W14
Fagus sylvatica-Rubus fruticosus woodland

Synonymy

Beechwood association Moss *et al.* 1910 *p.p.*; *Fagetum sylvaticae* plateau beechwoods Adamson 1922 *p.p.*; Beech associes, seres 1 & 2 Watt 1924; Chalk plateau beechwoods (b) Watt & Tansley 1930; Beech associes, seres A *p.p.* & B Watt 1934*b*; Beech consociation, seres 1 & 2 Watt 1934*b*; Beech consociation, seres A *p.p.* & B Watt 1934*b*; *Fagetum rubosum* Tansley 1939 *p.p.*; Beech-Oak-Ash Association, types 3 & 7 McNeill 1961; Beech-oak-holly woods Peterken & Tubbs 1965 *p.p.*; Cotswold beechwoods Barkham & Norris 1967 *p.p.*; Beechwood Rackham 1980 *p.p.*; Beech stand type 8D Peterken 1981; Woodland plot types 17 & 20 Bunce 1982.

Constant species

Fagus sylvatica, Ilex aquifolium, Rubus fruticosus agg.

Rare species

Epipactis purpurata.

Physiognomy

The *Fagus sylvatica-Rubus fruticosus* woodland is a floristically simple community organised on a very large scale. Typically, in mature stands, the canopy is overwhelmingly dominated by *Fagus sylvatica* which forms a closed, even-topped cover of trees that can attain a magnificent stature. It is in this community that beech makes its best general height growth in Britain with individuals commonly attaining 30 m or more and yielding timber of the top-quality classes (e.g. Watt 1934*b*, Brown 1953, McNeill 1961). Where the trees are well spaced, tall and unbranched below, they give the canopy an architectural quality, creating the impression of a vast, spacious vault. Even here, however, growth is frequently not so good as this, varying considerably, even on the most favourable soils, with exposure, and becoming distinctly poorer where edaphic conditions are not so congenial (Watt 1934*b*, Brown 1953, 1964). Moreover, stands often have a greater measure of

structural complexity related to patterns of natural invasion or treatment or both. In younger, sub-spontaneous woodlands of this kind, the height and density of the beech can be much less uniform, and it is sometimes possible to distinguish older, more richly branched pioneers that led the colonisation of open ground from subsequent generations of straighter, more crowded trees that followed (Watt 1924, 1934*b*). Even in more long-established stands, grouped age-classes and physiognomic variation may give some clues to the history of the vegetation, as Peterken & Tubbs (1965) demonstrated in the New Forest (see also Tubbs 1968). Many tracts of the community show signs of treatment. Some have obviously been planted, with regularly-disposed, morphologically-similar and even-aged trees giving the canopy great structural uniformity. Others, especially in the Chilterns where the *Fagus-Rubus* woodland is common, have been managed on a selection system which produced no clear segregation of age-classes but which has often left a legacy of smaller, less well grown trees with removal of the best timber (Brown 1953, 1964, Peterken 1981). Coppiced *Fagus-Rubus* woodland is very rare, though beech seems to have been extensively cut as underwood in medieval and later times (Mansfield 1952, Roden 1968), and some stands may have developed by overgrowth of coppiced *Quercus-Pteridium-Rubus* woodland (e.g. Adamson 1921). Pollarding of beech, on the other hand, is quite commonly seen here: it is a striking feature of older stands in the New Forest, where the practice was forbidden by statute in 1698 (Peterken & Tubbs 1965, Tubbs 1968), and can be seen in Burnham Beeches in Buckinghamshire.

The most characteristic associate of *Fagus* in this community is oak, almost invariably *Q. robur*, very locally on lighter soils *Q. petraea*. *Q. robur* grows well here, maintaining itself at the same height as *Fagus* even in the tallest canopies and sometimes exceeding it where soil conditions are somewhat less favourable for *Fagus* (Watt 1934*b*). Generally speaking, it is only occasional in mature canopies but it can become more frequent and

locally co-dominant in transitions to the *Quercus-Pteridium-Rubus* woodland. In some places, as in the New Forest, mosaics of these two communities are common (Peterken & Tubbs 1965, Tubbs 1968): their edaphic requirements overlap extensively and, in younger woodlands, oak may have an invasive advantage and, in larger gaps, a regenerative edge, over *Fagus* so that stands resembling *Quercus-Pteridium-Rubus* woodland become prominent for some time before beech exerts its final dominance (e.g. Watt 1924, 1934*b*). Transitional stands with a greater proportion of *Q. robur* are also characteristic of zonations to soils which show more consistent gleying, where this oak is better able than *Fagus* to maintain itself as a permanent dominant: this is well seen on the sequence of soils on the Chiltern plateau (Avery 1958, 1964). In some older stands of the *Fagus-Rubus* woodland in the New Forest, oak, like the beech, has been pollarded (Peterken & Tubbs 1965, Tubbs 1968).

Other tree species of the main canopy tier are scarce. Birch (usually *Betula pendula* though sometimes *B. pubescens*) is generally the first and most common coloniser of gaps and individuals can persist for 70–80 years in intact canopies though they are rare. *Fraxinus excelsior* and *Acer pseudoplatanus* can also be found very occasionally maintaining themselves at the same height as *Fagus*, sometimes as survivors of a pre-existing woodland cover that beech has invaded (e.g. Watt 1924, 1934*a*), more often as remnants of regeneration cores in gaps, which they are both eminently successful at colonising if seed-parents are close. But neither of these is as common here as in the more calcicolous *Fagus-Mercurialis* woodland or the oak-dominated *Quercus-Pteridium-Rubus* woodland and, in some New Forest stands, their presence may originate from trees planted as ornamentals (Peterken & Tubbs 1965, Tubbs 1968).

Prunus avium can sometimes be found: it was locally abundant in Watt's (1934*b*) Chiltern stands and can be a conspicuous feature when in full flower before the beech comes into leaf. *Sorbus aria* can also occur but it is not so characteristic here as in the *Fagus-Mercurialis* woodland. *Pinus sylvestris* may be locally prominent: it is quite common in younger stands in the New Forest having seeded in from extensive nearby plantations, and sometimes colonises gaps.

Very characteristically here, there is no understorey of shrubs but a second tier of trees beneath the beech canopy, the most frequent and distinctive species being *Ilex aquifolium*. Generally speaking, this is also the most abundant woody associate of beech and oak in this community, though its cover is very variable. In more oceanic areas, like Sussex and the New Forest, it is especially prominent, sometimes forming a dense layer of trees and occasionally being a local dominant in scrubby enclaves or isolated stands which may or may not have emergent trees, as in the holms (or 'hats') of the New Forest (Peterken & Tubbs 1965, Peterken & Newbould 1966, Tubbs 1968). In Chiltern stands, by contrast, *Ilex* is much sparser, though it usually remains the numerically most frequent of the smaller woody species of the community (Watt 1934*b*, Tansley 1939). Although well able to tolerate the dense shade of the *Fagus* canopy (Peterken 1965, 1966, Peterken & Lloyd 1967), *Ilex* is, however, very susceptible to browsing and this often affects its cover and the height of the trees in open woodlands and is probably a major factor in hindering regeneration, especially where light approaches critically low levels (Peterken 1966). Hollies here can be reduced to a low, procumbent underscrub or occur as conical bushes, sometimes with an apical tuft of inaccessible growth; and though larger trees can reach 5–8 m, their lower branches may be nibbled away to form a clean, horizontal browse line. Where grazing and shade are both heavy, *Ilex* can be largely limited to gaps and margins. Older hollies in the New Forest have often been pollarded, apparently repeatedly in some cases (Peterken & Tubbs 1965, Tubbs 1968).

Occasionally in the New Forest and sometimes in Surrey and Sussex, much more rarely in the Chilterns, there is also some *Taxus baccata*, scattered among the *Ilex* and usually taller, except in dense young holms. *Sorbus aucuparia* occurs occasionally, too, and there may be a very little *Crataegus monogyna*, *Sambucus nigra*, *Corylus avellana*, *Ligustrum vulgare* or *Salix caprea*, and spindly, overtopped specimens of *Fraxinus* or *Acer pseudoplatanus*. Younger saplings are never abundant except in gaps. Those of *Fagus* are the most frequent throughout and some can usually be found even under intact canopies, as scattered individuals making slow growth, but their prominence varies ultimately with masting and is much affected by the predations of grey squirrel, mice and woodpigeons on the seed and whether the young saplings have been able to penetrate the underscrub of *Rubus* (Watt 1923, 1925, 1934*b*). Where creation of gaps coincides with good mast years, *Fagus* saplings can be very prominent beneath the parent trees around the edge of gaps (Watt 1924), though the cores are generally filled by young *B. pendula*, *Fraxinus* and *A. pseudoplatanus*, with occasional *Q. robur* in larger openings, forming a dense thicket which can retain its distinctive composition for many years and from which any of these associated trees may promote themselves to the canopy.

In younger stands of the *Fagus-Rubus* woodland (which, in Sussex, Watt (1924) considered could include tracts up to 80 years or so), the ground beneath the densely-crowded beech can be totally bare and, even where the canopy has begun to open up somewhat, the field layer is often very sparse with extensive areas of beech litter and nothing else. But the most characteristic

plant in well-established *Fagus-Rubus* woodland is *Rubus fruticosus* agg. Where the shade is less intense, brambles can come to form a virtually continuous cover up to 1 m or more in height, impassable to the human visitor and, having some evergreen shoots, of very great significance to the prominence of potential herbaceous companions and the regeneration of the trees, a role which Watt (1934*b*) characterised as mischievous in its frustration of the expression of the associated flora here.

Essentially, the *Fagus-Rubus* woodland is the beech-dominated counterpart of the south-eastern *Quercus-Pteridium-Rubus* 'bluebell woodland' but because *Rubus* deepens the shade of the beech canopy even further, many of the typical species of that community are very poorly represented here. *Hyacinthoides non-scripta* itself, for example, is very infrequent, even in longer-established stands where it has had ample time to migrate in, often being confined to more open margins: typically, therefore, this community has no marked vernal aspect. The other two components of the under-scrub trio, *Pteridium aquilinum* and *Lonicera periclymenum* are quite frequent, but generally not abundant, though they can increase locally and temporarily in gaps; but, in so far as they gain higher covers, they further reduce the light reaching the ground by mid-summer. Against this kind of competition, even *Hedera helix* seems to suffer: it is not common here and, even in more oceanic areas, does not often form an extensive carpet so typical of more south-westerly *Quercus-Pteridium-Rubus* woodlands, though deer-grazing may also play some part in reducing its cover in unenclosed stands.

The general effect of this intense shade on the remaining species of the community is that it so reduces their cover that they typically occur as widely-scattered individuals, whose frequency is very low if small field-layer samples are taken. Many of the plants are very typical of this kind of woodland but they are not found very often unless extensive areas of ground are covered. Among the most characteristic of these associates is *Oxalis acetosella*: Watt (1924, 1934*b*) found this species to be especially prominent in the decade or so before the *Rubus* underscrub attained dominance but later to be largely overwhelmed, despite its great shade tolerance (e.g. Packham & Willis 1977, Packham 1978). Then, there are typically some scattered tussocks of grasses, notably *Holcus mollis*, *Milium effusum*, *Melica uniflora* and, on heavier soils, *Deschampsia cespitosa* with, less frequently, *Dactylis glomerata*, *Poa trivialis*, *Agrostis capillaris*, *Bromus ramosus*, *Festuca gigantea*, *Brachypodium sylvaticum* and *Holcus lanatus*. *Luzula pilosa* is quite common, too, and there can be scattered crowns of *Dryopteris filix-mas* and *D. dilatata*.

More noteworthy is the presence in some stands of *Galium odoratum*, sometimes in local abundance, a feature which suggests that, though the soils here are usually quite acidic and have no free calcium carbonate, the exchange capacity in the better-structured mulls may be quite high (e.g. Avery 1958). In general, however, species characteristic of more calcicolous woodlands, like *Mercurialis perennis*, *Circaea lutetiana*, *Geum urbanum*, *Sanicula europaea* and *Arum maculatum*, are rare here. They may make an appearance on profiles transitional to brown calcareous earths but Watt's beech-woods of sere 3 in Sussex (Watt 1924) and seres A_0 and part of A in the Chilterns (Watt 1934*b*), where such plants are common, are considered to fall within the *Fagus-Mercurialis* woodland. More exacting calcifuges such as *Deschampsia flexuosa* and certainly ericoid sub-shrubs are likewise absent. On moister soils, *Deschampsia cespitosa* is occasionally accompanied by *Anemone nemorosa*, *Lamiastrum galeobdolon*, *Carex sylvatica*, *C. remota* or even *Juncus effusus*, but such plants are not widely distributed throughout nor ever more than locally abundant in contrast to some wetter *Quercus-Pteridium-Rubus* woodlands. The Carices and *J. effusus*, for example, often mark tractor and cart ruts where water lies in winter.

In more open areas, as in gaps and around the margins of stands, other species may become prominent. *Rubus idaeus* can be very plentiful along with brambles where trees fall and there is often some *Digitalis purpurea*, *Euphorbia amygdaloides* or *Arctium minus* agg. in such places. *Epipactis helleborine* is sometimes found on the more open edges of the *Fagus-Rubus* woodland and the rarer *E. purpurata* can occur too, its distinctive clusters of pale flower spikes appearing late in the summer and sometimes in deep shade. One other occasional plant worthy of note is *Ruscus aculeatus*.

Finally, growing among the herbs, there are usually some tree seedlings. Those of *Fagus* itself are the most frequently encountered, though their abundance is very dependent on the irregular masting. Following good years, they can be extraordinarily plentiful, though the vast majority succumb to the predations of small mammals and invertebrate damage or to the dense shade cast by the *Rubus* underscrub (Watt 1925, 1934*b*). *Fraxinus* seedlings can also be quite common and can perhaps more readily penetrate a bramble cover; maybe *Q. robur* too, though its seedlings are quite rare, except in larger gaps. But this greater tolerance may give both these species an edge over *Fagus* in short-term regeneration, beech bringing up a slow rear but eventually benefiting by the shading out of bramble, tolerating the canopy shade of ash and oak and finally overtopping them (Watt 1934*b*).

Ilex seedlings can also be abundant, but they are of patchy occurrence both through time and spatially, according to the pattern of fruiting, which is somewhat irregular, and the activities of the birds which eat the

berries and excrete the seeds (Peterken 1965, 1966). The seedlings are shade-tolerant but very susceptible to being nibbled by larger herbivores and, though they show remarkable persistence in the face of such damage (Peterken 1966), it may be critical in denser shade. *Sorbus aucuparia* seedlings, like those of *Ilex*, can often be found beneath bird-perches and there may also be some *Taxus* and *A. pseudoplatanus* seedlings.

Bryophytes are not a consistently prominent feature of this kind of woodland and their total cover is generally low but, again, certain species are very characteristic and, though occurring as widely-scattered patches, they can provide virtually the only splash of green in shadier stands. The most frequent species are *Mnium hornum* (especially on twiggy litter and humus), *Isopterygium elegans* (on humus), *Hypnum cupressiforme s.l.* (often *H. mammilatum* over exposed beech roots), *Atrichum undulatum* (on exposed mineral soil), *Polytrichum formosum* and *Dicranella heteromalla*. Less common are *Thuidium tamariscinum*, *Eurhynchium praelongum* and *Isothecium myosuroides*. *Dicranum scoparium* and *Leucobryum glaucum* are rare here and much more characteristic of the *Fagus-Deschampsia* woodland.

Habitat

The *Fagus-Rubus* woodland is confined to brown earths of low base-status and with moderate to slightly impeded drainage in southern England. It probably represents the climax forest in such situations within the natural British range of beech but, although some stands are undoubtedly old, very many have been modified by sylvicultural treatments and grazing and some are relatively young plantations.

Within the broad spectrum of soil types on which *Fagus* can become dominant, the *Fagus-Rubus* woodland occupies a middle ground between rendzinas and brown calcareous earths on the one hand and podzolised soils on the other. It occurs widely over the southern Chalk but only where the influence of the underlying limestone is masked by a cover of superficials: on its very typical Chalk plateau sites, it is characteristic of Clay-with-Flints and Plateau Drift, probably with some local admixture of loess (Watt 1924, 1934*b*, Brown 1953, Avery 1958, 1964, Loveday 1962). But, on such deposits, it does not extend far on to more free-draining materials where the tendency for surface-leaching is very pronounced. Likewise, where it is found on soils derived directly from the underlying bedrock, acidic and pervious arenaceous substrates are usually avoided: in the Weald, for example, the community occurs on certain of the Cretaceous Lower Greensand beds and, in the New Forest, Oligocene Headon Beds and Eocene Barton Clays provide important parent materials (Tubbs 1968).

Typically, the brown earths derived from such deposits under the *Fagus-Rubus* woodland are of the classic *sol brun lessivé* type (Duchaufour 1956). Superficial pH is low, generally between 4 and 5, but leaching is usually limited to eluviation of any free calcium carbonate and the mobilisation of clay minerals with accumulation below in an often distinctly argillic B horizon. Some of these soils have a good mull structure: there is a surface accummulation of spongy beech and bramble litter, but steady integration by an active soil fauna in which earthworms figure quite prominently. Fairly often, however, there is a tendency towards the development of mor, with coated or laminated humus building up beneath the leaf litter and a much more compact subsurface horizon, a textural difference often detectable to the foot (Watt 1934*b*, Avery 1958, 1964). There may even be some mobilisation of humus and sesquioxides such that a discontinuous bleached layer forms in the top few centimetres of the A horizon, constituting a micropodzol (Brown 1953, Avery 1958). Such trends may be influenced by *Fagus* itself, more especially by certain treatments of beech (see below), but they are also affected by topography (mor formation being more pronounced on exposed brows: Avery 1958) as well as by variation in the parent material itself. Quite commonly, the *Fagus-Rubus* woodland is disposed over mosaics of brown earths, some areas tending to mull soils, some to mor.

The general association with leached brown earths sets much of the floristic character of the field and ground layers here and helps define the limits of the community against the two other kinds of beech woodland in Britain. This is especially well seen in the Chilterns where all three communities occur in close proximity over a sequence of profiles running from rendzina to podzolised soils, disposed over the free Chalk scarp and the dip slope with its mantle of superficials (Watt 1934*b*, Avery 1958, 1964). Here, the *Fagus-Rubus* woodland is confined to more base-poor brown earths in the Batcombe, Winchester and Charity series (Avery 1958, 1964), largely on the plateau, sometimes running over its edge where there is appreciable downwash of superficials or deposition of decalcified head in shallower valleys. Wherever profiles of the mull type become richer in calcium carbonate, as where the superficials are not so deep or are themselves more calcareous, there is an edaphic switch to the *Fagus-Mercurialis* woodland. Within the *Fagus-Rubus* woodland, the beginnings of this transition are probably marked by the appearance of *Galium odoratum*, a slight increase in *Fraxinus* and often extremely good growth of beech, but it is the appearance of such plants as *Mercurialis perennis*, *Geum urbanum*, *Circaea lutetiana* and *Viola reichenbachiana* and the increasingly patchy chlorotic cover of *Rubus* which provide the best separation between these communities. In the Chilterns, the changeover is well

under way on the Coombe brown calcareous earths and completed on the Upton (one-time Icknield) rendzinas on the scarp. On the South Downs (Adamson 1921, Watt 1924) and in some Cotswold woodlands (Barkham & Norris 1967, 1970), the contrast is not always so clearly associated with a topographic difference, because brown rendzinas are quite widespread there on the limestone dip slopes.

Towards the opposite extreme on the Chilterns, fully-developed podzols are rare, but any strong tendency towards mor accumulation and strong eluviation in the Batcombe soils is characterised by the appearance beneath beech of *Deschampsia flexuosa*, *Calluna vulgaris* (in more open places) and markedly calcifuge bryophytes. Such species are typically absent from the *Fagus-Rubus* woodland and mark the change to the *Fagus-Deschampsia* woodland (Watt 1934b, Avery 1958). An identical soil-related contrast between these two kinds of beechwood can be seen in moving from brown earths to more strongly developed podzols on sands in the Weald and on sands and Pleistocene Plateau Gravels in the New Forest.

With some change in definition of one of its floristic boundaries (to exclude the more calcicolous plateau woods of Watt 1924, 1934b), the *Fagus-Rubus* woodland thus takes its place as the central example of three kinds of beechwood developed over soils of differing acidity and calcareousness (Watt 1934b, Tansley 1939, Rackham 1980). But a further important edaphic limit is set by drainage impedence. Typically, here, though the soils can be distinctly argillic, there is no more than slight gleying and then only in the B horizon, a feature well seen in the Batcombe brown earths on the Chilterns (Avery 1958, 1964). Any increase in this tendency is marked by a rising prominence of *Quercus robur* on these brown earths and a switch to the oak-dominated analogue to this community, the *Quercus-Pteridium-Rubus* woodland, the characteristic forest type of more base-poor stagnogleys on argillaceous bedrocks and heavier-textured superficials throughout the south-east of Britain. Transitional stands with more *Q. robur* and an increase in such herbs as *Deschampsia cespitosa*, *Lamiastrum galeobdolon* and *Anemone nemorosa*, are quite common and intimate mosaics of the two communities can be seen, for example, in the New Forest where they are disposed over more and less impeded profiles of the Wickham stagnogleys and Bursledon stagnogleyic brown earths (Soil Survey 1983).

Within the bounds set by these edaphic conditions, beech has attained natural dominance in the *Fagus-Rubus* woodland by late (and perhaps man-assisted) expansion in the post-Glacial within those parts of southern Britain that are relatively warm but not too drought-prone (Watt 1923, 1925, Watt & Tansley 1930, Godwin 1975, Rackham 1980). As in the other beech woodlands, *Fagus* tends to show better growth here in areas with a moister, milder climate, like Sussex and the New Forest (Watt 1934b, Brown 1964) and the greater prominence of *Ilex* in these localities is a further testimony to their more oceanic character (Tansley 1939, Iversen 1944). But of much more obvious importance to the floristics of the community is the microclimate which beech itself, and the evergreen *Ilex* when it is present, create, casting a very dense shade which is unrelieved until the beech canopy begins to open up. The field layer is thus slow to develop here and in its early stages consists largely of a carpet of the shade-bearing *Oxalis* with only scattered grasses and ferns. Moreover, any further development of the herbs in this community is very severely constrained by the slow but often extensive establishment of the *Rubus* underscrub, which increases the shade still further and, being partly evergreen, precludes any abundance of vernal plants: *Hyacinthoides* would be the expected spring dominant here, but it is actually infrequent and often very sparse (Watt 1924, 1934b).

Root competition with *Fagus* may also play some part in the contrast between the very open herb cover in this community and the more extensive field layer typical of the *Quercus-Pteridium-Rubus* woodland because beech, unlike oak and the other common dominants of that community, is a surface-rooter. This may not be so widely important here as in the *Fagus-Mercurialis* woodland where the substrates are pervious and the soils often shallow and excessively-draining, but it may be more critical in drier areas like the Chilterns: Watt (1934b) noted that *Oxalis*, for example, which has a high demand for surface moisture (Packham 1978), was less abundant there than in Sussex stands.

It has also been suggested that beech dominance in the *Fagus-Rubus* woodland modifies the environment by influencing pedogenesis. Especially on inherently poorly-draining soils, its shallow rooting may reduce aeration and nutrient turnover, leading to a deterioration in sub-soil structure (Brown 1953, Manil 1956) and this, together with accumulation of beech mor, could favour clay deflocculation and an increased tendency to podzolisation. More likely, according to Avery (1958), is that it is certain treatments of *Fagus* that enhance such trends, mor being especially associated with dense stands of undersized, slow-grown trees, such as develop with repeated application of the selection system (Brown 1953, 1964). In curtailing this development, *Rubus* may play an important role: it can spread rapidly where gaps form, adding its own less acid litter to the humus and increasing nutrient turnover. Moreover, as Watt (1923, 1925, 1934b) noted, and as practitioners of the selection system discovered, a bramble cover can suppress beech regeneration but allow *Fraxinus* and, in larger gaps, *Q. robur*, to develop and maintain their

occasional presence in the canopy and, beneath these trees, there is a less dense shade, a more luxuriant herb cover and a local development of mull. In such situations, *Fagus* should theoretically be able to come through given time, regaining its position as the canopy dominant, shading out the field layer and shifting the humus regime back towards mor: a cyclical pattern of mor and mull formation would thus be a natural feature under stands of this community (Avery 1958). In practice, masting in *Fagus* is very erratic, its fruits are not transported far and, even if the seedlings get away, predation by a variety of invertebrate and vertebrate pests (especially, now, grey squirrel attacking at the pole stage) severely reduce the chances of the trees reaching maturity (Watt 1923, 1925, Brown 1953). The cycle of regeneration may thus be very slow and unreliable and, in larger gaps, vegetation approximating to the *Quercus-Pteridium-Rubus* woodland may be in occupation for some time (Rackham 1980, Smith 1980).

Hopeful attendance on natural regeneration in gaps created by timber removal was the essential feature of the selection system, applied extensively to beech woodlands in the Chilterns in the nineteenth and early twentieth centuries (Brown 1953, 1964, Peterken 1980). Here, the *Fagus-Rubus* woodlands of the Chalk plateau have been a major contributor to the local beech-based economy for many centuries, supplying coppice underwood for fuel from medieval times (e.g. Mansfield 1952, Roden 1968) and later, with the rise of the furniture industry, timber, small material being worked in the woods by itinerant 'chair-bodgers', larger material going to factories. Applied with skill, the selection system, drawing timber of varying sizes from coupes at intervals of 8–15 years, seems to have been adequate to ensure regeneration. But increased mechanisation and the use of imported timber meant that cuts became less regular and concentrated on larger timber, such that stands developed an over-abundance of densely-placed small trees beneath which regeneration, never very reliable, became extremely difficult. Some tracts of the community still show signs of this neglect; others have a structure related to the subsequent change to shelterwood and clear-felling treatments with planting of beech from outside the Chilterns; many are derived from restocking after the heavy fellings of the Second World War, sometimes with intermixtures of conifers (Brown 1953, 1964). Beech from the *Fagus-Rubus* woodland still finds a ready market: although quality varies greatly with topographic situation, the community can yield timber of class I or II on the better mull soils, especially in less drought-prone areas like Sussex (Brown 1953, 1964, McNeill 1961).

Planting or sowing of beech has also played a part in the origin of some stands of the community in the New Forest (Tubbs 1968), as in the statutory enclosures of the eighteenth and mid-nineteenth centuries and in the more recent Forestry Commission plantations, within which there is an undertaking to maintain a proportion of hardwoods. In this region, however, the *Fagus-Rubus* woodland also constitutes a large proportion of the 'Ancient and Ornamental Woodlands' which are an unenclosed element of a landscape derived from the medieval Royal Forest with common grazing rights. In fact, the bulk of the woodlands in which beech predominates are not very ancient (Tubbs 1964, 1968, Peterken & Tubbs 1965) and its prominence may be partly due to the preferential extraction of oak for ship timber in the eighteenth and nineteenth centuries. But it does seem to have been a very successful invader of open ground or derelict or cleared woodland in the first wave of woodland development, which Peterken & Tubbs (1965) dated to the period from the mid-seventeenth to the mid-eighteenth centuries. The cause of this phase of regeneration, which seems to have been matched in other Royal Forests, is unknown: deliberate enclosure against grazing and browsing animals may have played some part but does not seem a totally adequate explanation.

Canopy closure in these older stands, which now comprise a mosaic of *Fagus-Rubus* and *Quercus-Pteridium-Rubus* woodlands, together with their calcifuge counterparts, the *Fagus-Deschampsia* and *Quercus-Betula-Deschampsia* woodlands, seems to have been sufficiently sustained in some stands to prevent any extensive internal regeneration. Of much more general importance here, though, was the long-continued intensive grazing and browsing of these woods by deer (mostly fallow, with some roe and red), ponies and cattle, and the turning out of pigs in the pannage season. Not until this pressure fell with the Deer Removal Act of 1851 was there any marked regeneration. From this time onward dates the second age-class group of stands, apparently mostly *Quercus-Pteridium-Rubus* woodlands, with a wide variety of canopy species, including sometimes *Ilex* as a scrubby dominant, and among which *Fagus* found only an occasional place. Such stands occupy gaps within the *Fagus-Rubus* woodlands and represent some marginal expansion. Regeneration in this phase seems to have been checked by a variety of factors: dense shading by holly, an increased incidence of heath-burning and a renewed burst of pony-browsing towards the end of the First World War. However, a further decline in pony-browsing and cattle-grazing in the Second World War permitted another phase of regeneration, often represented by woodlands with much *Ilex, Fraxinus* and *Acer pseudoplatanus*. With deer and stock numbers again reaching very high levels, these woodlands provide one of the best examples of woodpasture in Britain and an evocative reminder of an earlier landscape, whose openness is much valued by huge numbers of visitors. But continued browsing

makes further regeneration of the *Fagus-Rubus* wood-lands unlikely and precludes the possibility of seeing whether any of the younger *Quercus-Pteridium-Rubus* woodland will succumb to eventual beech-dominance.

Zonation and succession
Zonations from the *Fagus-Rubus* woodland to other vegetation types most commonly reflect edaphic differences or represent stages in seral successions, though both of these kinds of transition are much affected by sylvicultural treatments and grazing or by the isolation of stands within predominantly agricultural landscapes.

Some of the most intact edaphic zonations are to be seen on the Chilterns. Here, though the stands of beech are of diverse origin and have canopy structures derived by manipulations pursued, in large measure, independently of soil variation, the *Fagus-Rubus* woodland can still be seen in direct continuity with *Fagus-Mercurialis* woodland on the one hand and *Fagus-Deschampsia* woodland on the other, disposed in the soil-related sequence given classic expression by Watt (1934*b*: see also Brown 1953 and Avery 1958). Incomplete sequences, lacking the *Fagus-Deschampsia* woodland, occur on the South Downs (e.g. Adamson 1921, Watt 1924), and the more calcifuge end of the series can be seen in the Weald and the New Forest.

The sharpness of the transitions between the different kinds of beech-dominated woodlands is very variable. Zonations from the *Fagus-Rubus* woodland to the *Fagus-Mercurialis* woodland can be very striking, with an abrupt switch from a vigorous bramble underscrub on the plateau brown earth to a luxuriant carpet of *Mercurialis* on the scarp rendzina. But, where there is some downwash of Clay-with-Flints over the scarp brow or deposition of decalcified head in shallow valleys, the junction between the communities may be ill defined and not so clearly coincident with topography. And plateau superficials may themselves be more calcareous so that the *Fagus-Mercurialis* woodland extends some way on to the typical *Fagus-Rubus* site-type, a feature especially widespread on the South Downs.

Transitions from the *Fagus-Rubus* to the *Fagus-Des-champsia* woodland are often less sharp, partly because the plateau superficials from which their soils are often derived are very variable in composition. In some localities on the Chilterns (e.g. Watt 1934*b*), the zonation relates clearly to increasing depth of superficials with increasing distance from the scarp edge, *Rubus* under-scrub and the more mesophytic grasses passing in well-ordered fashion to *Deschampsia flexuosa*, *Calluna* and calcifuge bryophytes. But local sandy patches and exposed brows swept clear of loose litter by wind (e.g. Avery 1958) may show unexpected transitions to the *Fagus-Deschampsia* woodland and there may be local development of mor beneath dense plateau beech so that

mosaics of the two communities develop.

Throughout these zonations, long and intensive exploitation for beech often makes canopy distinctions between the different communities very much less obvious than those of the field layer. Even in more natural circumstances, of course, *Fagus* is an overwhelming dominant in each but changes in woody associates can sometimes also be seen. In mature stands, *Fraxinus*, *Acer pseudoplatanus* and *Sorbus aria* appear in the canopy more frequently with the move to the *Fagus-Mercurialis* woodland and *Ilex* is often replaced by *Corylus* as the leading smaller companion. In the *Fagus-Deschampsia* woodland, the differences are much less: both *Q. robur* and *Ilex* remain common but there is sometimes more *Betula pendula* and, less often, a little *Q. petraea*. More recently, treatments have fragmented larger stretches of these beech-dominated sequences, interposing stands with some pine and larch or plantations composed entirely of conifers. The more recent kinds of landscape with beech are well illustrated for the Chilterns by Figure 68 in Tansley (1939) and for the New Forest by the map in Tubbs (1968).

The other common kind of woodland zonation involving the community, that to the *Quercus-Pteridium-Rubus* woodland, is more complex. Sometimes this, too, is related to soil differences: there seems little doubt that, within the natural range of beech, that kind of woodland is an edaphic replacement for *Fagus-Rubus* woodland on strongly-gleyed soils (e.g. Watt 1934*b*, Noirfalise 1968), and such transitions form part of the variation in the proportions of *Fagus* and *Q. robur* in the Weald, on the Chiltern plateau and in the New Forest. But complex mosaics are frequent because of fine differences in drainage impedence on gently-undulating surfaces (especially where the soils derive from superficials), and the situation is complicated by the fact that the *Quercus-Pteridium-Rubus* woodland seems to be a seral precursor to the *Fagus-Rubus* woodland. Thus, where neglected farmland or heathland on moderately base-poor soils is being colonised, or where *Fagus-Rubus* woodland has been felled and the site abandoned, or where large gaps develop within it, there is an initial, sometimes lengthy, period of oak-dominance before beech wins through (Watt 1924, 1934*b*, Tansley 1939, Peterken & Tubbs 1965). Similarly, where *Fagus-Rubus* woodlands have been coppiced, they may have an underwood and sapling population more like that of the *Quercus-Pteridium-Rubus* woodland (Adamson 1921). That *Fagus* can effect the conversion seems undeniable from the careful studies of Watt (1924, 1934*b*); that it is a precarious and sometimes very protracted process is also clear (e.g. Watt 1923, 1925, 1934*b*, Peterken & Tubbs 1965, Rackham 1980).

The ultimate precursors to the eventual development of the *Fagus-Rubus* woodland are probably the less

calcicolous kinds of mesotrophic sward (various sub-communities of the *Arrhenatheretum* and neglected meadows and pastures of the *Centaureo-Cynosuretum* and the *Lolio-Cynosuretum*) and the less extreme kinds of calcifuge sward in the *Festuca-Agrostis* grasslands and perhaps also, around the New Forest, the grassier types of *Ulex minor-Agrostis curtisii* heath. More open stands of *Pteridium* may also be colonised. Spinose shrubs are important invaders of all these communities, typically forming patchy *Crataegus-Hedera* scrub with a marginal tangle of *Rubus-Holcus* underscrub (e.g. Tansley 1922, Tansley & Adamson 1925, Watt 1924, 1934*b*). On more free-draining soils, *Ulex europaeus* may figure prominently in these early stages. Quite commonly, however, *Q. robur* and *Ilex* invade early and, if there is a seed source close by, *Fagus* itself. How long it takes for open herbaceous vegetation to progress fully to *Fagus-Rubus* woodland is unknown, but beech high forest of this type has clearly grown up in the New Forest within the last 300 years or so (Peterken & Tubbs 1965) and on the Chilterns in perhaps 200 years (Watt 1934*b*). Active development is now rare: stands are often embedded within commercial forests with much coniferisation or are sharply marked off from intensive arable land; where they remain unenclosed, as in the New Forest, heavy grazing prevents expansion.

Finally, there remains the possibility that the three kinds of beech forest in Britain are themselves related in a seral sequence, the *Fagus-Rubus* woodland developing from the *Fagus-Mercurialis* woodland and progressing to the *Fagus-Deschampsia* woodland, the process being assisted by the dominance of beech itself. Duchaufour (1950) has proposed that the establishment of a beech cover plays some part in the evolution of rendzinas to brown earths on the Lorraine Jurassic limestones but, in the Chilterns, Avery (1958) could adduce little evidence for progression beyond calcareous lithomorphic soils on drift-free Chalk, more acidic profiles being primarily related to the presence of superficials and largely independent of whether there was a cover of beech woodland. Over calcareous drift, matters are not quite so clear. Here, brown calcareous soils (which typically carry the *Fagus-Mercurialis* woodland) and brown earths (usually with the *Fagus-Rubus* woodland) may well represent successive stages of leaching and suggest a succession of one community by the other. Certainly, the floristic boundary between these two woodlands can be very indistinct but this is much affected by differences in the superficials and topography (Avery 1958): again,

such pedogenic variation also occurs outside beech forests, notably between calcicolous and calcifuge grasslands on limestone brows.

Development of the *Fagus-Rubus* woodland to the *Fagus-Deschampsia* woodland is likewise unattested. Mor accummulation and the development of micropodzols certainly occur under beech in the *Fagus-Rubus* woodland, both in the Chilterns (Watt 1934*b*, Brown 1953, Avery 1958) and the New Forest (Dimbleby & Gill 1955, Tubbs 1968) but, once more, variation in parent materials and topography play a part and a beech canopy is not a necessary pre-requisite: even when *Fagus* is present, how it is treated may be very important (Avery 1958). On balance, podzolisation under the *Fagus-Rubus* woodland does not seem to be widespread or progressive.

Distribution
The natural range of the *Fagus-Rubus* woodland is confined to southern England with especially good representation on the dip-slope plateaus of the Chilterns and, less commonly, the North and South Downs, and in the New Forest. Where beech has been planted as a replacement for oak on moderately base-poor soils in lowland England and Wales beyond its natural limit, such stands could be included here.

Affinities
Apart from the exclusion of more calcicolous woodlands on brown calcareous earths, a change also advocated in Peterken (1981), the *Fagus-Rubus* woodland corresponds with the *Fagetum rubosum* of Watt's classic beechwood series (Watt 1924, 1934*b*, Watt & Tansley 1930, Tansley 1939, Rackham 1980). Similar woodlands are quite widespread on more base-poor, but not excessively leached, soils in Europe and are now usually placed in the Galio odorati-Fagion sub-alliance, separated off from the more calcicolous forests of the Cephalanthero-Fagion. The community is thus the British equivalent of associations like the *Melico-Fagetum* Knapp 1942 described from Germany (Oberdorfer 1957) and Poland (Matuszkiewicz 1981) and the less calcifuge forms of the *Fagetum arduennense* (LeBrun *et al.* 1949) from Belgium. The more Atlantic character of this kind of beech woodland in north-west Europe is acknowledged in such designations as the *Endymio-Fagetum* (Noirfalise & Sougnez 1963, Klötzli 1970) and *Ilici-Fagetum* (Durin *et al.* 1968, Noirfalise 1968, Klötzli 1970).

Floristic table W14

Fagus sylvatica	V (6–10)		*Carex sylvatica*	I (1–3)
Quercus robur	II (2–7)		*Circaea lutetiana*	I (1–3)
Betula pendula	I (2–3)		*Digitalis purpurea*	I (1–3)
Betula pubescens	I (3–4)		*Fraxinus excelsior* seedling	I (1–3)
Fraxinus excelsior	I (1–4)		*Galium verum*	I (1–2)
Acer pseudoplatanus	I (1–4)		*Euphorbia amygdaloides*	I (1–3)
Prunus avium	I (2–6)		*Thuidium tamariscinum*	I (2–4)
Sorbus aria	I (1–4)		*Acer pseudoplatanus* seedling	I (2–4)
Ulmus glabra	I (2–4)		*Holcus lanatus*	I (2–8)
Pinus sylvestris	I (6)		*Urtica dioica*	I (3–4)
			Bromus ramosus	I (3–5)
Ilex aquifolium	IV (1–8)		*Atrichum undulatum*	I (3–4)
Fagus sylvatica sapling	IV (1–5)		*Dicranum scoparium*	I (3–4)
Taxus baccata	I (5)		*Sorbus aucuparia* seedling	I (1–2)
Corylus avellana	I (1–4)		*Ranunculus repens*	I (2–3)
Sambucus nigra	I (1–3)		*Polytrichum commune*	I (3–5)
Fraxinus excelsior sapling	I (1–4)		*Isothecium myosuroides*	I (3–5)
Acer pseudoplatanus sapling	I (3–4)		*Eurhynchium praelongum*	I (2–4)
Sorbus aucuparia	I (2–3)		*Geum urbanum*	I (2–3)
Betula pendula sapling	I (3)		*Agrostis stolonifera*	I (3)
Salix caprea	I (3)		*Carex remota*	I (3)
Ligustrum vulgare	I (3)		*Deschampsia flexuosa*	I (1–3)
			Hyacinthoides non-scripta	I (5)
Rubus fruticosus agg.	V (1–7)		*Taxus baccata* seedling	I (3)
Fagus sylvatica seedling	IV (1–7)		*Plagiothecium undulatum*	I (2)
			Anemone nemorosa	I (1)
Pteridium aquilinum	III (1–6)		*Arum maculatum*	I (1)
Mnium hornum	III (1–8)		*Fissidens taxifolius*	I (3)
Milium effusum	II (3–6)		*Viola riviniana*	I (2)
Oxalis acetosella	II (1–4)		*Brachythecium rutabulum*	I (4)
Deschampsia cespitosa	II (2–7)		*Stellaria media*	I (4)
Luzula pilosa	II (2–4)		*Poa nemoralis*	I (3)
Melica uniflora	II (3–7)		*Moehringia trinervia*	I (3)
Holcus mollis	II (2–5)		*Mercurialis perennis*	I (3)
Lonicera periclymenum	II (1–4)		*Hypericum pulchrum*	I (2)
Dryopteris filix-mas	II (1–4)		*Festuca gigantea*	I (4)
Hedera helix	II (2–4)		*Epipactis helleborine*	I (2)
Ilex aquifolium seedling	I (1–3)			
Poa trivialis	I (1–8)		Number of samples	49
Isopterygium elegans	I (2–3)		Number of species/sample	12 (6–27)
Hypnum cupressiforme	I (2–3)			
Galium odoratum	I (4–5)		Tree height (m)	20 (10–30)
Polytrichum formosum	I (4–6)		Tree cover (%)	96 (60–100)
Dryopteris dilatata	I (2–4)		Shrub height (m)	4 (1–9)
Rubus idaeus	I (2–7)		Shrub cover (%)	15 (0–70)
Ruscus aculeatus	I (1–4)		Herb height (cm)	23 (1–80)
Dicranella heteromalla	I (2–5)		Herb cover (%)	41 (1–100)
Plagiothecium denticulatum	I (1–4)		Ground height (mm)	12 (10–20)
Quercus robur seedling	I (1–3)		Ground cover (%)	6 (0–20)
Brachypodium sylvaticum	I (2–7)			
Dactylis glomerata	I (3–4)		Altitude (m)	155 (20–226)
Lamiastrum galeobdolon	I (2–4)		Slope (°)	2 (0–15)
Agrostis capillaris	I (3–4)			

W14   *Fagus sylvatica-Rubus fruticosus* woodland