
W12

Fagus sylvatica-*Mercurialis perennis* woodland

Synonymy

Beechwood association Moss *et al.* 1910 *p.p.*; *Fagetum sylvaticae calcareum* Tansley & Rankin 1911; *Fagetum sylvaticae* beechwoods on Chalk Adamson 1921; Beech associates, seres 3 & 4 Watt 1924; Beech consociation, Juniper and Hawthorn seres Watt 1934a; Beech consociation, seres 3 & 4 Watt 1934b; *Fagetum sylvaticae calcicolum* Tansley 1939; *Fagetum rubosum* Tansley 1939 *p.p.*; Beech-Ash-Yew Association McNeill 1961; Beech-Oak-Ash Association McNeill 1961 *p.p.*; Cotswold beechwoods Barkham & Norris 1967 *p.p.*; Beechwood Rackham 1980 *p.p.*; Beech stand types 8Cb & 8Cc Peterken 1981; Woodland plot types 1 & 8 Bunce 1982 *p.p.*

Constant species

Fagus sylvatica, *Mercurialis perennis*.

Rare species

Buxus sempervirens, *Cephalanthera longifolia*, *C. rubra*, *Cynoglossum germanicum*, *Epipactis leptochila*, *Epipogium aphyllum*, *Hordelymus europaeus*, *Orchis purpurea*.

Physiognomy

The *Fagus sylvatica*-*Mercurialis perennis* woodland is one of three woodland communities in Britain characterised by the great pre-eminence of *Fagus sylvatica*. In this community, *Fagus* is the only woody species that is constant throughout and is always the most abundant tree: in mature stands, it is an overwhelming dominant in a usually quite distinct topmost tier to the canopy. In general, though, and especially on the more shallow soils of the *Sanicula* and *Taxus* sub-communities, the individual trees do not attain the majestic stature so typical of the *Fagus sylvatica*-*Rubus fruticosus* woodland. There can also be considerable variation in the overall canopy height and in the distribution and physiognomy of the trees according to the age of the woodland and younger sub-spontaneous stands can continue to betray the pattern of invasion by *Fagus* for some time. In some of

the woodlands which Watt (1924, 1934a) examined, for example, he detected varied mixtures of pioneers, families and groups of different sizes and degrees of maturity and noted a contrast between the stocky, richly-branched early invaders with their spreading crowns and individuals of subsequent generations with taller, thinner boles, often obliquely set and with lop-sided crowns crowded by the existing trees. With increasing age, however, the *Fagus* cover takes on a more even and regular look and younger trees become progressively confined to gaps with slow and sometimes sporadic regeneration.

As defined here, this community also includes semi-natural or planted stands in which gap creation and regeneration have been controlled by a selection system of timber extraction (Troup 1966), an uncommon form of forest management in Britain but one especially associated with Chiltern stands of *Fagus*-*Mercurialis* woodland (Watt 1934b, Peterken 1981), and also stands treated by clear-felling and replanting or under a shelter-wood regime (Troup 1966, Peterken 1981). Coppiced stands, however, are rare: *Fagus* pollards well but it produces rather weak coppice shoots or is perhaps more prone to disease when coppiced, and is only very occasionally seen as the dominant in coppice underwood forms of the community (Rackham 1980, Peterken 1981). But, quite commonly, sites which would be expected naturally to carry the *Fagus*-*Mercurialis* woodland seem to have been converted to *Corylus* or mixed small coppice by the removal of *Fagus* (Watt 1934b, Tansley 1939), usually the total removal since *Fagus* standards have a strong shading effect on the underwood (Rackham 1980). In this scheme, such vegetation would fall within the *Fraxinus*-*Acer*-*Mercurialis* woodland, though neglect and *Fagus*-invasion means that many stands are reverting to this community.

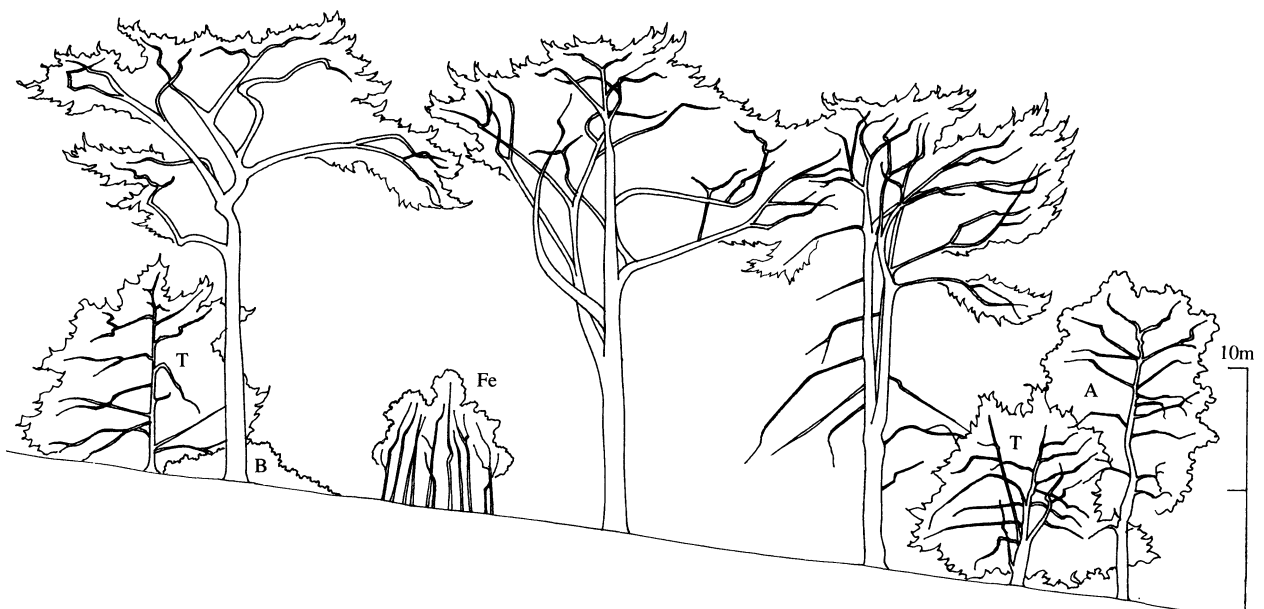
Apart from *Fagus*, no other tree is consistently frequent throughout the community or dominant over more than very local areas. Overall, the commonest companion is *Fraxinus excelsior*, especially in the *Mer*-

curialis sub-community, where older trees can be survivors from the *Fraxinus-Acer-Mercurialis* woodland that typically precedes this community in successions over somewhat deeper soils in less exposed situations (Watt 1924, 1934a). Occasional individuals can persist in mature *Fagus* canopies here, though they very often have a drawn-up and rather spindly appearance. *Fraxinus* is also the most frequent coloniser of gaps here and, when *Fagus* mast is in short supply, a leading ash maiden may grow up and fill the space in the canopy (Watt 1923, 1925). *Quercus robur* can also remain as a scarce associate though, in the end, it does not persist as well here as on the substantially deeper and moister soils that come to support the *Fagus-Rubus* woodland. But it is more shade-tolerant than *Fraxinus* and can be proportionately more abundant in the early stages of *Fagus* invasion, to be eventually overtaken again by *Fraxinus* because of the more prolific seeding-in of the latter (Watt 1924): it can, however, regenerate in larger gaps. Another very successful gap-coloniser in areas of higher rainfall like the western end of the South Downs is *Acer pseudoplatanus* and this likewise can be found as an occasional in developing and mature canopies (Watt 1924, 1934a). *Ulmus glabra*, which often accompanies *A. pseudoplatanus* in calcicolous woodlands in the wetter north and west, is noticeably rare in this community.

Two other characteristic trees here are *Sorbus aria* and *Taxus baccata*. Both can be relics of the early stages of invasion and, on shallower soils where *Fagus* does not grow so tall, they can survive as occasional components of the main canopy tier. This is the usual role here of *S. aria*, but the more slow-growing *T. baccata* is often overtaken to remain as a distinct lower contributor to the woody cover and, being very shade-tolerant, it can persist and regenerate to attain some local abundance (Figure 22). Then it is often possible to distinguish the older early colonisers branching from the ground and the later more diffusely branched invaders (Watt 1924). Both these trees can occur occasionally in each of the sub-communities, though increased frequencies of both, especially of *T. baccata*, help define the *Taxus* sub-community.

Other trees are generally very sparse. Birch, almost always *Betula pendula*, occurs occasionally throughout, though the dense shade here limits it to gaps. A somewhat better and rather surprising low-frequency survivor is the seventeenth-century Balkan introduction *Aesculus hippocastanum*: though widely planted in Britain, this tree seems to have seeded into this community naturally in some places and it performs quite well. *Prunus avium* can also be found, though it is more characteristic of the *Fagus-Rubus* woodland. *Carpinus betulus* is very infrequent and, though *Fagus* and *Tilia cordata* occur together in certain kinds of *Fraxinus-Acer-Mercurialis* woodland (the *Teucrium* sub-community in the Wye valley, for example), this association is not characteristic here. *Tilia platyphyllos* and *T. vulgaris*, however, both occur in close proximity to

Figure 22. Canopy and understorey in *Fagus-Mercurialis* woodland at White Hill, Surrey. Section shows a canopy of tall beech with occasional horse-chestnut (A) and an understorey of yew (T), box (B) and ash saplings (F) in a regeneration core beneath a gap.



stands of the *Taxus* sub-community at Box Hill in Surrey.

The main feature of the shrub layer of the *Fagus-Mercurialis* woodland is that it is very poorly developed, especially in mature stands. A thicker understorey may persist around the margins of stands or within enclaves where invasion of the preceding woodland is not so far advanced; and there may be a resurgence of shrubs within gaps. Generally speaking, however, shrub cover becomes increasingly patchy as *Fagus* asserts its dominance and the shade increases and the feeble growth of most of the survivors is very marked.

Overall, the most common elements of this lowest tier of woody vegetation are *Corylus avellana*, *Crataegus monogyna*, *Acer campestre*, *Sambucus nigra* and *Ilex aquifolium* with *Euonymus europaeus*, *Cornus sanguinea*, *Ligustrum vulgare*, *Viburnum lantana* and *V. opulus* rather less frequent; in other words, very much the same suite as is characteristic of the south-eastern kinds of *Fraxinus-Acer-Mercurialis* woodland. Here, however, none of these species survives to constancy through the community as a whole; indeed, none persists to constancy in any of the sub-communities, though some are preferentially frequent in different kinds of *Fagus-Mercurialis* woodland and can have locally high cover there. *Cornus*, *Ligustrum* and *V. lantana* tend to be more characteristic of the *Sanicula* sub-community and, though the last two are quickly extinguished as *Fagus* invades, they can show a marked resurgence in gaps over shallow, stony soils. *Juniperus communis*, which is a locally prominent species with these shrubs in the scrub which precedes this kind of *Fagus-Mercurialis* woodland, only very rarely persists long enough to qualify as a living member of this woodland, but its woody skeletons quite commonly testify to its previous abundance (Watt 1934a). *Crataegus* and *Corylus*, by contrast, are a little more frequent in the *Mercurialis* sub-community and the former especially can remain as drawn-up individuals in more mature woodlands. Overall, however, the best survivor among all these species seems to be the evergreen *Ilex* and this small tree can persist in some abundance, taller individuals sometimes growing up to contribute to a lower canopy tier with *Taxus*. Where *Taxus* itself is very prominent, as in the *Taxus* sub-community, the shade is doubly dense and very few of the smaller woody associates of the community can survive, though *Buxus sempervirens* appears as a distinctive companion at some sites.

Tree saplings, like the shrubs and smaller trees, are also noticeably patchy. Generally, the most frequently encountered are those of *Fraxinus* and *A. pseudoplatanus* but these are very much more common on the deeper soils of the *Mercurialis* sub-community and, even there, are largely confined to gaps. Here, though, they can be extremely abundant, forming distinctly domed regene-

ration cores (Watt 1924). Young *Fagus* are most frequent in these situations, too, but their abundance is much more sporadic through time because of the pronounced mast-year pattern of fruiting (Watt 1923, 1925). *Taxus* and *Sorbus aria* saplings can also sometimes be found. *Quercus robur* generally regenerates poorly in this community.

By and large, climbers and lianes are scarce, apart from the evergreen *Hedera helix* which, as well as forming a sometimes abundant ground carpet here, is sometimes found up the trunks and among the branches of the trees. In more open stands of the *Sanicula* sub-community, *Clematis vitalba*, *Tamus communis* and *Bryonia dioica* sometimes occur.

In qualitative terms, the field layer of the *Fagus-Mercurialis* woodland shows a general similarity to that of the *Fraxinus-Acer-Mercurialis* woodland with plants characteristic of more base-rich soils providing the core of the herbaceous component of the vegetation. Thus, among the most frequent species here are *Mercurialis perennis*, *Sanicula europaea*, *Geum urbanum*, *Circaea lutetiana*, *Arum maculatum*, *Brachypodium sylvaticum*, *Geranium robertianum* and *Viola riviniana/reichenbachiana* (incompletely separated in the available data but probably mostly *V. reichenbachiana*, e.g. Watt 1934a). However, by contrast with the geographically close south-eastern kinds of *Fraxinus-Acer-Mercurialis* woodland, plants typical of moister calcareous soils are relatively uncommon in this community. *Primula vulgaris*, *Poa trivialis*, *Ajuga reptans*, *Lamium galeobdolon*, *Carex sylvatica*, *Deschampsia cespitosa*, *Anemone nemorosa* and *Ranunculus ficaria* can all attain a measure of local prominence in particular stands but overall they are no more than occasionals here. *Hyacinthoides non-scripta* is also much less common in this community and even *Mercurialis perennis*, though it is the most frequent species throughout and the only herbaceous constant, is a common vernal dominant only on the deeper soils of the *Mercurialis* sub-community. This means that the field layer of this woodland, especially in the *Sanicula* sub-community, shows a much closer general kinship to that of the north-western kinds of *Fraxinus-Acer-Mercurialis* woodland typical of more free-draining substrates.

Two other frequent species can attain some measure of prominence in the field layer. *Hedera helix* can form a ground carpet of varying density and *Rubus fruticosus* agg. (often *R. vestitus* or members of the *Triviales* section) is sometimes sufficiently thick as to constitute a local underscrub, though it is not so consistent here as in the *Fagus-Rubus* woodland and, even in older stands, is hardly ever accompanied by *Oxalis acetosella*, so characteristic a herald of *Rubus*-dominance in well-established woodlands of that community (Watt 1934b). Less common than these two but sometimes attaining

patchy abundance are ground-cover herbs such as *Fragaria vesca* and *Veronica chamaedrys* and, more distinctively here, *Galium odoratum*, *Mycelis muralis* and *Melica uniflora*, the last two clearly preferential to the *Sanicula* sub-community. *Urtica dioica* and *Galium aparine* can be found occasionally, too, though they are not so frequent as in north-western *Fraxinus-Acer-Mercurialis* woodlands, and ferns, likewise, are rarely a prominent feature here: *Dryopteris filix-mas* occurs in some stands and, less commonly, *D. dilatata*. Other occasional species include *Rumex sanguineus*, *Campanula trachelium*, *Teucrium scorodonia*, *Milium effusum*, *Bromus ramosus*, *Euphorbia amygdaloides* and, especially associated with gaps, *Verbascum thapsus*, *Atropa belladonna* and *Epilobium angustifolium*. More locally, there are records for *Daphne laureola*, *Aquilegia vulgaris*, *Polygonatum multiflorum*, *Helleborus viridis*, *Iris foetidissima* and *Hordeolum europaeus*. There are quite commonly some seedlings of *Fraxinus*, *A. pseudoplatanus*, *Taxus* and, after good mast years, of *Fagus*.

Rich and fairly luxuriant field layers are quite widespread in this community but they are by no means as consistently common as in the *Fraxinus-Acer-Mercurialis* woodland. As with the understorey, much of this effect can be due to the increasingly dense shade that the developing *Fagus* canopy casts: in stands of thickly-set pioneers and in more mature woodland that has not yet opened up (especially where *Fagus* and *Taxus* are both abundant, as in the *Taxus* sub-community), the herb cover may be negligible or nil. Where the field layer is very sparse, very large samples are necessary to gain an adequate impression of its constitution and, where there are next to no herbs at all, only an examination of gaps will give a sure diagnosis of the community. When a reasonably regular turnover of canopy trees has been established, a much more balanced and complete field layer can become prominent. In general, the herbs which withstand the heavy shade best are those which put up their leaves before the canopy foliage emerges, like *Mercurialis* and *Sanicula*, or which are evergreen like *Hedera*; *Rubus* may also carry out much of its vegetative growth during the winter. These four are the commonest field-layer species of the community and, since they all retain their leaves throughout the growing season, they can themselves exert some controlling influence over the prominence of their herbaceous associates where they are themselves dense; and they may also influence the success of tree seedlings in getting away (e.g. Watt 1923, 1925, Wardle 1959).

But other kinds of quantitative variation can also be encountered. Stands on shallower and drier soils, for example, tend to have more open and less luxuriant field layers, and here a general shortage of moisture is probably exacerbated by the very thorough ramification of the soils by the tree roots which are all concentrated in

sometimes but a few centimetres of mantle above the bedrock (e.g. Adamson 1921, Watt 1934a, Tansley 1939). In stands on steeper slopes, there can also be exposures of bare bedrock or unstable tumbles of talus which help to keep the field layer open. Such conditions are especially associated here with the *Sanicula* and *Taxus* sub-communities. Even in well-illuminated stands of the *Mercurialis* sub-community, however, where deeper and somewhat moister soils can theoretically support a better cover of herbs, root competition may be important and, on the exposed margins of woodlands, wind too may play a part in keeping herb cover down. Where there is no protective marginal fringe or little understorey to break their force, winds can blow about the substantial quantities of *Fagus* litter, blanketing smaller species and exposing bare soil. Then the most prominent feature of the woodland floor may be the snaking pattern of tree roots and the intervening stretches of decaying litter.

All these factors also have an effect on the bryophytes of the community which are few in number, infrequent and often sparse. The most widespread species on exposed soil are *Brachythecium rutabulum* and *Eurhynchium praelongum* with, less commonly, *Fissidens taxifolius*, *Plagiomnium undulatum*, *Mnium hornum*, *Thamnobryum alopecurum* and *Ctenidium molluscum*. A clothing of *Hypnum mammilatum* is often a conspicuous feature of the bases of the tree boles and the exposed surfaces of roots and their immediate surrounds.

Sub-communities

***Mercurialis perennis* sub-community:** Beech associates, seres 3 & 4 Watt 1924; Mercury beechwoods Watt & Tansley 1930; Beech consociation, Hawthorn sere Watt 1934a; Beech consociation, seres 3 & 4 Watt 1934b; *Fagetum sylvaticae calcicolum*, Hawthorn-Mercury sere Tansley 1939; *Fagetum rubosum* Tansley 1939 *p.p.*; Beech-Ash-Yew Association type 6 McNeill 1961; Beech-Ash-Oak Association type 7 McNeill 1961; Cotswold beechwoods, mercury type Barkham & Norris 1967; Cotswold beechwoods, ivy type Barkham & Norris 1967 *p.p.* *Fagus* is very much the dominant tree here and, on the somewhat deeper and moister soils characteristic of this sub-community, it makes manifestly better growth than in the other kinds of *Fagus-Mercurialis* woodland, forming the bulk of a canopy that is usually 15–25 m tall (mean 19 m). But other trees can be quite common, either as survivors of a preceding woodland cover that has been invaded by *Fagus*, or within gaps. *Fraxinus* is the most frequent of the associates with *A. pseudoplatanus* a little less so and more restricted to areas with higher rainfall; occasional *Q. robur* can be found too. Each or all of these trees can attain a measure of local abundance as canopy sub-

dominants and transitions to *Fraxinus-Acer-Mercurialis* woodland are quite widespread. Less common woody companions are *Taxus* (often forming a distinct lower tier), *Sorbus aria*, *Betula pendula* (with *B. pubescens* also making a very occasional appearance here), *Aesculus*, *Prunus avium* and *Carpinus*. Conifers such as larches and pines occasionally seed into gaps from nearby plantations.

The understorey, though it is rarely dense, often patchy and quite frequently very sparse, is generally better developed than in the other sub-communities. Both *Corylus* and *Crataegus* are more frequent here and there is occasionally some *Acer campestre*, *Sambucus* and *Ilex*. *Cornus sanguinea*, *Viburnum lantana*, *V. opulus*, *Euonymus europaeus* and *Ligustrum vulgare* occur at lower frequencies but are very much confined to margins and gaps. In gaps, too, saplings of *Fraxinus*, *A. pseudoplatanus* and, following good mast years, *Fagus*, can be very prominent.

Provided that shade, root competition and exposure to winds blowing between the trees are not too severe, the somewhat deeper and moister soils typical of this sub-community favour the development of the kind of extensive and quite tall field layer characteristic of many *Fraxinus-Acer-Mercurialis* woodlands. *Mercurialis* is very common here, can make good growth and is the usual vernal dominant but, as always where it attains this kind of prominence, it exerts a strong control over the cover and variety of its associates because of the dense shade that its own leaves cast from early spring right through to late summer (Watt 1934a, Wardle 1959, Wilson 1968, Martin 1968). Overall, then, its most frequent companions are hemicryptophytes with taller leafy stems, most notably here *Circaea lutetiana*, *Brachypodium sylvaticum* and *Galium odoratum*, which protrude here and there through the *Mercurialis* carpet, and the shade-bearing evergreen *Hedera* which very typically forms a ground cover beneath it. Indeed, *Hedera* may replace *Mercurialis* as the field-layer dominant in the areas of deepest shade (Barkham & Norris 1967), though available samples of this kind of vegetation are not sufficiently distinct to warrant the erection of a *Hedera* sub-community. *Rubus* is also much commoner here than on the drier, shallower soils of the *Sanicula* and *Taxus* sub-communities: usually it occurs as rather sparse spindly shoots sprawling over the other herbs but it can thicken up locally to form a patchy underscrub which can itself limit the dominance of *Mercurialis*, though not usually the extent of *Hedera*. In contrast to these species, *Sanicula*, a rosette hemicryptophyte, is notably infrequent here.

Other herbs which occur a little more frequently than in the other two sub-communities are *Arum maculatum*, *Dryopteris filix-mas* and, sometimes with local abundance, *Lamium galeobdolon* and *Hyacinthoides non-*

scripta, all of them perhaps indicative of the somewhat moister soils here. *Allium ursinum*, *Anemone nemorosa*, *Ranunculus ficaria* and *Deschampsia cespitosa* can also be found with patchy prominence, though they are generally infrequent and the striking patterns of zoned dominance involving these species so typical of the *Fraxinus-Acer-Mercurialis* woodland are not a regular feature here. There are certainly insufficient samples to erect parallel sub-communities in which these plants are preferential, though Rackham (1980) distinguishes an *Allium* field layer in the beechwoods of the Cotswolds.

Community occasionals found in this kind of woodland include *Viola* spp., *Geranium robertianum*, *Urtica dioica*, *Galium aparine*, *Fragaria vesca* and *Primula vulgaris* but seedlings of the woody species are usually infrequent. Under the denser covers of *Mercurialis*, bryophytes too are sparse but *Brachythecium rutabulum* and *Eurhynchium praelongum* can sometimes be found and *Fissidens taxifolius* is quite common on litter-free patches of soil.

***Sanicula europaea* sub-community:** Sanicle beechwoods Watt & Tansley 1930; Beech consociation, Juniper sere Watt 1934a; *Fagetum sylvaticae calcicolum*, Juniper-Sanicle sere Tansley 1939; Beech-Ash-Yew Association type 5b McNeill 1961; Cotswold beechwoods, hawkweed type Barkham & Norris 1967. The tree canopy is more overwhelmingly dominated by *Fagus* here with only very occasional records for *Fraxinus*, *A. pseudoplatanus* or *Q. robur*. However, the individual trees are usually obviously less well grown than in the *Mercurialis* sub-community, forming a less tall canopy that is generally only 10–15 m high (mean 14 m). Occasional *Taxus*, *S. aria* or large *Ilex* can be represented in the tree layer.

The shrub cover, too, is typically less extensive than in the *Mercurialis* sub-community with *Corylus* and *Crataegus* noticeably less common, though the latter persists longer in younger sub-spontaneous stands than does its local co-dominant in the preceding scrub, *Juniperus*. *Sambucus* and *Ilex* occur occasionally and, where invading *Fagus* makes slow progress, *Cornus sanguinea* and *Viburnum lantana* may survive for some time. In older stands, though, these more light-demanding species are confined to margins or gaps where, with *Ligustrum vulgare*, *Clematis vitalba* and *Tamus communis*, they can form a dense tangle of woody growth. Saplings of all the major trees of the community are infrequent.

Although quite extensive and luxuriant field layers can be found in woodlands of this type, the herb cover is often a little sparser than in the *Mercurialis* sub-community and, even in areas of good illumination, intense root competition in the shallow soils and instability of slope helps keep the cover open. *Mercurialis* in

particular, though still common here, is generally less abundant and vigorous (e.g. Watt 1934a) and, though it can attain a patchy local prominence, it is not usually the vernal dominant. Here, this role is assumed by *Sanicula europaea* which, though often very abundant, is a rosette hemicryptophyte casting much less shade than *Mercurialis* and thus not exerting such a controlling influence on the distribution and variety of the associated flora. The herbaceous component here is thus a little richer and somewhat more diverse.

Among the associates are some strong preferentials, most notably *Mycelis muralis*, here attaining a tall, delicate, almost stately form far removed from its sturdy physiognomy on sunlit walls, and *Melica uniflora* and *Poa nemoralis* which, together with occasional *Brachypodium sylvaticum*, help give the field layer an open grassy appearance. Then, there are occasional scattered plants of such species as *Rumex sanguineus*, *Heracleum sphondylium*, *Anthriscus sylvestris*, *Arctium minus* agg., *Bromus sterilis*, *Cynoglossum officinale* (and in some sites, its rare relative *C. germanicum*) and, especially in more open sunny situations, Glandulosa Hieracia such as *H. exotericum* and *H. pellucidum*, all of which can lend a distinctly weedy feel to the vegetation.

The other striking component of the field layer comprises geophytes, more particularly a variety of orchids which, when flowering in early summer, can present a splendid sight. Most characteristic among these is *Cephalanthera damasonium*, a Continental Southern helleborine whose British distribution almost exactly matches the range of the *Fagus-Mercurialis* woodland but which is clearly preferential to this sub-community, quite common within it, locally very consistent and sometimes abundant. The more showy but rarer *C. longifolia* can also sometimes be found, particularly in Hampshire, but this species is not so confined, geographically and ecologically, to this kind of woodland. The now very rare *C. rubra* survives in this sub-community in the Chilterns and the Cotswolds and seems to have some preference for scrubby stands, or at least to flower better under a more open cover (Tansley 1939, Summerhayes 1968). *Epipactis helleborine*, which is widely distributed in Britain, also occurs here, again in the more open conditions of rides and margins. Much more characteristic of a denser tree cover and sometimes appearing locally in great numbers is the saprophytic *Neottia nidus-avis*, which seems to favour the moist accumulations of rotting leaves over a permeable substratum that shadier stands of this vegetation provide. Our other saprophytic bird's nest, the non-orchidaceous *Monotropa hypopitys* s.l. (both sub-species: Perring 1968), is sometimes also found and similar situations have provided some of the few and very sporadic British records for *Epipogium aphyllum*. Other orchids recorded rarely here are *Epipactis leptochila*, *Orchis purpurea*,

Ophrys apifera, *O. insectifera* and *Listera ovata*.

In addition to these more distinctive elements, there is usually some *Hedera* in this vegetation, again often forming a ground carpet, very occasional *Rubus* and *Rosa canina* agg. and scattered plants of *Geum urbanum*, *Viola* spp., *Veronica chamaedrys*, *Geranium robertianum*, *Urtica dioica*, *Galium aparine*, *Primula vulgaris* and, preferential here at low frequency, *Carex flacca*, usually not flowering in the shade. Tree seedlings are a little commoner here in the more open herb cover and bryophytes, too, can be more extensive with some enrichment by species typical of stony base-rich soils such as *Ctenidium molluscum*, *Homalothecium sericeum* and *Encalypta streptocarpa*.

***Taxus baccata* sub-community:** Beech consociation, Juniper sere Watt 1934a p.p.; *Fagetum sylvaticae calcicolum*, Juniper-Sanicle sere Tansley 1939 p.p.; Beech-Ash-Yew Association type 5a McNeill 1961. As in the *Sanicula* sub-community, the growth of *Fagus* here is generally poor: indeed, on average, the canopy is even lower than there with a mean height of only 12 m. But *Taxus* is a constant and can be present in abundance in a lower tier beneath the *Fagus*. *Sorbus aria* is somewhat more frequent in this kind of woodland too, and there is occasionally some *Fraxinus*. When all these trees are in leaf, the scarps on which this sub-community typically occurs present an unmistakeable patchwork of colour with the predominant mid- and dark green of the *Fagus* and *Taxus* and the scattered pale green and dusty white crowns of the *Fraxinus* and *Sorbus*.

In the very deep shade which this canopy casts, shrubs and small trees are very sparse indeed. The typical understorey species of the community are all poorly represented and such individuals as do persist present a very spindly appearance. The usual picture is of infrequent and much drawn-up *Sambucus* and *Crataegus* with, in somewhat more open places, a little *Ligustrum* and scrambling *Clematis*. At some sites, however, *Buxus sempervirens* is a distinctive (and probably native: Pigott & Walters 1953) associate in this sub-community, tolerating the gloom to form a patchy understorey or growing up among the trees and adding further to the shade with its dense evergreen foliage.

Very few herbs are able to survive the combination of this intense shade and the usually very inhospitable soil conditions, with intense root competition from both *Fagus* and *Taxus*, and the most obvious feature of the woodland floor is often the great extent of bare, rubbly substrate with litter and loose rock tumbling down between the tree boles. *Sanicula* and *Mercurialis* occur only occasionally and are generally very sparse, thickening up only locally where there is a little more light or a somewhat more extensive and stable soil cover. *Rubus* is likewise very infrequent and even *Hedera* largely fades

out here. A few widely-scattered plants of *Mycelis muralis*, *Melica uniflora*, *Arum maculatum*, *Geum urbanum*, *Circaea lutetiana*, *Viola* spp., very sparse tree seedlings and pale wisps of *Eurhynchium praelongum* and *Brachythecium rutabulum* complete the impoverished scene.

Habitat

The *Fagus-Mercurialis* woodland is the kind of beech forest which has developed where *Fagus* has attained dominance on free-draining, base-rich and calcareous soils in the south-eastern lowlands of Britain. It is essentially a community of limestone scarplands in this region and, at the present time, seems to represent a stable end-point of successions in such situations. However, although the *Fagus-Mercurialis* woodland has some claim to be a natural climax, individual stands of the community are not necessarily very old. Some are certainly relatively recent plantations and human agency may have been very widely important for the great pre-eminence of *Fagus* in this kind of woodland.

Despite early doubts to the contrary, we now know that *Fagus* is a certain native in Britain but, though the limits of its natural distribution are generally agreed, they are not very simply explained. It gained ascendancy as a forest dominant before the great era of tree-planting in the warmer and drier south-eastern corner of the country, within a line from The Wash, across to south Wales and down to Dorset (e.g. Tansley 1939, Noirfalise 1968, Godwin 1975, Rackham 1980): all the three kinds of *Fagus* woodland recognised in this scheme are centred in this region. It is possible that, in the more continental parts of East Anglia, seedling establishment and survival are limited by summer drought (e.g. Watt 1923, 1925, Rackham 1980), especially over more permeable substrates like the Chalk, a characteristic bed-rock of the *Fagus-Mercurialis* woodland, the range of which stops short there in the Chilterns. Towards the north and west, late frosts, low summer temperatures and heavier rainfall may hinder *Fagus*-dominance by their effects on masting and regeneration (e.g. Watt 1923, 1925, 1931, Watt & Tansley 1930, Godwin 1975): in this direction, it is the Oolite scarp of the Cotswolds and Lincolnshire that forms the general bounds of this community and the north-western limit of widespread *Fagus*-dominance in our woodlands. But correlations between this apparently natural range and present climatic conditions are not entirely convincing. *Fagus* is widely planted further north, it can grow very well there and can actively regenerate (even in Scotland: see Watt 1931): plantation stands of the *Mercurialis* sub-community of the *Fagus-Mercurialis* woodland, for example, occur in South Yorkshire and South Humberside. It is possible, then, that *Fagus* never reached its northern limit in Britain and that, in the way the three

beech woodlands are concentrated in the south-east, we see the results of some hindering of its spread here.

The post-Glacial advance of *Fagus* in Britain, as elsewhere in north-west Europe, was certainly late: it seems to have had a quite widespread distribution, though no more than local prominence, until the Sub-Atlantic (e.g. Firbas 1949, van Zeist 1959, 1964, Godwin 1975, Huntley & Birks 1983). Climatic conditions during this period would hardly seem to have favoured an extensive natural migration and the gathering consensus is that it expanded from existing small, scattered populations in response to some anthropogenic change, such as more systematic clearance of the natural woodland cover and the associated abandonment of traditional farmlands. The assumption here is that it had been previously largely excluded from the mixed deciduous forest but was then able to compete supremely well against other tree species in the invasion of newly-opened ground. As far as the *Fagus-Mercurialis* woodland is concerned, it has been suggested that the community now occupies sites which perhaps first became widely available for *Fagus*-dominance with the shift in population from the southern limestones to the heavier claylands in Roman and Anglo-Saxon times (Godwin 1975). Certainly, the studies of Watt (1924, 1934a) have shown just how successful *Fagus* can be as an invader of abandoned agricultural land over the Chalk and documentary and archaeological evidence confirms the general south-eastern bias in the distribution of *Fagus* within historic time (Rackham 1980). But there is room for much further work here on the exact status of *Fagus-Mercurialis* woodland within this region and on its absence further north: for example, why, when *Fagus* seems to have been quite well represented in Derbyshire in the Sub-Atlantic, did it not take off there to become a major dominant in woodlands over limestone slopes which now experience a climate not far removed from that characteristic of the western end of the South Downs?

Whatever the climatic and historical reasons for the geographical distribution of the *Fagus-Mercurialis* woodland, its edaphic relationships within its range are quite clear. *Fagus* is a fairly catholic tree as far as soil conditions are concerned: it can become dominant in soils that range from the very base-rich and highly calcareous through to markedly surface-acid podzols; and, though it avoids profiles with strongly-impaired drainage, it can extend some way on to moister or more heavy-textured soils (e.g. Watt & Tansley 1930, Watt 1934b, Tansley 1939, Rackham 1980). Within this broad spectrum, the *Fagus-Mercurialis* woodland is associated with the more base-rich extreme: typically, it is found over rendzinas which are shallow, free-draining, rich in free calcium carbonate and with a surface pH generally within the range of 7–8 (e.g. Adamson 1921, Watt 1924,

1934a; Avery 1958, 1964). In the south-east, such profiles are generally limited to the steeper drift-free faces of the escarpments of the Chalk and the Oolite and this is very much the type site of the community, along the North and South Downs, westwards into Hampshire, where Gilbert White long ago extolled the beauties of the 'beech hangers' (White 1788), on into parts of Wiltshire and up the cuestas of the Chilterns and the Cotswolds. These soils can also be found, more patchily, over the steeper slopes of the gaps cut through the Chalk and in some dry valleys.

In this region, these profiles are now mapped as Upton grey rendzinas (Soil Survey 1983), though they were long known as the Icknield series for which Avery (1958, 1964) provided classic descriptions from the Chilterns (see also Curtiss *et al.* 1976, Smith 1980). Typically, there is a shallow, quite well structured A horizon, within which the tree roots are concentrated and where, provided drainage is not too excessive, a numerous and varied soil fauna, including earthworms, incorporates the beech litter to produce a mull humus well-bound with the clays into crumbly aggregates. Where the soils are shallower, clay-deficient and more sharply draining, structural integration can be much poorer and, as we shall see, this is of major importance in influencing floristic variation within the community. But, throughout, the A horizon is never very deep (usually less than 20 cm), is rich in calcium carbonate (up to 60% or more) and quickly passes through a rubbly, humus-stained A/C to the bedrock proper at 40–60 cm or so below the surface.

These general soil conditions are reflected in the community as a whole by the predominance of more calcicolous associates among the woody and herbaceous components: *Fraxinus*, *Taxus*, *Acer campestre*, *Cornus sanguinea*, *Rhamnus catharticus*, *Euonymus europaeus*, *Mercurialis*, *Circaea lutetiana*, *Geum urbanum*, *Viola reichenbachiana* and *Arum maculatum*. Also, they help define the *Fagus-Mercurialis* woodland against its counterpart on deeper, moister and less base-rich brown earths, the *Fagus-Rubus* woodland where these species fade and *Rubus* and *Pteridium* exert a major influence on the structure and composition of the field layer. *Rubus* is quite common in the *Fagus-Mercurialis* woodland but only occasionally and locally abundant and often chlorotic on the shallower soils; *Pteridium* is hardly ever present. It is not until the strong influence of the underlying permeable limestone is masked by a cover of superfcials that these species become really abundant and sometimes a very sharp switch between these communities can be seen in beech-dominated woodlands that run up a scarp and on to the dip slope (see, for example, the striking Figure 8.3 in Smith 1980). In other situations, the distinction is not so clear and, as defined here, the *Fagus-Mercurialis* woodland takes in a little of

what early workers would have included within *Fagetum rubosum* (like the sere 3 woodlands of Watt (1924) where *Fraxinus* and *Mercurialis* were frequently recorded). Such more marginal stands can be found where the *Fagus-Mercurialis* woodland extends on to brown rendzinas (like the Andover series) or brown calcareous earths (like the Coombe series) on the somewhat gentler slopes on scarp crests and the upper parts of Chalk dry valleys (Avery 1958, 1964, Hodgson 1967, Jarvis 1973). Here the soils may be partly derived from a thin downwash of superfcials like Clay-with-Flints and loess, can have a fragmentary (B) horizon and show some superficial decalcification with a surface pH as low as 6 (Soil Survey 1983). However, on more base-rich brown soils where the drainage becomes impeded, as where heavy-textured superfcials have contributed to the parent materials, the *Fagus-Mercurialis* woodland is replaced by the *Fraxinus-Acer-Mercurialis* woodland. Such soils are rarely contiguous with the types characteristic here, but they replace them in the clay vales that alternate with the limestone scarps and dips in the south-east. The edaphically-related switch between these two kinds of calcicolous woodland is a very distinctive feature of this region and of the geologically similar parts of northern France and Belgium (e.g. Noirfalise 1968).

Within the fairly narrow range of soils characterised by the *Fagus-Mercurialis* woodland, the importance of edaphic differences for the structure and composition of the community was hinted at by Adamson (1921) on the South Downs but first given unequivocal expression by Watt (1934a) in his study of the Chiltern beechwoods. It has since been confirmed by Barkham & Norris (1967, 1970) in the Cotswolds, related more thoroughly to profile structure by Avery (1958, 1964) and to the performance of *Fagus* as a commercial timber tree by Brown (1953, 1964) and Wood & Nimmo (1962). All these studies indicate that the major axis of floristic variation within the *Fagus-Mercurialis* woodland can be related to a complex of edaphic differences of which soil moisture or soil depth can serve as a convenient summary. Thus, the *Mercurialis* sub-community is characteristically found on deeper grey rendzinas (and some brown rendzinas and brown calcareous earths) which are more moisture-retentive, the *Sanicula* sub-community on shallower, more fragmentary grey rendzinas where drainage tends towards excessive. In the latter, though organic matter can be quite high, there is usually not a well-developed and stable aggregation into a good mull. Earthworms are noticeably sparse, insect larvae, millipedes and ants comprise the bulk of soil fauna and the A horizon is often of the type which Kubiena (1953) termed a mull-like rendzina moder with recognisable litter fragments and invertebrate droppings (Avery 1958, 1964). The *Taxus* sub-community, though it has not traditionally been distinguished from the 'mercury'

and 'sanicle' types, can be regarded in part as a continuation of this edaphic trend: typically it occurs on the most fragmentary of soil covers where much of the ground consists of talus and exposed bedrock.

Within individual stands of the community or in stands which occur in close proximity in the same region, this kind of edaphic contrast is often expressed in terms of slope: commonly, the *Mercurialis* sub-community occupies the more gently sloping ground, the *Sanicula* and *Taxus* sub-communities the steeper. Or, it may be related to the degree of exposure to drying winds (not always a simple function of aspect on markedly embayed scarps like the Chilterns) or to sun: the *Sanicula* sub-community tends to be associated with more exposed sites and the majority of the stands of the *Taxus* sub-community face south. Or, again, it may reflect differing degrees of susceptibility to weathering in the underlying bedrock: the *Mercurialis* sub-community can thus pick out softer strata, the *Sanicula* sub-community the harder, like Chalk Rock. Often, more than one of these kinds of physiographic variation can be invoked to understand sub-community distribution as in Watt's (1934a) Chiltern stands or in the pair of woodlands which Barkham & Norris (1970) contrasted. It should be remembered, too, that, in moving from one district to another, differences in regional climate can result in a shift in the absolute definition of sites occupied by the different sub-communities. As Watt (1934a) noted, on the moister South Downs the *Mercurialis* sub-community described by Adamson (1921) occupied some of the ground that, in the drier Chilterns, would have carried the *Sanicula* sub-community. This is why, when samples are pooled from throughout the range of the *Fagus-Mercurialis* woodland, sharp correlations between the different sub-communities and variables like slope and aspect do not emerge.

Although the general effect of edaphic variation is clear, its influence on the vegetation is quite complex and partly indirect. First, there is the control it exerts on the growth of the trees, especially *Fagus*. It was a major part of Watt's (1934a) seral scheme for this community that this effect began very early by its influence on the kind of scrub and woodland that could precede *Fagus* and affect its pattern of invasion, but it is also clearly visible in mature stands of the community whether these are of sub-spontaneous or planted origin. Among more natural populations of beech, there is often quite a wide variation in tree physiognomy which perhaps suggests some genetic differences (Watt & Tansley 1930) but, even here, it is usually possible to see that *Fagus* makes distinctly better growth on deeper, moister soils. In the available data, there is a small but obvious increase in the mean height and height range of the trees in moving from the *Taxus*, through the *Sanicula* and to the *Mercurialis* sub-community. Girth was not measured but early

surveys (Adamson 1921, Watt 1924, 1934a) showed that this, too, is greater in the *Mercurialis* than in the *Sanicula* type and commercial foresters have observed that there is often a whole quality class difference between the beech timber from the two sub-communities (Brown 1953, McNeill 1961; see also Wood & Nimmo 1962). The exact reasons for this are uncertain: mycorrhizal growth does not seem to be poorer on the shallower soils (Harley 1937, 1949) and variation in water content itself and in the amounts of iron, nitrogen and phosphorus have all been suggested as of importance (Day 1946, Fournier in Smith 1980). Again, it needs to be remembered that such differences may be visible in comparative rather than absolute terms: on the South Downs, for example, *Fagus* generally makes better growth overall than in the drier Chilterns (Watt & Tansley 1930, Brown 1964).

Some other trees of the community, such as *Fraxinus*, *A. pseudoplatanus* and *Q. robur*, also tend to grow better in the *Mercurialis* sub-community. They are more frequent there since they can survive from the mixed woodland that can precede this sub-community on deeper, moister soils and the first two are common gap-colonisers. But, since *Fagus* also does so well, its shading effect on these woody associates is that much greater and they maintain or gain their position in the canopy only with some difficulty. On the other hand, although these species are much scarcer in the *Sanicula* and *Taxus* sub-communities, *Fraxinus* especially can sometimes keep pace with *Fagus* there. In the *Taxus* sub-community, too, *Sorbus aria* is not so readily overtopped and the slow-growing *Taxus* can sometimes break the lower *Fagus* canopy.

Another effect of better *Fagus* growth is probably felt through root competition for available water and nutrients, the former likely to be in generally short supply here where the A horizon is so shallow, the substrates so permeable and the ground water-table so low. Apart from the early observations of Watt & Fraser (1933), we know next to nothing about how this factor operates, though a visit to a stand of *Fagus-Mercurialis* woodland where trees have been wind-thrown will readily demonstrate the great extent of the horizontal beech root system through the thin soil mantle. It might be expected that, since *Fagus* makes better growth on soils which are somewhat deeper and more retentive, the greater extent of its root system in such situations would help even out natural variations in moisture content. As Barkham & Norris (1967) observed with respect to *Fagus* density, a *Fagus-Mercurialis* woodland on sheltered, gentle slopes with closely-packed trees can thus have a similar field layer to one on exposed, steep slopes where the *Fagus* density is much lower. Their study of Cotswold beechwoods certainly showed a strong negative correlation between *Fagus* density and soil moisture, though, in

managed woodlands, tree density may not be a reliable indicator of the natural capacity of the soils: thinning may be delayed over more unfavourable soils because the trees make slower growth there. Clearly, there is room here for much research.

Whatever the interactions between the beech cover and the natural water content of the soils here, the amount of available soil moisture certainly has a strong influence on the field layer, an effect seen most clearly in the simple contrast between the *Sanicula* and *Mercurialis* sub-communities (the *Taxus* sub-community being a little more complex: see below). On drier, shallower soils, there is probably an edaphic limitation on the representation of the more mesophytic species of the *Mercurialis* sub-community within the *Sanicula* sub-community, most importantly a reduction in the vigour and abundance of *Mercurialis* itself. On deeper, moister soils where this species can produce an extensive canopy of foliage, there is probably a competitive exclusion of species typical of the *Sanicula* sub-community within the *Mercurialis* sub-community (Watt 1934a). To the dense and long-lasting shade of *Mercurialis*, Watt (1934a) attributed the general scarcity of rosette hemi-cryptophytes, notably *Sanicula*, in the 'mercury' field layer, the virtual exclusion there of *Mycelis muralis* and most of the grasses, which perhaps require high light intensities for seed germination, and a general impoverishment of the bryophyte flora, floristic distinctions which were, in general, confirmed here in the separation of the two sub-communities. The predominant association of orchids with the 'sanicle' field layer, again confirmed here, Watt (1934a) found more puzzling: we still do not have an explanation for this.

In one way or another, then, soil differences can account for a considerable amount of the floristic and physiognomic variation within the *Fagus-Mercurialis* woodland. The other important factor is canopy shade, already touched upon in noting how the trees of the community compete for a place in the topmost structural tier but very obvious, too, in its influence on the understorey and field and ground layers. *Fagus*, of course, can cast a very deep shade: it is one of the few British deciduous trees that can eliminate everything beneath it, a feature which causes problems in classifying the darkest stands and which means that the field layers here are seen in their characteristic form only where there has been some lessening of competition among the components of the canopy and a measure of opening up (Watt 1924, 1934a). Even then, the cover and composition can be decidedly patchy, varying from an extensive and varied carpet of herbs beneath the places where adjacent crowns join, through a sparser clothing in which a mantle of *Hedera* is often the most conspicuous feature, to very bare areas around the bases of the trees, where occasional bryophytes and the smears of

algae down the trunks and over the roots provide the only splash of green. In general, however, this kind of variation does not work in line with the floristic trends noted above in the *Sanicula* and *Mercurialis* sub-communities: rather, it cuts across it to produce an additional range of variation (see, for example, the ordinations in Barkham & Norris 1967, 1970). The *Taxus* sub-community is perhaps an exception to this. Although it can be seen as a continuation of the edaphic trend visible in the other kinds of *Fagus-Mercurialis* woodland, the combination of *Fagus*, *Taxus* and occasional *Buxus*, makes for a more consistently dense shade here than elsewhere. For the most part, though, shade differences are best considered as producing variants.

The appearance of gaps creates a further range of variation in response to the local, sudden and temporary increase in light. In unmanaged stands, this happens naturally as individual trees age and succumb to disease. In practice, since so many beechwoods are under commercial forestry, such degeneration of the canopy is often pre-empted, though the selection system was essentially a way of creating artificial gaps in which natural *Fagus* regeneration was supposed to occur. But, even in managed stands, *Fagus* can fall early because of beech-snap following infestation with beech-bark disease (Brown 1953, Parker 1974) or be wind-thrown where exposed trees are rooted in thin soils. Conditions in gaps are very variable, much probably depending on their size, but a fairly natural pattern of recolonisation can often be observed, with a flush of growth among the herbaceous survivors and stunted shrubs and saplings of the preceding shade flora and a rapid appearance of young trees from seed. In more disturbed areas, adventive herbs can mask for a time the more usual kind of field layer with plants such as *Verbascum thapsus*, *Epilobium angustifolium*, *Arctium minus* agg., *Atropa belladonna* and *Scrophularia nodosa* becoming very prominent; on somewhat moister soils, *Deschampsia cespitosa*, generally speaking an uncommon grass here, may spread and, in sunnier spots over more stony soils, *Hieracium* spp. and *Inula conyza* can appear in abundance. Again, such vegetation has not been recognised here as constituting a distinct sub-community but is regarded as small-scale variation within the overall framework.

The commonest woody invaders in this kind of situation here are *Fraxinus* and, more locally in areas of higher rainfall, *Acer pseudoplatanus*, and, in smaller gaps, dense thickets of their young saplings commonly form the distinctive dome-shaped regeneration cores described so graphically by Watt (1924, 1925). Single survivors of the intense competition can eventually take their place in the canopy unless the neighbouring *Fagus* crowns expand to fill the space above, but they are often very drawn: perversely, on the deeper and moister soils

where these species grow best, *Fagus* itself tends to have a taller canopy. *A. pseudoplatanus*, being more shade-tolerant than *Fraxinus*, may be a better survivor in this respect (e.g. Watt 1925). Theoretically, *Fagus* itself should be able to emerge from enough gaps sufficiently frequently to maintain its own position in the canopy, but as Watt (1923, 1925) demonstrated, and as many foresters have found to their dismay, its natural regeneration is very unreliable. In essence, only where nearby trees produce sufficient fruit is there any great likelihood of *Fagus* getting away in gaps and, even then, intense shade and invertebrate and vertebrate pests can severely hinder its chances of reaching maturity. Grey squirrel (*Sciurus carolinensis*) damage at the pole stage is now a particularly widespread cause of failure. Where the appearance of small gaps within *Fagus* stands coincides with a mast year, conditions can therefore approach the optimal but, where the seed source is more remote, as in the centre of large gaps, and when fruiting is poor, canopies dominated by *Fraxinus* and *A. pseudoplatanus* may persist for some considerable time, perhaps decades (Rackham 1980, Smith 1980). Such stands are best classified as *Fraxinus*-*Acer*-*Mercurialis* woodland which, on free-draining but moister, base-rich soils within the natural range of *Fagus*, is regarded in this scheme as a seral precursor to *Fagus*-*Mercurialis* woodland.

Quite apart from the fact that this community may have originally attained prominence only as a biotically-assisted climax over the south-eastern limestones, many stands bear obvious signs of more recent treatment. In a very few places, there is evidence of the apparently extensive local use of *Fagus* as an underwood crop, as for example in the Chilterns from medieval times until the eighteenth century, where it was grown with oak or ash standards and cut mainly for fuel (Mansfield 1952, Roden 1968). For the most part, though, over the past 300 years, *Fagus* has been valued as a timber tree, extracted from and encouraged in existing stands of all three kinds of *Fagus* woodland and extensively planted. The present disposition of tracts of the *Fagus*-*Mercurialis* woodland and the canopy structure of individual stands can thus reflect a complex pattern of the waxing and waning interest in ornamental and commercial forestry in recent centuries. In the Chilterns, for example, evidence can be seen of the abandonment of the older coppices, the natural invasion of neglected land after enclosure, early ornamental and shelterbelt planting, the treatment of existing stands and plantations on a selection system to supply local industry, the shift to shelterwood or clear-felling regimes with the rise of modern forestry and the depredations of the wartime fellings (e.g. Brown 1964).

In this region and elsewhere, since *Fagus*-*Mercurialis* woodlands typically occupy the relatively narrow scarp-

land portion of the landscape, they have contributed much less to the beech economy than the more extensive *Fagus*-*Rubus* woodlands of the dip slopes. Also, growing on poorer soils, they yield lower-quality timber (commonly class III or worse: Brown 1953, 1964, McNeill 1961), so promise a lower return on investment. But, in former days, when foresters had to be more content with what there was and labour was cheaper, this community seems to have been widely exploited under the selection system on the Chilterns. One lasting heritage of this seems to be a common preponderance there of smaller, less well formed and poorly-fruited trees as a result of the progressive removal of the larger and better timber (Brown 1953, 1964, Peterken 1981). In recent years, *Fagus* has been widely planted over former Chalk downs or on cleared land in Sussex, Hampshire, Wiltshire and Dorset, often with a short-lived conifer nurse crop, usually *Pinus sylvestris* or *P. nigra* var. *nigra* or var. *maritima*, and with a battery of techniques to encourage good establishment, such as land preparation, application of herbicides and fertilisers, and prevention of predation by rabbits and deer. Such stands have not been included in this survey and it remains to be seen whether they will, in time, progress to *Fagus*-*Mercurialis* woodland.

Zonation and succession

Zonation within individual stands of *Fagus*-*Mercurialis* woodland are generally related to edaphic differences, upon which are superimposed variations related to canopy shade, regeneration and treatment, a pattern very well illustrated in the Cotswold woodlands studied by Barkham & Norris (1967, 1970). In fact, though the sub-communities can be clearly defined in relation to soil differences, transitional stands are very common because of the fairly gentle character of many slopes over the southern limestones and the frequently contorted fronts of their scarps. Generally speaking, however, within individual woodlands which cover a fair range of topographic variation, the trend is for the *Mercurialis* sub-community to give way to the *Sanicula* sub-community over steeper, more exposed slopes with shallower, drier soils, with the *Taxus* sub-community making a more local appearance over the steepest, rockiest ground with high exposure to wind and sun. Very locally, as on Box Hill, in Surrey, the transition continues into *Taxus* woodland proper with a thick undercanopy of *Buxus*.

Many stands of the community now remain as remnant strips of woodland isolated on the more intractable ground of scarps by the conversion of the dip slope above and the vale beneath to intensive agriculture. But in some places, the *Fagus*-*Mercurialis* woodland may run on some way over the dip slope as the *Mercurialis* sub-community on brown rendzinas or brown calcar-

eous earths derived from but thin covers of superficials: this pattern seems most characteristic of the South Downs where fairly base-rich soils are quite extensive on the dip. Often, though, where there is continuity of woodland cover, there is an edaphically-related transition to the *Fagus-Rubus* woodland on deeper, more base-poor and patchily-gleyed brown earths formed from substantial thicknesses of superficials like Clay-with-Flints. Such zonations can be gradual but, where they are sharp, they can be very striking, with an abrupt termination of *Mercurialis*-dominance and a switch to thick tangles of *Rubus*, and a replacement of the poor *Fagus* of the scarp by magnificent trees on the dip.

Intensive farming and forestry of limestone slopes in the south-east, with conversion of the vegetation to improved pasture, arable or plantations, has severely restricted gradual transitions from the *Fagus-Mercurialis* woodland to more natural kinds of herbaceous communities, so that stands are now abruptly defined by artificial boundaries or have, at most, a very narrow fringe of marginal scrub and rank grassland. But, in larger gaps within existing woodlands, and where there is more long-lasting neglect of the surrounding land, fragmentary zonations can be seen which give some clue as to the seral development of this kind of woodland: these were the sorts of situations from which Watt (1924, 1934a) accumulated the data for his hypothesis on succession to beech-domination over more base-rich soils. Although Watt's proposals were based on observation of spatial patterns rather than monitoring through time and undertaken when a combination of severe agricultural depression and good masting in *Fagus* (in 1922) tended to maximise colonisation, his theory still provides a convincing account of how the *Fagus-Mercurialis* woodland can develop and how the major floristic differences within it are prefigured in the scrub, and perhaps also in the grassland, that precede it.

Although Watt recognised a continuous range of variation between both the two major types of mature *Fagus-Mercurialis* woodland, the *Sanicula* and *Mercurialis* sub-communities, and their seral precursors, he defined two extreme lines of succession, the 'Juniper sere' and the 'Hawthorn sere' (termed the 'Juniper-Sanicula sere' and the 'Hawthorn-Mercury sere' by Tansley 1939). In both, a calcicolous scrub was the first major development in pasture where grazing was neglected. Qualitatively, little difference was to be perceived within this vegetation but there was some quantitative polarisation in the frequency and abundance of certain shrubs and trees according to soil conditions. On the more drought-prone, shallower soils developed on steeper slopes in exposed situations, *Juniperus communis* was especially frequent, often abundant and quite vigorous, with a slightly better representation, too, of *Taxus*, *Ilex* and lianes. On deeper, moister soils over gentler slopes

with some measure of shelter, *Crataegus* was usually the dominant and, provided rabbit-grazing did not give it an advantage over *Crataegus*, *Juniperus* was not so prominent, being susceptible to shading. There was thus, early on in the succession, the same exclusion, in the one direction, by edaphic limitation and, in the other, by competition, as could be seen in the mature woodlands in the relationship between *Mercurialis* and *Sanicula*.

Fagus was found to invade both types of scrub though, even with abundant mast, colonisation was slow because of the frequent remoteness of seed-parents along the upper scarp slopes and the relative scarcity of denser patches of scrub to afford protection against rabbit-grazing. However, although the greater resistance of *Juniperus* to rabbit attack might have been expected to allow *Fagus* to thrive better there, it in fact colonised more extensively on the moister soils favoured by *Crataegus*: among the *Juniperus* scrub, there was a characteristically local pattern of dense young *Fagus* clumps; among the *Crataegus*, a more diffuse invasion over more extended areas of ground. More importantly in the short term, the moister soils also favoured a prominence of *Fraxinus* which, though eventually outgrown by the *Fagus*, could come to dominate in a temporary 'ash consociates' interposed between scrub and the mature 'beech consociation', and survive more frequently in the woodland derived from the 'Hawthorn sere' than from the 'Juniper sere'. In the end, however, both lines of succession terminated with the inexorable dominance of *Fagus*, though the different kinds of 'mercury' and 'sanicle' field layer preserved the important edaphic contrast that had been of major importance throughout.

In fact, in the relatively dry climate of the Chilterns, Watt's (1934a) 'ash consociates' was relatively rare but, on the moister South Downs, his earlier work (Watt 1924) and the initial survey by Adamson (1921) showed that woodlands dominated by *Fraxinus* or mixtures of *Fraxinus* and *Quercus robur* (termed 'ash-oak associates'), were of extensive and perhaps quite long-lasting occurrence, on ground which they presumed would eventually carry *Fagus-Mercurialis* woodland (Watt 1934b). As described earlier, large gaps or clear-felled areas within stands of the community can also carry this kind of vegetation, classified in this scheme as *Fraxinus-Acer-Mercurialis* woodland, for long periods before *Fagus* is able to reassert its dominance. Watt (1924) did demonstrate that *Fagus* was able to invade mature stands of this community (an interesting observation in the light of the supposed confinement of the tree in prehistoric forests) but this may be a very haphazard process. There may be some quite subtle edaphic limitations to its expansion, especially on transitional soils which tend to favour either *Fraxinus* or *Q. robur* (e.g. Watt 1934b) and some general climatic restrictions on its spread but, as

Rackham (1980) succinctly puts it, *Fagus* is much more sensitive to weather than to climate and we may have to concede that its local, as well as its regional, prominence and thus the balance between *Fagus-Mercurialis* and *Fraxinus-Acer-Mercurialis* woodlands in any particular area, are partly the result of coincidences of good fruiting and human disturbance, the details of which are frequently irrecoverable.

On the most extreme kinds of *rendzina*, where *Fraxinus* is very unlikely to gain any prominence in the developing woodland, it seems as if the main rival to *Fagus* is *Taxus*. No evidence is available to reveal the successional origin of the *Taxus* sub-community here but, edaphically, it can be seen as an extreme form of the *Sanicula* sub-community and, in the light of Watt's (1926) study of *Taxus* woodlands proper, it seems possible that it develops where *Taxus* gains early prominence in *Juniperus*-dominated scrub and where invasion by *Fagus* is not entirely excluded but where its growth is locally very restricted on extremely shallow and impoverished soils on steep, sun-baked slopes.

Distribution

The *Fagus-Mercurialis* woodland has a wide distribution within the natural range of *Fagus* in Britain, being especially characteristic of the scarps of the North and South Downs, the Chilterns and the western end of the Cotswolds. The *Sanicula* sub-community has been encountered somewhat less frequently than the *Mercurialis* sub-community which has also been recorded in *Fagus* plantations in North Humberside and West Yorkshire. The *Taxus* sub-community is much more local but good examples are to be seen on the south-facing scarp of the North Downs and within some gaps in the Chilterns.

Affinities

In general terms, there is a very good correspondence between this community and its major sub-types and the *Fagetum calcicolum* described in the classic studies of Watt (1924, 1934a, b) and summarised in Tansley (1939) and Rackham (1980), although, as defined here, the *Fagus-Mercurialis* woodland takes in a little of the early workers' *Fagetum rubosum* and some stands transitional to yew woods. In this respect, the treatment is similar to that adopted by Peterken (1981) in the recognition of his stand type 8C of calcareous pedunculate oak-ash-beech woods, though the internal division of his community is based on the representation of different woody species and does not therefore correspond to the sub-communities defined here. He also includes within this type certain woodlands with *Fagus* from south Wales which are considered in this scheme to fall within the *Teu-*

rium sub-community of the *Fraxinus-Acer-Mercurialis* woodland.

The widespread occurrence of calcicolous beech-woods throughout Europe was first revealed in the exchanges of the Fifth International Botanical Congress (Watt & Tansley 1930 and accompanying papers) and has since been amplified in a variety of phytosociological investigations. These reveal a close general similarity between the *Fagus-Mercurialis* woodland and a range of associations now usually grouped in the *Galio odorati-Fagion* or *Cephalanthero-Fagion* sub-alliances (*sensu* Ellenberg 1978) within the *Fagion*: for example, the *Fagetum boreoatlanticum* from north-west Germany (Tüxen 1937) and Belgium (LeBrun *et al.* 1949), the *Elymo europaei-Fagetum* from the Schwäbischer Alps (Kühn 1937) and the Mittelgebirge (Hartmann & Jahn 1967), the *Endymio-Fagetum mercurialetosum* from north-west France (Noirfalise & Sougniez 1963), the *Carici albae-Fagetum* from the Swiss Jura (Moor 1952), the *Viola reichenbachianae-Fagetum* from Czechoslovakia (Moravec 1979) and the *Cephalanthero-Fagetum* in which Oberdorfer (1957) subsumed a number of communities previously described from southern Germany and France. Within and between some of these woodland types, it is possible to see a reflection of the differences which characterise the different sub-communities here: in the contrasts between the *Cephalanthero-Fagetum typicum* and *caricetosum digitatae* and the closely-related *Taxo-Fagetum* which Oberdorfer (1957) describes, for example, and in the woodlands compared in Moravec's (1979) synopsis. But these Continental *Fagion* woodlands are often much richer in species which are only occasional or often rare in British stands (e.g. *Cephalanthera damasonium*, *Neottia nidus-avis*, *Polygonatum multiflorum*, *Convallaria majalis*, *Daphne mezereum*, *Hordelymus europaeus*, *Cardamine bulbifera*) and they span a much greater altitudinal range, since calcareous bedrocks occur commonly in more mountainous areas within the range of *Fagus*-prominence, a combination of circumstances not met with in this country (see, for example, Ellenberg 1978).

As in other parts of north-west Europe, the occurrence of more calcicolous *Fagus* woodlands in Britain is strongly restricted by edaphic conditions since many of the more base-rich soils are of too impeded drainage for *Fagus* to thrive. Our *Cephalanthero-Fagion* community (*Fagus-Mercurialis* woodland) and our major calcicolous Carpinion community (*Fraxinus-Acer-Mercurialis* woodland) thus show the same general edaphic replacement but close floristic relationships that their counterparts exhibit in northern France, Belgium and The Netherlands (e.g. Noirfalise 1968).

Floristic table W12

	a	b	c	12
<i>Fagus sylvatica</i>	V (4–10)	V (3–10)	V (5–10)	V (3–10)
<i>Aesculus hippocastanum</i>	I (2–6)	I (2)	I (2–5)	I (2–6)
<i>Betula pendula</i>	I (1–3)	I (4)	I (2)	I (1–4)
<i>Fraxinus excelsior</i>	IV (1–7)	I (2–5)	II (3–5)	III (1–7)
<i>Acer pseudoplatanus</i>	III (1–6)	I (2–6)	I (3–5)	II (1–6)
<i>Quercus robur</i>	II (1–6)	I (2)	I (3)	I (1–6)
<i>Prunus avium</i>	I (2)		I (3)	I (2–3)
<i>Carpinus betulus</i>	I (2–4)			I (2–4)
<i>Betula pubescens</i>	I (3)			I (3)
<i>Taxus baccata</i>	I (1–5)	I (3)	V (3–8)	II (1–8)
<i>Sorbus aria</i>	I (3)	I (2)	II (3–5)	I (3–5)
<i>Corylus avellana</i>	III (2–7)	II (2–6)	I (3)	II (2–7)
<i>Crataegus monogyna</i>	II (1–7)	I (2–7)	I (3–5)	II (1–7)
<i>Acer pseudoplatanus</i> sapling	III (2–6)	I (3–5)	I (3–5)	II (2–6)
<i>Fagus sylvatica</i> sapling	III (1–7)	I (1–4)		II (1–7)
<i>Acer campestre</i>	II (2–4)	I (2–7)	I (4)	I (2–7)
<i>Sambucus nigra</i>	II (2–4)	I (2–5)	I (3–4)	I (2–5)
<i>Fraxinus excelsior</i> sapling	II (2–6)			I (2–6)
<i>Euonymus europaeus</i>	I (1–3)	I (2)	I (5)	I (1–5)
<i>Viburnum opulus</i>	I (2–4)	I (4)		I (2–4)
<i>Betula pubescens</i> sapling	I (1–4)			I (1–4)
<i>Ulmus glabra</i> sapling	I (3–4)			I (3–4)
<i>Taxus baccata</i> sapling	I (3–4)			I (3–4)
<i>Sorbus aria</i> sapling	I (3)			I (3)
<i>Quercus robur</i> sapling	I (3)			I (3)
<i>Ligustrum vulgare</i>	I (3–5)	II (2–4)	I (3–6)	I (2–6)
<i>Viburnum lantana</i>	I (3–4)	II (1–5)	I (2)	I (1–5)
<i>Ilex aquifolium</i>	I (2–7)	II (2–4)	I (5)	I (2–7)
<i>Cornus sanguinea</i>	I (2–3)	II (3–5)		I (2–5)
<i>Buxus sempervirens</i>			II (4–6)	I (4–6)
<i>Mercurialis perennis</i>	IV (2–10)	IV (2–7)	II (2–7)	IV (2–10)
<i>Rubus fruticosus</i> agg.	IV (1–10)	II (2–7)	II (2–4)	III (1–10)
<i>Circaea lutetiana</i>	II (2–8)	I (3–4)	I (3)	I (2–8)
<i>Hyacinthoides non-scripta</i>	II (2–10)	I (3)	I (3)	I (2–10)
<i>Arum maculatum</i>	II (2–4)	I (2–4)	I (2)	I (2–4)
<i>Fissidens taxifolius</i>	II (2–5)	I (3)	I (4)	I (2–5)
<i>Galium odoratum</i>	II (1–5)	I (2–4)		I (1–5)
<i>Dryopteris filix-max</i>	II (1–3)	I (3)		I (1–3)
<i>Lamium galeobdolon</i>	II (3–7)	I (3)		I (3–7)
<i>Allium ursinum</i>	I (3–7)			I (3–7)
<i>Anemone nemorosa</i>	I (3–7)			I (3–7)
<i>Dryopteris dilatata</i>	I (1–4)			I (1–4)
<i>Ranunculus ficaria</i>	I (3–6)			I (3–6)

<i>Epilobium montanum</i>	I (1–5)			I (1–5)
<i>Phyllitis scolopendrium</i>	I (1–6)			I (1–6)
<i>Thamnium alopecurum</i>	I (3–8)			I (3–8)
<i>Solidago virgaurea</i>	I (1–3)			I (1–3)
<i>Sanicula europaea</i>	I (3–4)	III (3–8)	II (2–3)	II (2–8)
<i>Mycelis muralis</i>	I (1–3)	III (2–4)	I (2–3)	II (1–4)
<i>Melica uniflora</i>	I (3–6)	III (3–6)	I (3)	II (3–6)
<i>Poa nemoralis</i>	I (3–5)	III (3–6)		II (3–6)
<i>Tamus communis</i>	I (1–3)	III (2–6)	I (1)	II (1–6)
<i>Clematis vitalba</i>	I (1–4)	II (2–5)	I (1–8)	I (1–8)
<i>Bromus ramosus</i>	I (1–4)	II (2–7)	I (3)	I (1–7)
<i>Rumex sanguineus</i>	I (1–2)	II (3–4)		I (1–4)
<i>Cephalanthera damasonium</i>		II (3–5)	I (2–3)	I (2–5)
<i>Heracleum sphondylium</i>		I (2–4)		I (2–4)
<i>Ranunculus bulbosus</i>		I (2–3)		I (2–3)
<i>Galium mollugo</i>		I (2–5)		I (2–5)
<i>Anthriscus sylvestris</i>		I (3–4)		I (3–4)
<i>Arctium minus</i> agg.		I (2–3)		I (2–3)
<i>Arrhenatherum elatius</i>		I (2–4)		I (2–4)
<i>Carex flacca</i>		I (1–2)		I (1–2)
<i>Ajuga reptans</i>		I (2–3)		I (2–3)
<i>Neottia nidus-avis</i>		I (2)		I (2)
<i>Cynoglossum officinale</i>		I (2)		I (2)
<i>Bromus sterilis</i>		I (3)		I (3)
<i>Hypericum hirsutum</i>		I (2)		I (2)
<i>Hedera helix</i>	IV (3–10)	IV (2–10)	I (6)	III (2–10)
<i>Brachypodium sylvaticum</i>	III (2–5)	II (2–5)		II (2–5)
<i>Viola riviniana/reichenbachiana</i>	II (2–6)	II (2–4)	I (2–3)	II (2–6)
<i>Fraxinus excelsior</i> seedling	II (1–5)	II (2–3)	I (3–4)	II (1–5)
<i>Fagus sylvatica</i> seedling	I (1–3)	III (2–8)	II (2–4)	II (1–8)
<i>Brachythecium rutabulum</i>	I (2–4)	II (3–4)	II (3–4)	II (2–4)
<i>Eurhynchium praelongum</i>	II (2–5)	I (3)	II (2–4)	II (2–5)
<i>Urtica dioica</i>	II (2–4)	II (1–4)		I (1–4)
<i>Geranium robertianum</i>	II (1–5)	II (2–7)		I (1–7)
<i>Galium aparine</i>	I (2–3)	II (2–4)	I (3)	I (2–4)
<i>Veronica chamaedrys</i>	I (4)	II (2–3)	I (2)	I (2–4)
<i>Acer pseudoplatanus</i> seedling	I (1–3)	II (1–3)	I (2)	I (1–3)
<i>Taxus baccata</i> seedling	I (1–3)	II (2)	I (1–2)	I (1–3)
<i>Fragaria vesca</i>	I (3–5)	I (2–3)	I (2)	I (2–5)
<i>Geum urbanum</i>	I (1–4)	I (2–5)	I (2)	I (1–5)
<i>Iris foetidissima</i>	I (6)	I (2)	I (3)	I (2–6)
<i>Carex sylvatica</i>	I (2–5)	I (2–3)		I (2–5)
<i>Rosa canina</i> agg.	I (1–3)	I (2–3)		I (1–3)
<i>Crataegus monogyna</i> seedling	I (1–4)	I (2–3)		I (1–4)
<i>Epilobium angustifolium</i>	I (2–3)	I (2–3)		I (2–3)
<i>Stachys sylvatica</i>	I (2–4)	I (2–5)		I (2–5)
<i>Primula vulgaris</i>	I (3–4)	I (3–4)		I (3–4)
<i>Campanula trachelium</i>	I (2–3)	I (5)		I (2–5)
<i>Mnium hornum</i>	I (3–4)	I (3)		I (3–4)

Floristic table W12 (*cont.*)

	a	b	c	12
<i>Teucrium scorodonia</i>	I (3–6)	I (3)		I (3–6)
<i>Dactylis glomerata</i>	I (3)	I (2–3)		I (2–3)
<i>Milium effusum</i>	I (3–4)	I (3)		I (3–4)
<i>Daphne laureola</i>	I (1–3)	I (1–2)		I (1–3)
<i>Alliaria petiolata</i>	I (2–4)	I (3)		I (2–4)
<i>Ilex aquifolium</i> seedling	I (1–5)	I (3)		I (1–5)
<i>Plagiomnium undulatum</i>	I (3–4)	I (5)		I (3–5)
<i>Euphorbia amygdaloides</i>	I (1–3)	I (3)		I (1–3)
<i>Listera ovata</i>	I (2–3)	I (2–4)		I (2–4)
<i>Silene dioica</i>	I (3–4)	I (2–3)		I (2–4)
<i>Deschampsia cespitosa</i>	I (1–7)	I (4)		I (1–7)
<i>Lonicera periclymenum</i>	I (2–4)	I (3)		I (2–4)
<i>Glechoma hederacea</i>	I (3)	I (4)		I (3–4)
<i>Poa trivialis</i>	I (2–5)	I (3)		I (2–5)
Number of samples	57	30	22	109
Number of species/sample	21 (9–43)	24 (16–36)	9 (3–16)	19 (3–43)
Tree height (m)	19 (10–35)	14 (8–25)	12 (8–15)	16 (8–35)
Tree cover (%)	92 (50–100)	90 (50–100)	97 (90–100)	93 (50–100)
Shrub height (m)	4 (2–10)	2 (1–5)	3 (1–7)	3 (1–10)
Shrub cover (%)	18 (0–60)	10 (0–50)	8 (0–40)	14 (0–60)
Herb height (cm)	37 (15–100)	31 (10–75)	14 (2–40)	31 (2–100)
Herb cover (%)	87 (25–100)	81 (10–100)	19 (0–100)	72 (0–100)
Ground height (mm)	13 (0–50)	10 (10–20)	10	12 (10–50)
Ground cover (%)	8 (0–90)	9 (0–100)	1 (0–10)	7 (0–100)
Altitude (m)	129 (30–260)	112 (56–200)	143 (60–210)	127 (30–260)
Slope (°)	10 (0–85)	8 (2–15)	9 (0–30)	9 (0–85)

a *Mercurialis perennis* sub-communityb *Sanicula europaea* sub-communityc *Taxus baccata* sub-community12 *Fagus sylvatica*-*Mercurialis perennis* woodland (total)

