency of these trees has very frequently been accentuated by generations of cropping for large-coppice underwood and now they can be found as dominants, alone or in mixtures of the two, in extensive tracts of woodlands in which oaks have been reduced to occasional standards and from which birch has traditionally been eliminated. The impoverishment of the field layer in dense stands of these species, especially striking under *Tilia*, means that it may sometimes be difficult to separate lime- or hornbeam-dominated stretches of this community from areas of *Fraxinus-Acer-Mercurialis* woodland in which they are abundant and some schemes (e.g. Rackham 1980, Peterken 1981) unite them in 'lime-' and 'hornbeam-woodlands'. When the canopy is opened up, however, in coppicing or clearance, the flush of field-layer growth is rather different in each case.

Much more strictly confined to the *Quercus-Pteridium-Rubus* woodland and prominent on a more restricted geographical scale than *Tilia* or *Carpinus*, though with equally distinctive effect when it does occur, is *Castanea sativa*. This tree, which has a Sub-Mediterranean distribution in Europe, is almost certainly an introduction to Britain (Godwin 1975, Rackham 1980), but it is eminently successful on the moister soils over which this community occurs and has been strongly selected as a prolific coppice crop to supply poles and stakes. It is especially associated here with the *Anemone* sub-community though, again, there is little justification for separating off this kind of woodland from the community as a whole and erecting a separate 'chestnut-woodland' (cf. Rackham 1980).

Quite a wide variety of other tree species occurs at low frequency throughout the community and only very exceptionally at high cover. First, larger specimens of *Ilex aquifolium* and *Sorbus aucuparia* sometimes make a

contribution to the canopy. Both of these, and especially *Ilex*, are rather more common here than in the *Fraxinus-Acer-Mercurialis* woodland, though generally they form part of an understorey, occurring as scattered individuals or with patchy local prominence. But, in some situations, they can be the major woody associates of oak and birch in this community and then it may be difficult to separate samples from the *Quercus-Betula-Deschampsia* woodland on the basis of the trees and shrubs alone. Field-layer differences (see below) will usually effect a separation in such cases, though there are some quite widespread situations where these two communities grade one into another with their herbs distributed in complex mosaics.

The occasional presence of *Fagus sylvatica* here may also create problems of definition. Woodlands in which *Fagus* dominates over similar, though often rather impoverished, field layers to those found in this community, are treated separately in this scheme as the *Fagus-Rubus* woodland but, in certain circumstances, transitional stands can be found. *Fagus* is generally a sparse canopy component in *Quercus-Pteridium-Rubus* woodland and *Q. robur* similarly infrequent within *Fagus-Rubus* woodland but, where oak succeeds in regenerating in larger gaps within the latter community or where beech has been introduced into stands of the former, more balanced mixtures of the two trees can occur over the typical herbs. Often, this is in areas like the Chiltern plateau and the New Forest where established tracts of both communities occur in close proximity, though interplanting with *Fagus* has been widely pursued well beyond its natural British limit. *Taxus baccata*, a locally prominent associate of beech in the *Fagus-Rubus* woodland, is sometimes conspicuous here, too, as in some New Forest stands where it occurs in a patchy lower tier to a canopy of oak. Overall, however, it remains an infrequent tree in the community.

A further scarce associate is *Alnus glutinosa*. Generally speaking, this also occurs only as scattered individuals, in this case picking out areas of poorer drainage, and any increase in its cover usually marks out a transition to flushes (where it is a major canopy component in the *Alnus-Fraxinus-Lysimachia* woodland) or to alluvial flats (where it figures in the *Alnus-Urtica* woodland). But, since springs and streams are a common feature of *Quercus-Pteridium-Rubus* woodlands, some more gradual zonations between these communities should be expected.

As in the *Fraxinus-Acer-Mercurialis* woodland, wetter soils here can also have some *Populus tremula*, characteristically forming clones of small suckering trees. Another suckering tree which can also attain local prominence in the community is *Prunus avium*: very occasionally, it can dominate in this kind of woodland over considerable areas, as in some East Anglian sites

described by Rackham (1980), but frequently it is found as a solitary tree, sometimes of magnificent size and, with its peculiar angular branches, looking very distinctive. Much more strictly non-gregarious is *Sorbus torminalis*, which often needs an extensive search to find it, and *Malus sylvestris*.

Finally, among the canopy components, mention must be made of planted softwoods because this community, unlike the *Fraxinus-Acer-Mercurialis* woodland, can stand fairly intensive coniferisation without a complete destruction of its overall floristic integrity, though not, of course, without often irremediable damage to its historic continuity. Interplanting or replacement of the canopy with softwoods is quite widespread here and stands of such species as *Pinus sylvestris*, *P. nigra* var. *maritima*, *Pseudotsuga menziesii* and *Larix* spp. over field layers with *Pteridium aquilinum* and *Rubus fruticosus* agg. are best incorporated, on general ecological grounds, within this community.

Semi-natural high-forest stands of the *Quercus-Pteridium-Rubus* woodland generally have a distinct understorey of shrubs and small saplings, often quite low (less than half the height of the trees) though sometimes fairly dense, at least in patches. But, very commonly, and especially towards the south-east, this community has been treated as various kinds of coppice, sometimes with trees such as *Tilia*, *Carpinus* or *Castanea* forming the crop, but on a much more widespread scale with shrubs and smaller trees being cut. With the general neglect of coppicing, a complicated range of physiognomies, between well-defined coppice and high forest, can now be encountered, though traces of the treatment can still often be detected in stands of this woodland by careful observation.

As in the *Fraxinus-Acer-Mercurialis* woodland, *Corylus avellana* is the commonest shrub here and its high frequency helps separate this community from oak-birch woodlands of more acid soils where, in the southern lowlands at least, *Corylus* is scarce. This difference in representation was recognised by Peterken (1981) in his diagnosis of birch and hazel sub-types among his lowland birch-oak woodlands. Even in uncoppiced high forest, *Corylus* is usually the most abundant element in an understorey but, in coppiced stands, it has been very widely favoured, encouraged and perhaps planted so it is often here an effective dominant, with or without a tier of standards, almost always oak, above. With similar stands in the *Fraxinus-Acer-Mercurialis* woodland, these kinds of *Quercus-Pteridium-Rubus* woodlands constitute the vast bulk of hazel coppice in lowland Britain and, where uniform treatment has been imposed over natural boundaries between these two communities, an identical physiognomy can extend deceptively over different field layers. Usually, sufficient herbs occur to discern a switch from the one to the other but, where

there is especially dense shade, as in stands which are reaching the end of their rotation of growth or which have been long neglected, it may be difficult to draw a boundary; and, on soils which show a gradual change in their calcium content or base-status, the zonation may be continuous for quite natural, edaphic reasons.

As noted above, *Acer campestre* is rare in this community and the most frequent woody companions of *Corylus* are generally the hawthorns. *Crataegus monogyna* is very much the more common species overall and, though it rarely rivals *Corylus* in its abundance, it is a characteristic feature of the understorey in high-forest stands, sometimes growing very tall and breaking the canopy, and an occasional in coppice, where it has sometimes been included in the crop. To the north-west, *C. monogyna* is the usual woodland hawthorn here, but in the warmer and drier south-east, it is sometimes replaced, especially within longer-established stands of the community, by *C. laevigata* which is a naturally bushier plant and more readily coppiced. Hybrids between the two can also be found (Bradshaw 1953).

Smaller trees of *Ilex aquifolium* are also a quite frequent feature of the understorey or coppice-underwood here and there is occasionally some *Sorbus aucuparia*. *Viburnum lantana* and *V. opulus* occur sparsely and, in younger scrubby stands or along margins and rides, *Prunus spinosa* may join *Crataegus monogyna* in a dense spiny cover. *Sambucus nigra* can be patchily prominent, too, especially on more disturbed and enriched areas and, though it is not so frequent overall as in the *Fraxinus-Acer-Mercurialis* woodland, it shows the same tendency as there, in that it increases its representation towards the north-west where the soils are perhaps more consistently aerated and have a faster nutrient turnover as well as having the benefit of the rich foliage of *Fraxinus* and *Ulmus glabra*. In contrast to the *Fraxinus-Acer-Mercurialis* woodland, however, shrubs such as *Cornus sanguinea*, *Euonymus europaeus* and *Ligustrum vulgare* are noticeably rare on the typically less base-rich soils here. Indeed, where stands of this community are coppiced, the place of these species as invaders is sometimes taken by *Cytisus scoparius* or *Ulex europaeus*. The soils here are also sometimes sufficiently acid to support *Rhododendron ponticum* and, where this shrub has been planted into these woodlands, a widespread practice since its original introduction in the eighteenth century, as game cover or as ornamentation of what is sometimes visually dull vegetation, it can become a serious weed (Cross 1975).

Except in young, unthinned plantations and in older and neglected coppice, the cover of trees and shrubs in the *Quercus-Pteridium-Rubus* woodland is often not complete. Some stands occur more as wood-pasture than as woodland proper, being found in association

with open 'plains' (or 'lawns' or 'launds') in ancient parkland or forests in the old legal sense. Even in high forest, the shade cast is frequently quite light and, provided there is no intense competition from herbs or consistent predation by small herbivores, deer or stock, tree saplings can be quite common, thickening up in gaps to form dense regeneration cores. As noted earlier, young birch are often a conspicuous feature here but *A. pseudoplatanus* saplings can also be very prominent, more consistently in the wetter north-west, where, along with *Fraxinus*, this tree is usually the most prolific regenerator. After good mast years, *Fagus* saplings can also occur frequently, near to their parents. In marked contrast, the most characteristic woody species of the community, oak, is often the most poorly represented among younger trees, a feature which was noted early by Watt (1919), which may be a relatively recent development (Rackham 1980) and which probably has a complex number of causes (see below). Certainly, the general scarcity of oak saplings within established stands of *Quercus-Pteridium-Rubus* woodland is very different from the good representation of young trees where the community is developing by invasion of open ground.

The most obvious general feature of the field layer here, especially when it is compared with that of the *Fraxinus-Acer-Mercurialis* woodland, its counterpart on more base-rich soils, is its general species-poverty. In essence, the herbaceous component of this community as a whole comprises variations on the representation of only three constants and a very small number of occasional to frequent species. But the proportions of these plants are quite varied and the general impression created by the field layer can be very different from one stand to another. In common parlance, these are 'blue-bell woods' and a visit to a woodland of this kind when *Hyacinthoides non-scripta* is flowering in abundance from April to June can be an unforgettable experience. *Hyacinthoides* is the commonest vernal dominant here, indeed the only frequent vernal dominant apart from *Anemone nemorosa*, which tends to replace it on the moister soils occupied by the *Anemone* sub-community. But, though its leaves emerge in early spring, they have almost totally decayed by mid-summer (Blackman & Rutter 1954), so apart from a competitive relationship with *Anemone* (Pigott 1982), this species does not exert the same kind of controlling influence on its associates here as does *Mercurialis perennis* in the *Fraxinus-Acer-Mercurialis* woodland. *Hyacinthoides* is, of course, a frequent and often abundant plant in that community, too, but *Mercurialis* is characteristically very sparse here, even on the better-aerated soils where it can perform well. Indeed, if anything, its very occasional appearances in the *Quercus-Pteridium-Rubus* woodland tend to be on fairly moist soils because these often indicate some slight base-enrichment from streams or

flushes: typically, here, a few plants mark out little alluvial flats in stream-loops or transitions to *Alnus-Fraxinus-Lysimachia* flushes. Generally speaking, however, the soils here are too base-poor to support any abundant growth of *Mercurialis* or frequent representation of its typical associates in the *Fraxinus-Acer-Mercurialis* woodland: plants like *Geum urbanum*, *Circaea lutetiana*, *Arum maculatum*, *Viola reichenbachiana*, *Geranium robertianum* and *Brachypodium sylvaticum* are all markedly uncommon in this community. It is in the *Quercus-Pteridium-Rubus* woodland that *Hyacinthoides* extends on to the most acid of the woodland soils on which it is represented in Britain and the more species-poor 'bluebell woods' which this community comprises are actually of rather restricted distribution in Europe, being largely confined to the north-west of France, Belgium and the lowlands of this country (Noirfalise 1968, Neuhausl 1977).

Despite its characteristic pre-eminence here, *Hyacinthoides* is not a constant of the *Quercus-Pteridium-Rubus* woodland, though it probably would be were not so many stands long-overgrown and gloomy coppices or modified plantations. More frequent overall and, even where *Hyacinthoides* is well represented, more obvious by mid-summer, are *Pteridium aquilinum*, *Rubus fruticosus* agg. and *Lonicera periclymenum*, and various combinations and amounts of these species typically form a ferny underscrub that can attain a metre or more in height. One further component of the pattern, of patchy frequency to the south-east, more consistently common to the north-west, is *Holcus mollis*, lush swards of which can become prominent as *Hyacinthoides* is fading and before the *Pteridium* fronds have attained their full height and the *Rubus* its summer leaves. Spatial variations on this basic theme are very diverse: some stands are intimate mixtures or patchy mosaics of just *Hyacinthoides* and *Holcus*, in others there are intermixed sparse small fronds of *Pteridium* and a few strands of *Rubus*; or *Rubus* and *Lonicera* can form a virtually impenetrable underscrub with very little else; and *Pteridium* can increase its height and cover to present a virtual jungle of fronds, man-high, and with such a dense shade and thick litter that no associates, not even the other community constants, can gain a hold. All these variations, which are a complex function of canopy shade, soil moisture, grazing and competition between the plants themselves, can be found within each of the sub-communities here and, apart from the general feature of impoverishment with thicker cover, they are often unaccompanied by any consistent floristic differences among other species. These variations are therefore not employed here for distinguishing the sub-communities of the *Quercus-Pteridium-Rubus* woodland, though it should always be remembered what a distinct visual impression each of them can make and it may be useful to recognise variants according to the particular dominant.

The other component of the field layer that is sometimes physiognomically prominent consists of dryopteroid ferns. *Dryopteris filix-mas* occurs occasionally throughout and *D. dilatata* is quite common overall, too, though increased frequency of this species is a fairly good diagnostic feature of the north-western *Acer-Oxalis* sub-community. *D. borrieri* occurs much less often than these two and there is sometimes, again more so to the north-west, a little *Athyrium filix-femina*. All these ferns tend to be more obvious when *Pteridium* is less abundant, and scattered crowns, emerging through a low patchy underscrub of *Rubus* and sprawling *Lonicera*, are a very characteristic feature of many stands.

Against this general background, a variety of other species make a contribution to the field layer which is not more than occasional overall but which can, in certain circumstances, become prominent, helping to define some of the sub-communities of the *Quercus-Pteridium-Rubus* woodland. First, there is *Hedera helix* which, as well as occurring as a sometimes conspicuous climber, quite often forms a ground carpet here, except where *Pteridium* is very abundant. As in the *Fraxinus-Acer-Mercurialis* woodland, *Hedera* shows a distinct tendency to be a more frequent and extensive component here in more oceanic regions but it is also, as in that community, a marker of stands of *Quercus-Pteridium-Rubus* woodland where there has been a substantial period of uninterrupted canopy or underwood growth. The *Hedera* sub-community thus contains many neglected coppices, younger secondary woods and plantations approaching a first thinning.

Second, there are grasses. Many stands here have a grassy appearance, especially in the period between the spring dominance of *Hyacinthoides* and the summer dominance of *Pteridium*. But this cover is generally rather species-poor with *Holcus mollis* as the major component. *Deschampsia cespitosa* may make a locally conspicuous contribution on moister soils, as around transitions to flushes, and along the edges of paths and in rides, and there is sometimes a little *Poa trivialis*, *Milium effusum* or *Melica uniflora*. And on more free-draining soils, as on drier banks or on transitions to more leached brown earths, *Deschampsia flexuosa* can become more frequent in mosaics with *H. mollis*, occasional *Blechnum spicant* and patchily prominent *Luzula sylvatica*. In sharp contrast to the sub-montane *Quercus-Betula-Oxalis* woodland, however, *D. flexuosa* remains generally scarce and is not accompanied here by grasses like *Anthoxanthum odoratum* and *Agrostis capillaris* which, in that community, are such an obvious indicator of grazing on more surface-leached soils. Here, increased representation of grasses generally involves more mesophytic species, notably *Holcus lanatus*, less so *Dactylis glomerata*, and these are very much a marker of the kind of disturbance associated with replacement of the canopy with oak or conifers. Such vegetation is here

placed in a *Holcus lanatus* sub-community.

Then there is a wide range of low-frequency associates. Some of these, though not very common and not exclusive, are quite characteristic of this kind of woodland: *Stellaria holostea*, *Silene dioica*, *Luzula pilosa*, *Digitalis purpurea* and *Solidago virgaurea*. Often these occur as scattered individuals, though *S. holostea* is sometimes patchily prominent within swards of *Holcus mollis*, especially in the north-western *Acer-Oxalis* sub-community. But *S. dioica* and *D. purpurea* can increase very markedly where this community is opened up and disturbed and they are a frequent component here of post-coppice vegetation sometimes with *Corydalis claviculata*. Also, in such situations, *Epilobium angustifolium*, *Rumex acetosa*, *R. sanguineus*, *Urtica dioica*, *Teucrium scorodonia* and *Euphorbia amygdaloides* may increase their representation and shrubs like *Cytisus scoparius* and *Ulex europaeus* appear. Occasional plants of these species may survive for some time as the canopy closes.

Finally, among the herbs, there are ground-cover species which can attain local prominence over more open areas of bare soil, especially where this is heavy and moist and where the cover of *Pteridium* in particular is reduced. This is the kind of situation where some species very characteristic of south-eastern *Fraxinus-Acer-Mercurialis* woodlands may make an appearance. As well as *Poa trivialis* already noted, there can be some *Glechoma hederacea*, *Ajuga reptans* and *Lamium galeobdolon*, sometimes with *Veronica chamaedrys*, *Lysimachia nemorum* and *L. nummularia*. These plants, too, may show some vegetative spread here after coppicing.

It is in the more open areas of herb cover that tree seedlings are especially numerous. *Acer pseudoplatanus* is generally the best represented species with *Fraxinus*, *Crataegus monogyna* and, in drier situations, *Betula pendula*. Oak seedlings occur in larger gaps and in young stands where the canopy has not yet closed.

Bryophyte cover in the *Quercus-Pteridium-Rubus* woodland is usually low, especially where, as amongst lush *Holcus mollis* or beneath *Pteridium*, litter is extensive and thick. The commonest species throughout are *Eurhynchium praelongum*, on soil and less acidic litter, and *Mnium hornum* on fallen twigs and bark, around tree bases and on soil. Other less frequent species are *Brachythecium rutabulum*, *Thuidium tamariscinum*, *Pseudoscleropodium purum*, *Isopterygium elegans* and *Plagiothecium undulatum*. Strongly calcicole or calcifuge bryophytes are characteristically sparse but they may be represented in transitional stands.

Sub-communities

Typical sub-community: *Quercus robur* wood, *Pteris-Holcus* and *Holcus* societies Adamson 1912; *Quercus robur-Carpinus* woodland, *Pteris* and *Scilla* societies Salisbury 1916; *Quercus sessiliflora-Carpinus* woodland,

Pteris, *Rubus* and *Scilla* societies Salisbury 1918a; *Quercetum roboris* and *Quercetum petraeae*, *Pteridium*, *Rubus-Pteridium*, *Scilla* and post-coppice societies Tansley 1939; *Quercus-Betuletum* Klötzli 1970 p.p.; Ash-maple-hazel woodland Rackham 1980 p.p.; Hornbeam, hornbeam-ash and oak-hornbeam woods Rackham 1980 p.p.; Lime and lime-oak woods Rackham 1980 p.p.; Oakwoods Rackham 1980 p.p.; Lowland birchwoods Rackham 1980 p.p.; Hazel-ash stand types 3Aa & 3Ab Peterken 1981 p.p.; Ash-lime stand type 4A Peterken 1981 p.p.; Oak-lime stand type 5A Peterken 1981 p.p.; Birch-oak stand types 6Cc, 6Db & 6Dc Peterken 1981 p.p.; Hornbeam stand types 9Aa & 9Ba Peterken 1981 p.p.; Woodland plot types 17 & 24 p.p. Bunce 1982. This is the central type of *Quercus-Pteridium-Rubus* woodland over most of the south-eastern lowlands, forming the core of what has traditionally been described as 'dry oakwood' in Britain (Moss *et al.* 1910, Tansley 1911, 1939). Certainly, oak is the most frequent tree throughout, usually *Q. robur*, though in its distinctive enclaves and more generally on more free-draining soils, *Q. petraea*. In some stands, oak dominates in a high-forest canopy with frequent, though usually less abundant, *Betula pendula* and sometimes a little *Fagus*, *Acer pseudoplatanus* or *Pinus sylvestris*, seeding in from nearby or deliberately introduced for ornament. Oak is predominant, too, usually as *Q. robur*, in some long-established plantations here. Very often, however, oak is not of great abundance in stands of this sub-community, having been reduced to occasional standards in, or altogether eliminated from, coppice of hazel, lime, hornbeam or sometimes chestnut. *Tilia* and *Carpinus*, in fact, occur as low-frequency canopy trees in this kind of *Quercus-Pteridium-Rubus* woodland, typical as it is of the warmer and drier parts of the country and, when they do occur, the woody component of the vegetation can closely resemble that of continental Carpinion high forest. Very often, though, they have been coppiced and locally selected for as the basis of an underwood crop, so stands of this sub-community dominated by overgrown lime or hornbeam, or diverse mixtures of the two, are widespread. Those kinds of lime and hornbeam woodland characterised by Rackham (1980) and Peterken (1981) from more base-poor and free-draining soils therefore belong here in the scheme, together with the drier types of oak-hornbeam woodlands described in the early account of Salisbury (1916, 1918a). *Castanea* is occasionally found here in association with *Carpinus* and rarely it is locally dominant, but most chestnut coppice is best included in the *Anemone* sub-community.

Much more widespread than these kinds of coppiced versions of this sub-community are those dominated by *Corylus*, with or without a cover of standards, almost invariably oak, very occasionally *Fraxinus*. Even in high-forest stands, *Corylus* is generally the most promi-

ment shrub but here it is often extremely abundant in neglected coppice, the bushes growing dense and tall where the tree canopy remains more open but eventually thinning out with increasing age and canopy extension. Under such gloomy conditions, transitions to the *Hedera* sub-community are common.

The most frequent companions of *Corylus* in this sub-community are the hawthorns, usually *C. monogyna*, but quite commonly in older stands of these south-eastern woods, *C. laevigata*, with the former then characteristic of younger tracts and scrubby margins, where *Prunus spinosa* can also increase in abundance. *Ilex* occurs occasionally, together with less frequent *Sorbus aucuparia* and, on more base-poor, free-draining soils, these two species tend to become proportionately more prominent. Other associates are *Sambucus nigra*, often clearly associated with disturbed areas, *Viburnum opulus*, *Malus sylvestris* and introduced *Rhododendron ponticum*. In coppiced stands, *Crataegus laevigata*, *Ilex* and *Sorbus* would often have been included with *Corylus* in a mixed underwood crop. In high forest here, all these smaller trees and shrubs occur as a generally open and low understorey with, in gaps, saplings of *Betula pendula* (especially on the drier soils), *Acer pseudoplatanus* (more on the moister soils), *Fagus* and occasional *Fraxinus*.

In the field layer of this sub-community, *Hyacinthoides* is a very common and often extremely abundant vernal dominant. Completing the bulk of its growth before the canopy comes into leaf, it grows quite freely in stands with a fairly dense woody cover though, like most herbs here, it declines under thicker stands of *Carpinus* and especially of *Tilia* and beneath neglected *Corylus* underwood. With regular coppicing, it shows the characteristic flush of flowering in the second or third spring after the cut (Salisbury 1924), though this is apparently not so marked on the more acid soils on to which this kind of woodland extends (Rackham 1980). *Hyacinthoides* can also thrive amongst moderately dense *Pteridium* here, the fronds of which are still expanding as the former flowers, but it is much reduced where very vigorous bracken growth leads to an accumulation of thick litter.

By mid-summer, *Pteridium* is often the most prominent feature of the field layer, especially on the more free-draining soils which here tend to be the more acidic (though bracken cannot be seen as a simple calcifuge). Its abundance is also very dependent on light penetration, so its vigour and cover are at their maximum here under more open canopies such as are found in recently-cut coppices and clear-felled areas, in gaps, around glades and where young birch and oak are establishing themselves on previously open ground (Adamson 1912, Salisbury 1916, 1918a, Tansley 1939). In such situations, the fronds, which emerge in late May and are fully unfurled by early July, can be very densely

packed and robust, commonly reaching well over a metre high and producing a dense shade in which there is little other summer growth. *Pteridium* litter can then be very bulky, the dead fronds decaying only slowly into a layer 10 cm or more thick. This may prevent establishment of seedling trees or even regrowth of coppice shoots, especially if the additional hindrance of browsing is severe (Tansley 1939, Rackham 1980). Beneath denser canopies of trees or shrubs, the abundance of *Pteridium* is much reduced with sparser, shorter and less vigorous fronds occurring scattered through a richer summer field layer.

In stands of this kind, it is often *Rubus* and *Lonicera* which become most obvious as *Hyacinthoides*-dominance fades in early summer. Brambles, or some of them at least, have some advantage over *Pteridium* in denser woodlands, in that they have shoots which overwinter in full leaf (Taylor 1980). But maximum growth coincides with canopy closure, summer leaves unfolding on new lateral shoots which can form a dense underscrub with its own shading canopy of foliage beneath which other species are again quite sparse. Through this tangle of arching shoots, *Lonicera* sprawls, producing knee-high vegetation which is virtually impenetrable. As with *Pteridium*, however, *Rubus* grows best under more open canopies and it shows a similar response to coppicing. It is also sensitive to browsing and increases its cover dramatically if access to deer and stock is prevented.

Holcus mollis is not so consistent a feature of this kind of *Quercus-Pteridium-Rubus* woodland as it is to the north-west, but on moderately moist soils and where the canopy shade is not too dense, it can be prominent as a patchy sward in the short period between the waning of *Hyacinthoides* and the closure of a bramble or bracken cover. In this period, too, scattered crowns of *Dryopteris filix-mas* and *D. dilatata* become fully unfurled and occasional tussocks of *Milium effusum* and *Melica uniflora* flower. In more densely shaded stands, where sparse bluebells are replaced by a thin summer cover of bracken or brambles, ground-cover plants such as *Poa trivialis*, *Glechoma hederacea* and *Veronica chamaedrys* may attain prominence with small patches of *Eurhynchium praelongum*, *Mnium hornum*, *Isopterygium elegans* and *Atrichum undulatum*. This kind of very open, impoverished field layer is very characteristic of dense *Tilia* coppice here.

Vegetative expansion of more shade-tolerant ground-cover plants is often the first response when this kind of *Quercus-Pteridium-Rubus* woodland is coppiced, followed by increased flowering in *Hyacinthoides* and a marked spread of *Silene dioica*, *Euphorbia amygdaloides* and *Digitalis purpurea* which are normally only present as scattered individuals here. *S. dioica* may mark out areas of local nutrient enrichment but often much more obvious around brushwood bonfires are patches of

Epilobium angustifolium and *Urtica dioica*. Larger Rumices may also appear with occasional *Cytisus scoparius*, *Ulex europaeus* and *Rubus idaeus*. *Juncus effusus* and *Deschampsia cespitosa*, though they can become locally prominent on wetter soils, are not a consistent feature here and the more frequent gross physiognomic change in such post-coppice floras is the spread of *Pteridium* (especially on the free-draining substrates) and/or *Rubus* (extending on to moister soils). Increased cover of these species may initially hinder coppice regrowth and remain a prominent feature of the field layer until well into the cutting cycle. Bracken-dominated glades may develop within stands of this sub-community where there has been coppicing or clear-felling and intense browsing.

***Anemone nemorosa* sub-community:** Provisional hornbeam association Tansley 1911; *Quercetum sessiliflorae*, damp sub-association Moss 1911, 1913; *Quercus robur*-*Carpinus* woods, *Anemone* society Salisbury 1916; *Quercetum roboris*, *Anemone* society Tansley 1939; Sweet chestnut coppice Ford & Newbould 1970; Hornbeam & oak-hornbeam woods Rackham 1980 *p.p.*; Lime and lime-oak woods Rackham 1980 *p.p.*; Chestnut-woods Rackham 1980 *p.p.*; Hazel-ash stand type 3Ab Peterken 1981 *p.p.*; Ash-lime stand type 4A Peterken 1981 *p.p.*; Oak-hornbeam stand type 9Aa Peterken 1981 *p.p.* *Q. robur* is very much the characteristic oak of the *Anemone* sub-community and it can be found here as a dominant, along with a little *Betula pendula*, *Fraxinus*, *Alnus* and *Acer pseudoplatanus* and clones of *Populus tremula*, in high-forest stands, over a thin understorey of *Corylus* and usually much less hawthorn. *Tilia* and *Carpinus* occur as sparse associates in such woodland but, again, they can be locally dominant here in large-coppice underwood with a much-reduced canopy of oak standards, now commonly overtopped, and few associated shrubs. Hazel coppice is also a widespread form of this sub-community.

But the most striking peculiarity is the strong association between the *Anemone* field layer and the local prominence of *Castanea*. This long-standing introduction has been widely planted throughout the British lowlands (Perring & Walters 1962) but, in certain well-defined areas, notably Kent and eastern Essex, which seem to be the ancient centre of its distribution (Godwin 1975, Rackham 1980), it is a common dominant in coppiced versions of *Quercus*-*Pteridium*-*Rubus* woodland and these stands are very often of this sub-community. Some show obvious signs of having been planted, sometimes quite recently, chestnut having continued in favour as a source of hop-poles and cleft pales for fencing, but others have a much more natural appearance with ill-defined boundaries and stools of different sizes and ages in irregular arrangements (Rack-

ham 1980). *Castanea*, though it can be a long-lived tree, is a fast and prolific producer of underwood: stools put up a very large number of shoots which quickly self-thin to leave a few substantial poles. In Ford & Newbould's (1970) study of a Kent chestnut coppice, only about 6% of the flush of sprouts survived an 18-year growth cycle, though their winter biomass at the close was 88 tonnes ha⁻¹. Further work (Ford & Newbould 1971) showed that the leaf canopy was fully closed after eight years and quantified the very poor light transmission at less than 4% of visible radiation for a single leaf thickness, a formidable shading effect, not only on its own coppice shoots but on any herbs beneath. Denser stands of *Castanea*, like those of *Tilia*, can thus have a very sparse field layer beyond the middle years of their coppice cycle.

When there is a reasonable amount of light, however, the three community constants, *Pteridium*, *Rubus* and *Lonicera* are all frequent here, though the cover of *Pteridium* is often fairly low: it can become more prominent in the first year after coppicing but typically does not form the dense, tall stands found in other sub-communities. Before these plants have reached their summer maximum, *Hyacinthoides* can be prominent but the more characteristic vernal dominant here is *Anemone nemorosa*. This species does occur elsewhere in the community but at low frequency and cover: though it flowers before *Hyacinthoides*, its leaves emerge a little later and are shaded out by those of bluebell (Pigott 1982). On these typically moister soils, *Hyacinthoides* is, for reasons which are unclear, not so successful so *Anemone* is able to attain abundance before the canopy of trees and shrubs closes and the *Rubus* attains its summer leaves. In contrast to the *Fraxinus*-*Acer*-*Mercurialis* woodland, such a switch is not accompanied here by a rise to prominence of *Primula elatior* in those parts of East Anglia where this plant is such a feature of wetter woodland soils.

Other distinctive characteristics are weak. *Holcus mollis* tends to be less frequent here than in most other *Quercus*-*Pteridium*-*Rubus* woodlands: it can tolerate fairly moist soils in the community but is probably reduced here by the marked inclination to gleying. *H. lanatus*, on the other hand, makes an occasional appearance, though it is not so prominent here as in plantation stands. *Lamium galeobdolon* is sometimes present and it can become locally abundant after coppicing. The high frequency of dense stands of heavily-shading trees like *Tilia*, *Castanea* and *Carpinus* also produces a slight rise in the occurrence of *Atrichum undulatum* which, with *Mnium hornum*, scattered plants of *Anemone*, *Hyacinthoides*, *Lamium* and *Ajuga reptans* and a few trailing shoots of *Hedera* and *Rubus*, comprise the very sparse ground cover in many older coppices included here.

***Hedera helix* sub-community:** Hazel-ash stand type 3Aa, *Hedera-Ilex* sub-type Peterken 1981. This kind of *Quercus-Pteridium-Rubus* woodland has rarely been recognised as a distinct vegetation type, but it has some quite clear floristic and structural characteristics. Again oak is the most common tree, almost always *Q. robur*, and, with a little *Fagus* and *Fraxinus*, it can dominate here in high forest, forming a tall, often closed, canopy that sometimes shows clear signs of planting. In such stands, shrubs are often rather sparse, the understorey comprising some scattered *Corylus* and a little *Crataegus monogyna*, *Ilex* and *Sambucus*. In other cases, *Corylus* is extremely abundant in dense, long-abandoned coppice with few oak standards or none. Some old *Tilia*, *Carpinus* and *Castanea* coppices occur here too. Yet other stands look to be fairly young, but undisturbed, woodland derived by recent invasion: here *Crataegus monogyna* and *Prunus spinosa* can be abundant among scattered oaks. The striking scarcity of birch in all these kinds of woodland is a good indication of their closed and often gloomy character.

Beneath these canopies, *Pteridium* remains very frequent though its cover is usually low. *Rubus*, on the other hand, is often abundant, especially where it is trees, rather than shrubs, which constitute the bulk of the woody cover, and, with *Lonicera*, it can form a thick underscrub. *Holcus mollis* occurs fairly frequently and it is sometimes prominent in early summer but *Hyacinthoides* is uncommon and does not usually provide the striking springtime displays of flowers characteristic of the Typical and *Acer-Oxalis* sub-communities.

Much more obvious throughout the winter and spring is a ground cover of *Hedera helix* which can occur here as a virtually continuous carpet, thinning out only beneath the very densest bramble. *Dryopteris filix-mas* and *D. dilatata* occur occasionally and there can be patches of *Galium odoratum* and grasses such as *Milium effusum*, *Melica uniflora* and *Brachypodium sylvaticum*. In high-forest stands with these species, this kind of vegetation closely approaches the *Fagus-Rubus* woodland and transitional stands can be found.

***Holcus lanatus* sub-community:** Woodland plot types 19 & 20 Bunce 1982. In this again little-described but very widespread and distinctive woodland type, *Q. robur* is the most frequent tree and quite often it forms the bulk of a high-forest canopy, commonly with some *Betula pendula*. In some cases, such stands are young woodlands where oak and birch are invading together but have not yet formed a dense woody cover (in contrast to the closed sub-spontaneous canopies of the *Hedera* sub-community). But often here, there are clear structural indications that the oak has been planted and this sub-community incorporates many younger plantations or thinned stands of oak in their middle years. The other

distinctive feature here is the frequency of conifers, either naturally invading trees which have needed in from nearby (into gaps within established stands or amongst newly-planted oaks) or planted trees, introduced for occasional ornament or as a more substantial replacement of oak or as an oak nurse. The characteristic field layer of this kind of *Quercus-Pteridium-Rubus* woodland is thus commonly encountered under young or thinned stands of such softwoods as *Pinus sylvestris*, *P. nigra* var. *maritima*, *Pseudotsuga menziesii* and *Larix* spp., forming the characteristic herbaceous component of many conifer plantations on base-poor but less free-draining soils throughout the south-eastern lowlands.

In these woodlands, smaller trees and shrubs are very sparse and often there is no understorey at all. *Corylus*, especially, is strikingly infrequent and the usual picture is of scattered *Crataegus monogyna*, *Sambucus* and *Prunus spinosa*, very occasional *Ilex* or *Sorbus aucuparia*, birch saplings in more open areas and, locally prominent, *Rhododendron*.

In the field layer, all the community constants are very common and often extremely abundant. In sub-spontaneous stands and many younger plantations, *Pteridium* in particular can show high cover and vigorous growth, over a very impoverished associated flora. In other cases, the exclusion of grazing animals from plantations is accompanied by a marked spread of *Rubus* and *Lonicera*, early on among the newly-planted trees and again after thinning. Such field layers are not quite so species-poor as those under dense bracken, but this kind of bramble underscrub beneath an even-aged canopy of virtually identical oaks or conifers presents one of the dreariest scenes among British woodlands.

The most obvious loss in these kinds of *Quercus-Pteridium-Rubus* woodlands is *Hyacinthoides* which is extremely infrequent. It can sometimes be found here migrating in from marginal colonies around longer-established plantations or sub-spontaneous woods but it spreads only slowly (6–10 m per century in a Surrey stand: Pigott 1984). And it is eliminated under conifers by the time these reach an age of 15–20 years, so slow re-invasion under a subsequent rotation of oak will not allow it to regain dominance (Pigott 1984). *Anemone* likewise is absent from the moister soils here.

Most of the other characteristic species of the community are uncommon. *Holcus mollis* is occasionally prominent and there are sometimes scattered dryopteroid ferns and sparse plants of *Stellaria holostea*, *Silene dioica*, *Teucrium scorodonia* and, on heavier soils, some *Deschampsia cespitosa*.

Among this generally impoverished picture, the one striking preferential is *Holcus lanatus*, scattered tussocks of which are a typical feature here. And, accompanying this in more open stands there are occasional records for a number of species which increase the untidy appear-

ance of the vegetation. *Epilobium angustifolium* occurs with patchy prominence (as in the stands of Bunce 1982) and there can be some *Urtica dioica*, *Senecio jacobaea*, *Arrhenatherum elatius*, *Heracleum sphondylium*, *Rubus idaeus*, *Cytisus scoparius* and *Ulex europaeus*. Young plantations here thus have much in common with the post-coppice vegetation of the *Quercus*-*Pteridium*-*Rubus* woodland.

***Acer pseudoplatanus*-*Oxalis acetosella* sub-community:** *Quercetum sessiliflorae*, *Pteris-Holcus-Scilla* complementary society Woodhead 1906; *Quercetum sessiliflorae*, drier sub-association Moss 1911, 1913; *Quercetum petraeae*, *Pteridium-Holcus-Scilla* society Tansley 1939; *Blechno-Quercetum fraxinetosum* Klötzli 1970 p.p.; Hazel-ash stand type 3D Peterken 1981 p.p.; Birch-oak stand types 6Ac & 6Bc Peterken 1981 p.p.; *Lonicero-Quercetum*, *Endymion* subassociation (Birse & Robertson 1976) Birse 1984 p.p.. Oak is still a frequent and usually the most abundant tree in this sub-community but there is a marked shift here from *Q. robur* to *Q. petraea* and hybrids. And, very commonly, *Acer pseudoplatanus* and *Fraxinus* make some contribution to the woody cover with, less often, *Ulmus glabra*. Birch is surprisingly sparse, *Fagus* is rare and *Tilia* and *Carpinus* have not been recorded, though in some Lake District ravines, *Tilia* survives in close association with this kind of woodland (Pigott & Huntley 1978). A high-forest structure predominates, though some stands are obviously of fairly recent natural origin and others are clearly plantations or much-modified woods. There are also some coppices, though this treatment is not so universally widespread among these north-western *Quercus*-*Pteridium*-*Rubus* woodlands as it is to the south-east: the usual underwood crop is hazel, though oak itself has sometimes been cut and there are some sycamore coppices.

Corylus is the most frequent shrub here, even in high-forest stands where it forms the bulk of a generally open low understorey. Hawthorn is common, though it is often rivalled in frequency and cover by *Sambucus* and *Ilex*: the latter is sometimes locally very abundant, as around the Pennine fringes where it seems to have figured as a winter foliage crop for stock. *Sorbus aucuparia* also occurs occasionally and *Rhododendron* can be a prominent introduction or invader. Saplings are more numerous here than is usual in the community and there are commonly some young *Fraxinus* and *A. pseudoplatanus* with less frequent birch.

The basic components of the field layer are as in the Typical sub-community with *Hyacinthoides* a common vernal dominant, succeeded by various mixtures of *Pteridium* and *Rubus* and *Lonicera*. But here *Holcus mollis* is much more generally frequent, its lush cover developing as the bluebell flowers fade, and dryopteroid

ferns, especially *D. dilatata*, tend to be more prominent too, along with occasional *Athyrium filix-femina*. *Stellaria holostea* and *Deschampsia cespitosa* are also slightly preferential to this sub-community.

But the most distinctive herb in this woodland of the wetter north-west is *Oxalis acetosella* which attains constancy here and is one of the very few plants that will tolerate a dense cover of *Pteridium* (Packham 1978). As in the *Fraxinus-Acer-Mercurialis* woodland, this rise is accompanied by a less marked increase in the frequency of *Viola riviniana* and by a greater representation of bryophytes, though on these more base-poor soils, more calcicolous species are not involved. Most prominent are *Eurhynchium praelongum*, *Mnium hornum*, *Brachythecium rutabulum*, *Thuidium tamariscinum* and on more acidic litter and soils, *Plagiothecium undulatum* and *Isopterygium elegans*. Among the patches of mosses and on areas of open ground, seedlings of *A. pseudoplatanus* can be extraordinarily abundant in spring, though few get away except in gaps.

The other characteristic feature of the field layer here is that its herbs often occur in intimate mosaics with species of more free-draining and surface-leached soils, especially on steeper slopes where there can be frequent outcrops of rocks or terracing, as in some of the sites described by Woodhead (1906) and Scurfield (1953) from the Pennines. It is in this kind of situation that plants such as *Deschampsia flexuosa*, *Blechnum spicant*, *Vaccinium myrtillus* and, where there is grazing, *Anthoxanthum odoratum* and *Agrostis capillaris*, can appear. Strictly, patches with such species should be regarded as fragments of more calcifugous oak-birch woods, but, in practice, it is often impossible to sample separately every terrace riser and nidus-capped rock.

Habitat

The *Quercus*-*Pteridium*-*Rubus* woodland is characteristic of base-poor brown soils throughout the temperate lowlands of southern Britain. Here, its distinctive assemblage of species probably approximates to the natural climax forest on such soils, but the floristics and physiognomy of the community have been very widely affected by silvicultural treatments. Some stands are of known antiquity, but many have been derived by relatively recent invasion or planting.

Edaphically, this kind of woodland occupies a broad middle ground between rendzinas and brown calcareous earths on the one hand, and brown podzolic soils and true podzols on the other. It is thus absent from limestones unless they are overlain by non-calcareous superfcials, even towards the north-west of its range where higher rainfall induces extensive surface leaching in calcareous lithomorphous soils. It tends to be scarce, too, over calcareous superficial deposits like the Chalky Boulder Clay which typically weathers to produce pro-

files that can be quite acid above but which usually have much exchangeable calcium below. Over such rocks and soils as these, the community is characteristically replaced by the *Fraxinus-Acer-Mercurialis* woodland, the more calcicolous species of which make an appearance here only where there is some local base-enrichment, as along stream sides or around flushes.

Towards the other extreme, the *Quercus-Pteridium-Rubus* woodland does not extend far on to soils derived from more pervious, acidic deposits. It can be found in the south-east over some of the sandstones of the Cretaceous sequence in the Weald, on Eocene sands and gravels in Essex and Kent and around the Southampton Basin and over more free-draining acid superficials but, in general, it gives way in such situations to the *Quercus-Betula-Deschampsia* woodland where species such as *Deschampsia flexuosa*, *Vaccinium myrtillus* and calcifugous bryophytes become very important. Towards the north-west, these plants show an increasing tendency to move into all drier woodlands apart from those on freely-weathering limestones and they can make an occasional appearance in the *Acer-Oxalis* sub-community. Beyond the 1000 mm isohyet (*Climatological Atlas* 1952), which forms an effective limit to the *Quercus-Pteridium-Rubus* woodland, they become an important component of the *Quercus-Betula-Oxalis* woodland, its sub-montane analogue on moderately acid rocks and superficials.

Within these fairly wide limits, the *Quercus-Pteridium-Rubus* woodland is characteristic of soils with a superficial pH that is generally between 4 and 5.5 but which show a great variety of textures and of water and humus regimes. In the British lowlands, such profiles are widespread over many different deposits but this community is especially associated with argillaceous rocks and superficials. As mentioned above, it can be found on some sandstones and sands, but it is especially frequent on the Eocene London Clay north and south of the Thames and in Hampshire, on the Triassic Keuper Marl which crops out in Devon and forms very extensive parts of the Midlands and the Cheshire Vale, on Carboniferous Culm and Coal Measure shales, again in Devon, but particularly important in this community in the Pennine foothills, on Welsh Silurian shales and on long-weathered Granite in the South-West Peninsula and in south-west Scotland. Among superficial deposits, Clay-with-Flints forms a characteristic substrate over some of the southern Chalk (though here *Fagus-Rubus* woodland often replaces this community) and, in valleys on the upland fringes, this kind of woodland often marks out patches of glacial drift or head. It can occasionally be found on the drier alluvium of river terraces.

Among the more free-draining profiles derived from such parent materials, many approximate to the classic brown earth (Avery 1980: brown forest soil in the older

terminology). In some of these soils, mor accumulation can be quite marked and there may be some slight bleaching of sand grains in the A horizon, with a depression of surface pH down to 3.5, but podzolisation is typically no more than incipient. It is when the *Quercus-Pteridium-Rubus* woodland occurs in such situations that it makes its closest approach to the *Quercus-Betula-Deschampsia* woodland with an increase in *Betula pendula* and *Pteridium*. Stands of this kind occur quite commonly in the *Acer-Oxalis* sub-community to the north-west and, more locally, in the Typical sub-community in East Anglia and the Weald. Some locally dominant trees also seem to encourage the development of mor humus: *Castanea* is one, even oak and, of course, the coniferous replacements of the *Holcus* sub-community.

Generally, however, the most marked feature of these more free-draining soils is the mobilisation of clay minerals and very commonly here the B horizon shows a clearly argillic character. Where the clay fraction is not too dominant, the soil structure can be well developed with good incorporation of mull humus by an active soil fauna and brown earths of this type are quite frequent beneath the Typical, *Hedera* and *Holcus* sub-communities (except where conifers have been long established) and also in the *Acer-Oxalis* sub-community where, as is sometimes the case, it occurs on slopes with fairly free drainage.

However, very often here, there is so much clay in the profile that the soils are rendered impermeable to excess rain and seasonal surface-water gleying is very widespread beneath stands of the community, with the frequent characteristic signs of mottling above and sometimes manganese concretions below (e.g. Curtiss *et al.* 1976). This is true even to the south-east because, though rainfall there is considerably lower than to the north-west (less than 600 mm yr⁻¹ for the most part), the topography is typically flat or only gently undulating with little surface drainage. Frequently, then, the soils are stagnogleyic brown earths or true stagnogleys (though some clay-rich profiles would now be classed as pelosols: Avery 1980, Soil Survey 1983) and, on a national scale, there is a rather striking coincidence between the distribution of these profiles and that of the *Quercus-Pteridium-Rubus* woodland (e.g. Soil Survey 1974).

This tendency to surface-water gleying can be seen throughout the community and it probably plays a part in influencing the balance between some of the major species here. It is likely to be involved to some extent in controlling the proportions of the two oaks (Jones 1959), with *Q. robur* being more characteristic of the heavier soils, *Q. petraea* rising to prominence on the lighter, more freely drained (though not always drier) soils. And it is probably partly responsible for the variation in the amounts of *Hyacinthoides*, *Holcus mollis*

and *Pteridium* that is so characteristic a feature of the field layer in this kind of woodland. Most strikingly among the herbs, however, a pronounced tendency to winter and spring waterlogging is marked here, as in the *Fraxinus-Acer-Mercurialis* woodland, by a switch from *Hyacinthoides* to *Anemone* as the vernal dominant. This floristic transition, which seems to be based on a decreasing ability on the part of *Hyacinthoides* to maintain its competitive advantage against *Anemone* on the wettest soils, is a continuous one but the *Anemone* sub-community is very obviously associated with waterlogged plateaus and hollows over undulating topographies and becomes much commoner on the very heaviest substrates on which this community is found. It is particularly frequent, for example, on the sticky Eocene clays in Essex and Kent where many stands have been treated as hornbeam or chestnut coppice. It can also be found picking out areas of ground-water gleying as where this kind of woodland extends down on to small alluvial flats.

As in the *Fraxinus-Acer-Mercurialis* woodland, climate also plays a direct role in influencing the distribution and floristics of this community, as well as being involved in these edaphic relationships, and its effects here are similar, though not so sharply-defined. First, like its more calcicolous counterpart, the *Quercus-Pteridium-Rubus* woodland is confined to the warmer parts of Britain, where mean annual maximum temperatures are generally in excess of 26 °C (Conolly & Dahl 1970). In this community, though, a Continental/Southern element is not very prominent and only *Tilia cordata*, *Carpinus betulus*, *Sorbus torminalis*, *Crataegus laevigata*, *Euphorbia amygdaloides* and *Lamiastrum galeobdolon*, none of which is more than occasional throughout, serve to mark off the community from its analogue in the cooler uplands, the *Quercus-Betula-Oxalis* woodland. *Tilia*, though it tends to be a more extensive dominant in more southerly stands of the *Quercus-Pteridium-Rubus* woodland than in the *Fraxinus-Acer-Mercurialis* woodland, shows exactly the same complex pattern of reproductive behaviour here in relation to the progressively cooler summers as one moves north into the range of the *Acer-Oxalis* sub-community (Pigott & Huntley 1978, 1980, 1981).

The second more direct impact of climate is seen in the increasingly oceanic character of the community towards the west and north. Indeed, in comparison with similar woodlands throughout Europe (e.g. Noirfalise 1968, Neuhäusl 1977), the most distinctive feature of this woodland as a whole is the Atlantic aspect of its flora, with *Hyacinthoides* playing such a prominent role. But, in moving away from the south-east, other floristic elements reflect more clearly the shift to milder winters and a generally wetter climate. Increasingly to the south-west, for example, the *Hedera* sub-community replaces the Typical sub-community, even in longer-established

stands, where the abundance of an ivy carpet is not related to uninterrupted growth of underwood or canopy. *Ilex*, too, shows a slight increase throughout in more westerly stands of the community.

Much more obvious are the various characteristic features of the *Acer-Oxalis* sub-community where the *Quercus-Pteridium-Rubus* woodland extends on to base-poor soils in those parts of Britain with an annual rainfall approaching 800 mm or more (about 140 wet days yr⁻¹ or more: Ratcliffe 1968). Among the trees, *Acer pseudoplatanus* itself is the best marker of this shift, as in the *Fraxinus-Acer-Mercurialis* woodland, though its abundance here is not so consistently high, perhaps because of the tendency towards gleying in so many of the soils. But, where the profiles are free-draining and moist, it does supremely well. *Fraxinus* follows it in increasing its frequency in a marked transgression into less calcicolous woodlands noted by Tansley (1939), and *Ulmus glabra* shows a similar but smaller response.

Among the field layer species of the *Acer-Oxalis* sub-community, the marked increase in the frequency of *Oxalis acetosella* and, to a lesser extent, in *Viola riviniana*, are also probably a reflection of a more consistently moist soil surface than is usual among south-eastern *Quercus-Pteridium-Rubus* woodlands where even less free-draining soils can become severely droughted in summer (e.g. Packham 1975, 1978). Bryophytes, too, tend to be more extensive and lusher to the north-west and, marking the combination of fairly high soil moisture with surface acidity, there is a rise in the representation of *Dryopteris dilatata* and *Athyrium filix-femina*.

Variations in climate and soils set the basic framework of floristic variation within the community and influence the distribution of certain of the sub-communities but, as in the *Fraxinus-Acer-Mercurialis* woodland, silvicultural treatment has commonly influenced the physiognomy and composition of the vegetation here. Sometimes, such treatment has accentuated what are probably natural associations between certain trees and particular field layers, as with the selection for *Carpinus* and especially for *Castanea* on the moister soils of the *Anemone* sub-community. But often it has worked against natural patterns of variation, as with the reduction of *Q. robur* to occasional standards in many coppices or the favouring of this species as against *Q. petraea* in plantations on some lighter soils, or the introduction of exotic canopy dominants such as various conifers. In general terms, treatment has produced variation within the trees and shrubs that is not always consonant with differences in the field layer. Individual sub-communities can thus have a wide variety of underwood and canopy covers and different sub-communities exactly the same woody component.

The traditional treatment here has been coppicing with or without standards and, over more base-poor

lowland soils, the *Quercus-Pteridium-Rubus* woodland has been the major source of underwood and timber through historic times. Stands with obvious signs of coppicing are much more widespread and frequent to the south-east and here the Typical and *Anemone* sub-communities have been extensively cropped for hazel and mixed small underwood, for lime and hornbeam, occasionally for oak and, mostly in the *Anemone* sub-community, for chestnut. In many (though now fast-decreasing) woodlands in this region, tracts of these sub-communities survive as an irreplaceable record of past land use, often with archaeological features, like wood-banks and rides, marking out the coppice compartments (e.g. Rackham 1980, Peterken 1981). Almost universally now, such woodlands are not used in the traditional fashion. Many show a spread of birch with the neglect of cleaning after the last cuts and, where the underwood has remained undisturbed for a number of decades, there has often been a progression to the gloomy conditions that favour the development of the *Hedera* sub-community. To the north-west, evidence of coppicing is generally rarer but stands of the *Acer-Oxalis* sub-community can be seen converted to hazel or mixed coppice and also to sycamore coppice; there are even a few far-flung stands of lime coppice in this region.

With the neglect of coppicing, the distinctive post-coppice floras associated with this kind of woodland are now rarely seen but, where cutting continues, the general pattern of development is as in the *Fraxinus-Acer-Mercurialis* woodland (e.g. Salisbury 1916, 1918a, 1924, Rackham 1980). First, there is a spread of the more shade-tolerant herbs of the community, notably here *Silene dioica* and *Euphorbia amygdaloides*, and, in the second or sometimes third spring, a dramatic flush of flowering from *Hyacinthoides* and/or *Anemone*. Second, *Rubus* and *Pteridium* can show a marked increase, sometimes very early on and overwhelming these species. Then, more weedy plants can spread or appear anew, most commonly here *Epilobium angustifolium* and *Urtica*, Rumices and more calcifugous shrubs like *Cytisus scoparius* and *Ulex europaeus*, or even *Calluna vulgaris* on the most acid soils. Mixtures of these species present a rather different kind of flora to that characteristic of *Fraxinus-Acer-Mercurialis* coppices in their middle years though, as there, many of the adventives are eliminated as the new underwood growth closes over. But *Rubus* and, especially, *Pteridium* can compete with the springing shoots, especially where these are subject to the additional hindrance of heavy browsing and some bracken glades within stretches of these woodlands may have resulted from *Pteridium* gaining a firm hold after coppicing.

Many of the older coppiced stands of the *Quercus-Pteridium-Rubus* woodland have now been felled with a permanent loss in the extent of the community. How-

ever, plantation stands of this kind of woodland are quite widespread and, where these have a long-established canopy of hardwoods, usually here oak, sometimes with a little *Fraxinus* or *Fagus*, the full complement of the characteristic field-layer species can be present. Some older plantations of this kind are accommodated in the Typical and *Acer-Oxalis* sub-communities. Quite commonly, though, even hardwood plantations lack a good representation of *Hyacinthoides* and have the typically impoverished and untidy field layer of the *Holcus* sub-community. Many of these, of course, may be woodlands planted on previously open ground where there were no existing patches of *Hyacinthoides* to provide centres for subsequent migration. But, even where such plantations have been established on the site of clear-felled stands of the *Quercus-Pteridium-Rubus* woodland, *Hyacinthoides* may be eliminated or severely reduced by a combination of physical disturbance and a dense growth of, first, *Rubus* or *Pteridium* on the cleared ground or, second, the young trees. This certainly happens under conifers, such that *Hyacinthoides* can be completely suppressed by the second decade of their growth. Ornamentation with occasional softwoods is quite widespread in the community and, where the trees are not too densely spaced, the vegetation can retain the greater richness of the Typical or *Acer-Oxalis* sub-communities. But a dense canopy of conifers, with its heavy shade and accumulation of mor, excludes *Hyacinthoides* and alternations with oak may not allow time for re-invasion (Pigott 1984). Older softwood plantations, where there is more light, often have the *Holcus* sub-community and the development of this kind of *Quercus-Pteridium-Rubus* woodland may be very dependent on the opening up and disturbance that occurs with thinning. Fairly young and undisturbed woody covers here frequently show the *Hedera* sub-community and this may be the usual precursor to the *Holcus* sub-community under both softwood and hardwood replacement canopies.

The *Hedera* sub-community is characteristic, too, of young stands of this kind of woodland which have sprung up by natural invasion of open ground. With intensive agricultural pressure on many of the lowland clay areas, such sub-spontaneous tracts are not very common or extensive but they can be found quite widely in neglected field corners, old clay pits, on ungrazed commons and on waste ground. In such situations, the uniform or grouped age-classes of the trees and a prominent element of spinose shrubs can give a persistent clue as to the origin of the woodland.

Zonation and succession

Zonations between different kinds of *Quercus-Pteridium-Rubus* woodland and transitions to other woodland types are primarily related to edaphic variation.

Treatment differences produce effects of their own but they can also emphasise or confuse soil-related patterns. Marginal zonations sometimes represent successional changes but very often now agricultural use of the surrounding land produces artificially abrupt transitions to herbaceous vegetation.

By far the commonest kinds of edaphic zonations within stands of the community are related to differences in soil moisture, most frequently changes in the extent and frequency of surface-water gleying. Often these are related directly to variations in slope with the Typical or *Acer-Oxalis* sub-communities picking out areas with better surface drainage, often here on ground with only a very gentle slope, and the *Anemone* sub-community marking hollows and plateau tops. Similar patterns can be seen where ground-water gleying produces local areas of wetter soil along the sides of streams flowing through *Quercus-Pteridium-Rubus* woodland (as in the transect in Pigott 1982). Quite frequently, such zonations continue into some kind of alder woodland. Around slope flushes, for example, there is often a transition to the *Alnus-Fraxinus-Lysimachia* woodland. This may be quite gradual, with a progressive increase in herbs such as *Deschampsia cespitosa* or *Juncus effusus* and a slow switch to *Alnus*-dominance. In other cases, there is an abrupt appearance of *Carex remota* or *C. pendula* in sharply-defined patches. Both these kinds of zonation are very well seen along the base of the Lower Greensand in the Weald and on slopes cut into the Coal Measure shales of the Pennines. Where there is local peat accumulation in small river valleys, the *Quercus-Pteridium-Rubus* woodland may give way to small stands of the *Alnus-Carex* woodland, quite a common pattern in the Weald again and in some Essex woods (e.g. Rackham 1980, Wheeler 1980c). In other cases, it is the *Alnus-Urtica* woodland which terminates the sequence on alluvial flats, the appearance of *Urtica dioica* and *Galium aparine* marking the transition to more eutrophic soils.

The other very common kind of zonation to other woodland types is related to differences in the base status of the soils. Very often, sites in which the *Quercus-Pteridium-Rubus* woodland is represented cover geological transitions to bedrocks or superficiales which are either more or less calcareous. Where there is a switch to limestones, lime-rich shales or clays or to drift with more calcium carbonate, the community characteristically passes to the *Fraxinus-Acer-Mercurialis* woodland on more base-rich soils, usually brown earths, calcareous stagnogleys or pelosols, more rarely free-draining rendzinas. Sharp alternations of different bedrocks, especially typical here of the Cretaceous and Eocene sequences of the south-east, or abrupt differences in the nature of superficiales (as at Gamlingay: Adamson 1912), can be marked by equally well defined floristic zona-

tions, with an abrupt switch in dominance from *Pteridium* or *Holcus mollis* to *Mercurialis* and its calcicolous associates. In the south-east, such transitions generally involve a move from the Typical, *Anemone* or *Hedera* sub-community of the *Quercus-Pteridium-Rubus* woodland to the *Primula-Glechoma*, *Anemone* or *Hedera* sub-community of the *Fraxinus-Acer-Mercurialis* woodland respectively. To the north-west, the zonation is typically from the *Acer-Oxalis* sub-community of the former woodland to the *Geranium* sub-community of the latter. It should be remembered, though, that a number of important species occur in both these kinds of woodland and, where there is a continuation of a *Hyacinthoides* carpet, say, under a canopy of *Q. robur*, *Tilia*, *Carpinus* and *Corylus*, the boundary between the communities may be blurred. Such gradual transitions are especially characteristic of heavy superficial deposits in the south-east, where there may be diffuse variations in the calcium carbonate content of the parent material and a complex mosaic of brown earths or stagnogleys with small but critical differences in base-status.

Where the characteristic soils of the *Quercus-Pteridium-Rubus* woodland give way to strongly-leached brown earths, brown podzolic soils or podzols, the community is replaced by the *Quercus-Betula-Deschampsia* woodland. Typically, here, this kind of transition is related to a geological switch from shales or clays to some kind of arenaceous bedrock or sandy superficial deposit. Such patterns can be seen in the south-east in the Cretaceous sequences of the Weald and they are very common to the north and west where, in Carboniferous deposits, alternations of shales and grits form the basis of much of the scenery along the fringes of the Pennine uplands in Derbyshire, South and West Yorkshire and Durham. Here, the *Acer-Oxalis* sub-community characteristically occupies the much-weathered dips of cuestas and the lower slopes of the valley sides, with the *Quercus-Betula-Deschampsia* woodland clothing the more resistant grit scarps. Sharp transitions between these kinds of woodland are quite common and, though *Pteridium* continues through both with *Q. petraea* and *B. pendula* figuring in the canopy of each, the springtime boundary of *Hyacinthoides* and the restriction of *Fraxinus*, *A. pseudoplatanus* and *Corylus* to the *Quercus-Pteridium-Rubus* woodland generally serve to delimit the communities.

In some situations, though, the zonation is not so clear. On steeper slopes, slipping is quite common, with grit blocks tumbling down over the incompetent shales and then there can be a patchy inter-digitation of the two kinds of woodland along the slope foot. Even on more stable slopes, terracing is frequent and then every tread may be clothed with vegetation resembling the *Quercus-Pteridium-Rubus* field layer, every riser with *Quercus-Betula-Deschampsia* herbs (e.g. Woodhead 1906, Scur-

field 1953). When *Hyacinthoides* has faded from the patches of the former, such mosaics are typically marked by a patterning of *Holcus mollis* and *Deschampsia flexuosa* (Jowett & Scurfield 1949, 1952). *Holcus* seems to hold its own on the less sharply draining areas and also tends to hold the litter, the decay of which helps maintain the more mull-like qualities of the soils. Indeed, there is evidence that *Holcus* can invade the *Deschampsia* patches in these kinds of mosaic (Ovington 1953).

Particularly in the south-east, where the effects of traditional silviculture have persisted more extensively, coppicing treatments can confuse these soil-related transitions. Most obviously, where a uniform treatment has been applied across edaphic zonations, identical covers of underwood can continue over what are really the field layers of different communities. This is very common here across junctions between the *Quercus-Pteridium-Rubus* woodland and the *Fraxinus-Acer-Mercurialis* woodland, both of which have been widely cropped for hazel, lime and hornbeam. Under dense underwood, especially of the heavily-shading *Tilia*, herbs become very sparse so there may be only the very slightest indication of where one community ends and the other begins.

Even within sites made up wholly of *Quercus-Pteridium-Rubus* woodland, coppicing produces its own patterns of variation which are superimposed, often quite independently, over floristic differences related to, say, soil moisture. In actively-coppiced woodland, compartments marked out by varied and striking post-coppice herbaceous vegetation at different stages of development can thus provide an interruption to zonations between the Typical and *Anemone* sub-communities, or a cyclically changing patchwork of parcels within tracts of each. Treating a whole woodland in this way results in great spatial variation at any one time, though in any one section of a stand, the differences are essentially a temporal perturbation of an underlying floristic pattern related to natural variation in the soils. With neglect of coppicing, such edaphic transitions can become more obvious again, though after several decades of uninterrupted underwood growth the shape of old compartments can become marked on the ground once more by abrupt transitions to the *Hedera* sub-community with a dense woody cover. And many woodlands subject to intensive use in the past still preserve complex patterns of zonations between the *Quercus-Pteridium-Rubus* woodland and other vegetation types which reflect the structural organisation of the site. Commonest among these are the transitions in larger rides and glades which are here often picked out by stands of *Pteridium* or *Rubus-Holcus* underscrub, frequently now invaded by birch, *Crataegus monogyna* and *Prunus spinosa*.

External boundaries to stands of the community can

show similar zonations, though where the woodlands survive within intensive agricultural landscapes, there is generally only a very compressed fringe of *Crataegus* or *Prunus* scrub with *Rubus-Holcus* underscrub or, on more free-draining soils, a narrow strip of *Betula* and *Pteridium*, with an abrupt transition to pasture or arable.

In other situations, more extensive marginal transitions to herbaceous vegetation can be seen and these, together with young stands developing anew on railway verges (e.g. Sargent 1984) and on commons where grazing rights have fallen into disuse, can give some clues as to the seral development of the community. However, systematic studies of successions to the *Quercus-Pteridium-Rubus* woodland are very few (Salisbury 1918b, Adamson 1921, Tansley 1939), usually concerned with stands developing on abandoned arable land and set within a very broad understanding of what 'oak woodland' is or ought to be. The following observations are therefore very brief and generalised.

Within the lowlands, the natural limits to the development of the *Quercus-Pteridium-Rubus* woodland are set, for the most part, by the character of the soils such that the community is excluded from situations where the substrate is markedly base-rich, base-poor or very wet. Within this fairly broad compass, it probably approximates to the climax forest type, except within the natural range of *Fagus* which competes successfully with *Q. robur* for dominance over similar field layers to those characteristic here on all but the moister brown soils on which the *Quercus-Pteridium-Rubus* woodland can occur (e.g. Watt 1923, 1924, 1925, 1934a, b).

The natural herbaceous precursors to the community are probably very varied. Over the central type of brown earth, with free but not excessive drainage, less calcicolous types of the *Arrhenatheretum* are likely to figure prominently with, on more waterlogged mesotrophic soils, communities like the *Holco-Juncetum* and the *Holcus-Deschampsia* grassland. Towards the extreme of more strongly leached soils, this kind of woodland can probably supersede the less calcifuge types of *Festuca-Agrostis* grassland, though it is not usually a natural successor to ericaceous heath.

Where these types of vegetation are not regularly grazed, mown or burned, invasion by some of the characteristic shrubs and trees of the community can be very rapid. On moister soils, *Crataegus monogyna* and *Prunus spinosa*, *Rubus fruticosus* and *Rosa* spp. are frequent early colonisers, quickly thickening up to form a patchwork of scrub. In drier situations, *Betula pendula* becomes increasingly prominent in the early stages and it too may form dense thickets. In certain cases, this kind of young woodland can persist for some time: birch-dominated stands in particular seem to be more resistant

to further development than might be expected from the relatively short life of the individual trees (e.g. Rackham 1980).

But it is a very common feature of this type of succession that oak, especially *Q. robur*, invades very early. The present poor regeneration of this tree within closed woodlands is well known (e.g. Watt 1919, Jones 1959, Rackham 1980) and probably a fairly natural consequence of a number of factors, chiefly the neglect of coppicing which created a regular sequence of large well-lit gaps, and loss of seedlings to moth caterpillars and oak mildew (e.g. Jones 1959, Shaw 1974, Rackham 1980). In the open, however, young oaks can appear quickly and in profusion. Acorns are distributed much further from the parent tree than, for example, beech mast, being carried hundreds of metres by pigeons, corvids and squirrels (Jones 1959, Mellanby 1968) and they are readily able to germinate in closed swards, even if the shade cast by tall grasses, open bracken or nearby young shrubs is moderately dense (Jones 1959). Early growth may be slow but young oaks are very resilient and there seems little doubt that in many younger stands, *Q. robur* has played an important role from the outset.

We do not know how long it takes for *Quercus-Pteridium-Rubus* woodlands to acquire the richer field layers typical of the community. Young dense stands are often of the *Hedera* type, ivy carpets spreading even when the vegetation is in the scrub stage. And older stands derived from invasion may perhaps develop the character of the *Holcus* sub-community as the canopy opens and the woodland becomes more accessible to disturbance. But complete invasion by the more slow-spreading herbs probably takes centuries and, though *Carpinus* and *Castanea* may find a place in the developing woody cover in the south-east, the more diverse and complex mixtures of trees and shrubs characteristic of ancient stands are not found.

Distribution

The *Quercus-Pteridium-Rubus* woodland is widely distributed and common over the lowlands of England and Wales. It does extend into southern and eastern Scotland but, in the cooler and wetter upland fringes of the west and north, it is replaced by the *Quercus-Betula-Oxalis* woodland. The central types over the more south-easterly parts of the range are the Typical and *Anemone* sub-communities, the former more widespread, the latter more local, though particularly prominent on the heavy clays of the Weald and Essex. Towards the more oceanic south-west and especially in Devon and Cornwall, the *Hedera* sub-community becomes increasingly common, though this kind of woodland is quite widespread elsewhere in neglected

coppices and younger stands. The *Holcus* sub-community occurs throughout most of the range but has been most frequently recorded in plantations in the Weald, East Anglia and the Midlands. The *Acer-Oxalis* sub-community is confined to the upland margins of Wales, northern England and Scotland and represents a clear transition to the *Quercus-Betula-Oxalis* woodland.

Affinities

This community has long been recognised as one of the major kinds of woodland in lowland Britain but comparisons with early definitions are difficult because of the particular conceptions of 'oak woodland' which have long been current in the English descriptive tradition. In the first place, it has generally been the practice to make some kind of separation between different kinds of oak woodland according to whether *Q. robur* or *Q. petraea* was the dominant tree. Some schemes explicitly recognised that either or both could form a canopy over what was essentially the same kind of field layer, like Tansley's (1911) proposal for a *Quercetum arenosum roboris et sessiliflorae*. And, indeed, this fact was acknowledged in many accounts; but, generally, classifications have characterised a pair of communities, a *Quercetum roboris* and a *Quercetum sessiliflorae/petraeae* (e.g. Moss 1911, 1913; Tansley 1939), or equivalents in which other trees figured prominently, like the pair of oak-hornbeam woodlands described by Salisbury (1916, 1918a). Such communities were then diagnosed as having overlapping series of field-layer societies, many of which were shared, though some more consistently associated with the dominance of one or the other oak. A similar, though less exclusive division on the basis of *Quercus* spp. characterises the much more recent scheme of Peterken (1981) within his birch-oak woodlands proper and in his lime and hornbeam woods.

Among British woodlands, there certainly is a pattern in the distribution of the two oaks in relation to climate and soil but it is quite a complex pattern, even when the more obvious effects of silvicultural preferences are excluded, and it is not entirely consistent as one moves from calcicolous woodlands, through those of more neutral soils, to the most calcifuge. In this community, typical of soils of moderate to low pH and often with impeded drainage, the predominant oak is *Q. robur*, but *Q. petraea* is locally important to the south-east and becomes much more prominent to the wetter and cooler north-west. Overall, there is no justification for making a precise split within the community according to which oak is the dominant. Thus, although the *Quercus-Pteridium-Rubus* woodland approximates to the older *Quercetum roboris*, and to the pedunculate oak stand types in Peterken's (1981) scheme, the correspondence is not exact.

The second difficulty is that, in early accounts, oak-wood of the *Quercetum roboris* type was a very broadly defined amalgam of virtually all woodlands in which *Q. robur* was a frequent canopy component. It therefore often took in more calcicolous vegetation which is here considered part of the *Fraxinus-Acer-Mercurialis* woodland, where *Q. robur* is certainly common (*Q. petraea*, too, to the north-west) but which can hardly be described as oak woodlands. The *Quercus-Pteridium-Rubus* woodland does grade floristically into the *Fraxinus-Acer-Mercurialis* woodland, especially in its woody component, but the two communities are really quite distinct. In vernacular terms, the former comprise 'blue-bell woods', the latter 'mercury woods'.

The schemes of Rackham (1980) and Peterken (1981) also split off from the older *Quercetum roboris* more calcicolous woodlands like those separated here into the *Fraxinus-Acer-Mercurialis* woodland. But comparisons between what remains and the *Quercus-Pteridium-Rubus* woodland are difficult because of the concentration by these two authors on the woody component of the vegetation. Peterken (1981) does have a birch-oak woodland which corresponds in part with this community; Rackham (1980) does not and most of what he calls oak woodland would fit in this scheme into the *Quercus-Betula-Deschampsia* community. But in the classifications of both these workers, many of the kinds of woodland included here are placed in separate commu-

nities defined by the dominance of lime, hornbeam, chestnut or hazel. The approach in this scheme is to regard such stands as treatment-derived variants of sub-communities related primarily to differences in climate and soils.

Retaining such stands within the general ambit of the *Quercus-Pteridium-Rubus* woodland helps to integrate the community within a European framework. The presence of *Tilia* and *Carpinus* is especially important in this respect because both these trees are prominent components of this kind of woodland right across Northern Europe into the USSR (Neuhäusl 1977). What is especially distinctive about the British stands, like those of north-west France and southern Belgium is the presence of *Hyacinthoides* as the characteristic vernal dominant (Noirfalise 1968, Neuhäusl 1977). This community is thus a clear equivalent of woodlands like the *Querceto-Carpinetum* (Lemée 1937, Dethioux 1955), the *Quercetum atlanticum* (LeBrun *et al.* 1949) and the *Endymio-Carpinetum* (Noirfalise & Sougnez 1963, Noirfalise 1968, 1969) described from these areas and includes all our Carpinion woodlands on less calcareous soils. The north-western limit of this kind of woodland in Britain is mapped by Noirfalise (1969) and Neuhäusl (1977) at the supposed natural limit of *Carpinus* itself, but there is no strong reason to exclude lowland 'blue-bell woods' which lie beyond this line.

Floristic table W10

	a	b	c	d	e	10
<i>Quercus robur</i>	III (2–10)	IV (3–10)	IV (2–10)	IV (1–10)	II (1–8)	IV (1–10)
<i>Betula pendula</i>	III (2–9)	III (2–8)	I (1–8)	III (1–10)	I (1–8)	II (1–10)
<i>Fagus sylvatica</i>	I (1–10)	I (3)	II (1–10)	I (3–5)	I (1–6)	I (1–10)
<i>Sorbus aucuparia</i>	I (1–5)	I (3)	I (1–4)	I (3–5)	I (1–5)	I (1–5)
<i>Ilex aquifolium</i>	I (1–5)	I (2–7)	I (1–4)	I (2–6)	I (1–4)	I (1–7)
<i>Alnus glutinosa</i>	I (1–5)	I (4)	I (4–7)	I (9)	I (3–6)	I (1–9)
<i>Prunus avium</i>	I (3)	I (3–5)	I (2–3)	I (1–4)	I (2–4)	I (1–5)
<i>Betula pubescens</i>	I (4–7)	I (4–7)	I (2–9)	I (4–8)	I (1–7)	I (1–9)
<i>Taxus baccata</i>	I (1–5)	I (1–3)	I (2–6)	I (9)		I (1–9)
<i>Tilia vulgaris</i>	I (3–7)			I (3–4)	I (4)	I (3–7)
<i>Carpinus betulus</i>	I (1–9)	I (4–9)	I (3)			I (1–9)
<i>Tilia cordata</i>	I (2–5)	I (2–5)	I (1–4)			I (1–5)
<i>Populus tremula</i>	I (1–4)	I (1–4)		I (4)		I (1–4)
<i>Quercus petraea</i>	III (3–10)		I (3)	I (3–9)	II (3–9)	II (3–10)
<i>Castanea sativa</i>	I (1–5)	III (3–10)	I (3–7)	I (3–5)	I (2–4)	I (1–10)
<i>Pinus sylvestris</i>	II (3–4)	I (4)	I (3–4)	II (2–10)	I (1–10)	I (1–10)
<i>Pinus nigra</i> var. <i>maritima</i>				II (6–10)		I (6–10)
<i>Pseudotsuga menziesii</i>				II (6–10)		I (6–10)
<i>Larix</i> spp.				I (6–10)	I (1–8)	I (1–10)
<i>Acer pseudoplatanus</i>	II (1–9)	I (5)	I (5–8)	I (3–9)	III (1–7)	II (1–9)
<i>Fraxinus excelsior</i>	I (1–6)	II (2–7)	II (1–7)	I (1–6)	III (1–8)	II (1–8)
<i>Quercus</i> hybrids	I (1–8)				II (1–10)	I (1–10)
<i>Ulmus glabra</i>					II (1–7)	I (1–7)
<i>Corylus avellana</i>	III (1–9)	III (2–9)	IV (1–10)	I (3–7)	III (1–9)	III (1–10)
<i>Crataegus monogyna</i>	II (1–6)	I (3–7)	II (1–5)	I (4–6)	II (1–5)	II (1–7)
<i>Ilex aquifolium</i>	II (1–6)	I (2)	II (2–9)	I (3–7)	II (1–6)	II (1–9)
<i>Viburnum lantana</i>	I (2)	I (2–3)	I (3–4)	I (4)		I (2–4)
<i>Carpinus betulus</i> sapling	I (8)	I (3–5)	I (2–4)			I (2–8)
<i>Viburnum opulus</i>	I (1–4)	I (2–3)	I (1–3)			I (1–4)
<i>Crataegus laevigata</i>	I (3)	I (4)	I (2–3)			I (2–4)

Floristic table W10 (cont.)

	a	b	c	d	e	10
<i>Fagus sylvatica</i> sapling	II (1–5)		I (2–4)	I (1–8)	I (1–8)	I (1–8)
<i>Rhododendron ponticum</i>	I (1–8)		I (1–5)	I (2–5)	I (1–5)	I (1–8)
<i>Sorbus aucuparia</i>	I (1–4)		I (3–5)	I (3)	I (1–5)	I (1–5)
<i>Betula pendula</i> sapling	I (2–3)		I (3–4)	I (3–7)	I (1–5)	I (1–7)
<i>Betula pubescens</i> sapling	I (2–4)		I (2–6)	I (6)	I (1–4)	I (1–6)
<i>Malus sylvestris</i>	I (1–2)		I (2)		I (1)	I (1–2)
<i>Prunus spinosa</i>	I (1–3)		I (1–7)	I (4–5)		I (1–7)
<i>Quercus robur</i> sapling	I (2–3)		I (1–5)	I (1–4)		I (1–5)
<i>Acer campestre</i>	I (1–3)		I (2–4)			I (1–4)
<i>Quercus petraea</i> sapling	I (2–4)			I (4)	I (1)	I (1–4)
<i>Quercus hybrids</i> sapling	I (1–3)				I (1–4)	I (1–4)
<i>Castanea sativa</i>	I (1–3)	II (3–9)	I (1–3)	I (2–5)		I (1–9)
<i>Acer pseudoplatanus</i> sapling	II (1–7)	I (2–4)	I (1–5)	I (3)	II (2–5)	I (1–7)
<i>Fraxinus excelsior</i> sapling	I (1–5)	I (3)	I (1–4)	I (4)	II (1–6)	I (1–6)
<i>Sambucus nigra</i>	I (2–3)	I (2–3)	I (1–7)	I (3)	II (1–5)	I (1–7)
<i>Ulmus glabra</i> sapling					I (1–6)	I (1–6)
<i>Rubus fruticosus</i> agg.	V (3–10)	IV (2–9)	V (1–10)	IV (1–10)	III (1–8)	IV (1–10)
<i>Pteridium aquilinum</i>	IV (1–9)	III (2–7)	IV (1–10)	V (1–10)	III (1–8)	IV (1–10)
<i>Lonicera periclymenum</i>	III (2–8)	IV (3–7)	V (1–8)	III (1–7)	II (1–8)	IV (1–8)
<i>Anemone nemorosa</i>	I (1–2)	IV (3–8)	I (3–8)		I (1–6)	I (1–8)
<i>Atrichum undulatum</i>	I (1–4)	II (2–7)	I (2–4)	I (2)	I (1–4)	I (1–7)
<i>Lamium galeobdolon</i>	I (1–5)	II (2–5)	I (1–5)			I (1–5)
<i>Hedera helix</i>	II (2)	II (2–8)	IV (2–10)	I (2–4)	I (2–7)	II (2–10)
<i>Galium odoratum</i>			I (2–3)		I (1)	I (1–3)
<i>Geranium robertianum</i>			I (2–4)		I (1–5)	I (1–5)
<i>Holcus lanatus</i>	I (1–6)	II (3–9)	I (1–7)	IV (1–8)	I (1)	I (1–9)
<i>Dactylis glomerata</i>				I (3–4)	I (1–3)	I (1–4)
<i>Senecio jacobaea</i>				I (1–3)		I (1–3)

<i>Oxalis acetosella</i>	I (1–4)	I (2–3)	I (2)	I (2)	IV (1–9)	II (1–9)
<i>Holcus mollis</i>	II (1–10)	I (2–8)	II (2–10)	I (3–9)	IV (1–9)	II (1–10)
<i>Dryopteris dilatata</i>	II (1–7)	I (2–5)	II (1–6)	I (1–5)	III (1–8)	II (1–8)
<i>Eurhynchium praelongum</i>	II (1–7)	II (3–5)	I (1–6)	I (2–7)	III (1–8)	II (1–8)
<i>Mnium hornum</i>	II (1–5)	II (1–6)	I (1–5)	I (3–5)	III (1–9)	II (1–9)
<i>Viola riviniana</i>	I (1–3)	I (2)	I (1–3)	I (3–4)	II (1–4)	I (1–4)
<i>Thuidium tamariscinum</i>	I (1–8)	I (5)	I (2–7)	I (3)	II (1–5)	I (1–8)
<i>Stellaria holostea</i>	I (1–5)	I (2–4)	I (1–5)	I (3–4)	II (1–6)	I (1–6)
<i>Deschampsia cespitosa</i>	I (1–4)	I (2–4)	I (1–6)	I (1–8)	II (1–9)	I (1–9)
<i>Brachythecium rutabulum</i>	I (1–3)	I (3–5)	I (2–5)	I (3)	II (1–3)	I (1–5)
<i>Plagiothecium undulatum</i>	I (2)	I (3)	I (2–4)	I (2–3)	II (1–6)	I (1–6)
<i>Isopterygium elegans</i>	I (2–4)		I (4)	I (3–4)	II (1–4)	I (1–4)
<i>Pseudoscleropodium purum</i>	I (1)		I (1–8)	I (4)	II (1–5)	I (1–8)
<i>Athyrium filix-femina</i>	I (1–4)		I (2–4)		II (1–7)	I (1–7)
<i>Eurhynchium striatum</i>					I (1–5)	I (1–5)
<i>Thelypteris limbosperma</i>					I (1–5)	I (1–5)
<hr/>						
<i>Hyacinthoides non-scripta</i>	III (3–9)	IV (4–10)	II (1–10)	I (1–7)	III (1–9)	III (1–10)
<i>Acer pseudoplatanus</i> seedling	II (1–9)	I (3)	I (1–2)	I (1)	II (1–2)	II (1–9)
<i>Dryopteris filix-mas</i>	II (1–5)	I (2–6)	II (1–7)	I (1–8)	II (1–6)	II (1–8)
<i>Epilobium angustifolium</i>	I (1–6)	I (2–4)	I (1–4)	I (2–4)	I (1–3)	I (1–6)
<i>Conopodium majus</i>	I (1–4)	I (2–3)	I (2–4)	I (2–5)	I (1–3)	I (1–5)
<i>Poa trivialis</i>	I (1–5)	I (2–3)	I (1–4)	I (1–5)	I (1–7)	I (1–7)
<i>Luzula pilosa</i>	I (2–3)	I (4)	I (1–5)	I (4)	I (1–4)	I (1–5)
<i>Luzula sylvatica</i>	I (1–7)	I (2–4)	I (2–8)	I (2–4)	I (1–9)	I (1–9)
<i>Rumex acetosa</i>	I (4)	I (3)	I (3)	I (4–5)	I (1–4)	I (1–5)
<i>Silene dioica</i>	I (3)	I (3)	I (2–3)	I (1–6)	I (1–5)	I (1–6)
<i>Melica uniflora</i>	I (2–5)	I (2–5)	I (3–6)	I (3)	I (1–5)	I (1–6)
<i>Fraxinus excelsior</i> seedling	I (1–3)	I (3)	I (1–3)	I (3)	I (1–2)	I (1–3)
<i>Stellaria media</i>	I (3–4)	I (3)	I (2–3)	I (3–4)	I (3)	I (2–4)
<i>Teucrium scorodonia</i>	I (1–5)	I (2)	I (1–6)	I (2–6)	I (1–3)	I (1–6)
<i>Urtica dioica</i>	I (1–2)	I (4)	I (2–5)	I (2–3)	I (1–9)	I (1–9)
<i>Crataegus monogyna</i> seedling	I (1–3)	I (2)	I (1–3)	I (2–3)	I (1)	I (1–3)
<i>Dicranella heteromalla</i>	I (1–4)	I (2–3)	I (1–4)	I (1–3)	I (1–4)	I (1–4)

Floristic table W10 (cont.)

	a	b
<i>Hypnum cupressiforme</i>	I (1–4)	I (2–3)
<i>Carex sylvatica</i>	I (1–2)	I (2)
<i>Euphorbia amygdaloides</i>	I (3)	I (2–4)
<i>Heracleum sphondylium</i>	I (2–3)	I (2)
<i>Glechoma hederacea</i>	I (2–3)	I (2–3)
<i>Melampyrum pratense</i>	I (2–4)	I (4)
<i>Blechnum spicant</i>	I (5)	I (4)
<i>Rumex sanguineus</i>	I (3)	I (2–4)
<i>Solidago virgaurea</i>	I (2–5)	I (2)
<i>Quercus robur</i> seedling	I (3–4)	I (3)
<i>Sanicula europaea</i>	I (1–4)	I (2–3)
<i>Poa nemoralis</i>	I (2)	I (2)
<i>Milium effusum</i>	I (1–4)	I (3–8)
<i>Ligustrum vulgare</i>	I (2)	I (3)
<i>Circaea lutetiana</i>	I (1–4)	I (2)
<i>Ajuga reptans</i>	I (1–3)	I (2)
<i>Stachys sylvatica</i>		I (3–4)
<i>Veronica chamaedrys</i>	I (2–4)	I (2)
<i>Lysimachia nemorum</i>	I (1–3)	I (3)
<i>Amblystegium serpens</i>	I (3)	I (3–5)
<i>Agrostis capillaris</i>	I (1–9)	
<i>Anthoxanthum odoratum</i>	I (1–2)	
<i>Brachypodium sylvaticum</i>	I (2–4)	
<i>Deschampsia flexuosa</i>	I (1–5)	
<i>Digitalis purpurea</i>	I (1–3)	
<i>Galium saxatile</i>	I (2–3)	
<i>Juncus effusus</i>	I (2)	
<i>Betula pendula</i> seedling	I (2)	
<i>Vaccinium myrtillus</i>	I (2–5)	
<i>Rubus idaeus</i>	I (3)	
<i>Rosa canina</i> agg.	I (2–3)	
<i>Sorbus aucuparia</i> seedling	I (1–2)	
<i>Lophocolea bidentata</i> s.l.	I (1–3)	

c	d	e	10
I (1-3)	I (3-4)	I (1-3)	I (1-4)
I (1-3)		I (1)	I (1-3)
I (3)	I (3)		I (2-4)
I (1-3)	I (1-3)		I (1-3)
I (4)	I (3-6)		I (2-6)
I (3-5)	I (3-4)		I (2-5)
I (2-7)	I (2-3)		I (2-7)
I (2-3)	I (2-3)		I (2-4)
I (1-3)	I (2-3)		I (1-5)
I (1-3)	I (1-3)		I (1-4)
I (3)		I (2-3)	I (1-4)
I (2-7)		I (1-3)	I (1-7)
I (3)		I (1)	I (1-8)
I (2-4)		I (3)	I (2-4)
I (2-4)		I (1-2)	I (1-4)
I (1-2)		I (1-2)	I (1-3)
I (1-5)	I (2)	I (1)	I (1-5)
	I (3)	I (1)	I (1-4)
	I (2)	I (1-3)	I (1-3)
	I (3)		I (1-5)
I (1)	I (3-8)	I (1-7)	I (1-9)
I (3)	I (2-4)	I (1-5)	I (1-5)
I (2-4)	I (2-3)	I (1-4)	I (1-4)
I (3-6)	I (2-6)	I (1-9)	I (1-9)
I (1-3)	I (1-4)	I (1-6)	I (1-6)
I (3)	I (2-5)	I (1-7)	I (1-7)
I (3)	I (3-4)	I (2-4)	I (2-4)
I (1)	I (2)	I (1-3)	I (1-3)
I (5)	I (3-4)	I (1-2)	I (1-5)
I (2-3)	I (4-5)	I (1-4)	I (1-5)
I (1-6)	I (3-4)	I (1-2)	I (1-6)
I (2-3)	I (1-3)	I (1-2)	I (1-3)
I (2-3)	I (1-4)	I (1-4)	I (1-4)

<i>Plagiothecium denticulatum</i>	I (1–3)	
<i>Fagus sylvatica</i> seedling	I (1–4)	
<i>Isothecium myosuroides</i>	I (1–3)	
<i>Ilex aquifolium</i> seedling	I (1–4)	
<i>Polytrichum formosum</i>	I (1–4)	
<i>Cytisus scoparius</i>	I (1)	
<i>Ranunculus ficaria</i>	I (3)	I (3)
<i>Pellia epiphylla</i>	I (2)	I (4)
<i>Plagiomnium undulatum</i>	I (3)	I (5)
<i>Plagiomnium rostratum</i>	I (1)	I (3)
<i>Bromus ramosus</i>	I (3)	I (3)
<i>Fragaria vesca</i>		I (3)
<i>Potentilla sterilis</i>		I (2–3)
<i>Ranunculus repens</i>		I (3)
<i>Mercurialis perennis</i>	I (2–4)	
<i>Primula vulgaris</i>	I (3–4)	
<i>Dryopteris borreieri</i>	I (3)	
<i>Galium aparine</i>	I (2)	
<i>Dicranum scoparium</i>	I (3)	
<i>Ulex europaeus</i>	I (3)	
<i>Luzula multiflora</i>		
<i>Lysimachia nummularia</i>	I (2–3)	I (2)
<i>Dicranoweissia cirrata</i>	I (2)	I (2–3)
<i>Ceratodon purpureus</i>	I (4)	I (3)
<i>Prunella vulgaris</i>	I (3)	I (3)
<i>Aegopodium podagraria</i>		I (3)
<i>Anthriscus sylvestris</i>		I (2)
<i>Acer campestre</i> seedling		I (3)
<i>Narcissus pseudonarcissus</i>		I (3)
<i>Arrhenatherum elatius</i>		
<i>Corydalis claviculata</i>		
<i>Festuca ovina</i>		
Number of samples	51	22
Number of species/sample	18 (7–35)	13 (1–31)

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

77	150	79	379
16 (7-23)	10 (1-27)	24 (11-39)	15 (1-39)

Floristic table W10 (*cont.*)

	a	b
Tree height (m)	17 (5–25)	12 (8–20)
Tree cover (%)	89 (40–100)	88 (2–100)
Shrub height (m)	4 (1–8)	5 (1–10)
Shrub cover (%)	24 (0–90)	19 (0–95)
Herb height (cm)	51 (15–100)	33 (15–60)
Herb cover (%)	81 (20–100)	69 (1–100)
Ground height (mm)	15 (10–30)	13 (10–20)
Ground cover (%)	6 (0–60)	6 (0–40)
Altitude (m)	120 (10–250)	89 (16–190)
Slope (°)	7 (0–60)	1 (0–15)

a Typical sub-community

b *Anemone nemorosa* sub-community

c *Hedera helix* sub-community

d *Holcus lanatus* sub-community

e *Acer pseudoplatanus*-*Oxalis acetosella* sub-community

10 *Quercus robur*-*Pteridium aquilinum*-*Rubus fruticosus* woodland (total)

c	d	e	10
18 (8–32)	13 (2–30)	18 (6–30)	16 (2–32)
89 (60–100)	84 (0–100)	77 (20–100)	84 (0–100)
4 (1–8)	3 (1–8)	4 (1–10)	4 (1–10)
39 (0–100)	12 (0–100)	17 (0–85)	21 (0–100)
57 (1–130)	66 (10–200)	46 (5–150)	56 (1–200)
88 (20–100)	77 (1–100)	83 (1–100)	81 (1–100)
11 (10–20)	21 (10–50)	18 (5–30)	17 (5–50)
9 (0–100)	7 (0–80)	14 (0–90)	9 (0–100)
102 (8–270)	95 (4–250)	110 (9–282)	102 (4–282)
2 (0–30)	1 (0–30)	17 (0–45)	5 (0–60)



