W16
Quercus spp.-*Betula* spp.-*Deschampsia flexuosa* woodland

Synonymy

Oak-birch-heath association   Moss *et al.* 1910, Tansley 1911; *Quercetum arenosum roburis et sessiliflorae* Tansley 1911 *p.p.*; *Quercetum ericetosum* Tansley 1911, 1939; *Quercetum sessiliflorae* Moss 1911, 1913 *p.p.*; Dry oak-birchwood Hopkinson 1927 *p.p.*; Southern Pennine oakwoods Scurfield 1953 *p.p.*; Oakwoods Pigott 1955 *p.p.*; *Querco-Betuletum* Klötzli 1970 *p.p.*; Oakwoods Rackham 1980 *p.p.*; Birchwoods Rackham 1980 *p.p.*; Birch-oak woodland Peterken 1981 *p.p.*; Birch woodland Peterken 1981 *p.p.*; Woodland plot type 18   Bunce 1982 *p.p.*

Constant species

Betula pendula/pubescens, Quercus petraea/robur, Deschampsia flexuosa, Pteridium aquilinum.

Physiognomy

The *Quercus* spp.-*Betula* spp.-*Deschampsia flexuosa* woodland is a much less species-rich and less variable community than its mixed deciduous counterparts and much less complicated by the effects of treatment. In essence, these are oak-birch woodlands: oak and birch are very much the most frequent trees throughout and the usual dominants, alone or in mixtures. Both species of oak are well represented, their distribution showing the same general pattern as in the *Quercus-Pteridium-Rubus* woodland. *Quercus robur* predominates over most of the southerly parts of the range, apart from those striking enclaves, such as parts of the Weald, south-east Essex and Sherwood Forest in Nottinghamshire, where it is partly replaced by *Q. petraea* and hybrids (Jones 1959, Gardiner 1974). In these areas, the favouring of *Q. robur* as the plantation oak and the greater facility with which it colonises open ground, tend to sharpen up the difference between older stands, many of which are coppiced, with *Q. petraea*, and younger stands with *Q. robur*, a feature reflected in the views of Rackham (1980) on East Anglian examples of this kind of woodland. Towards the north-western fringes, *Q. petraea* prevails almost exclusively, even in younger tracts.

Oak can dominate here in high-forest canopies which are virtually closed, though the trees are not always tall, especially in more exposed sites at higher altitudes along the Pennine fringes (e.g. Moss 1911, 1913, Scurfield 1953, Pigott 1955). A complete cover of oak is also characteristic of some plantation stands included here. Quite commonly, however, the oak canopy is somewhat open, not only in younger woodlands where colonisation is not far advanced, but also in wood-pasture stands, in which form this community makes an important contribution to the landscape of some of our older Forests like Sherwood (Hopkinson 1927), Epping and parts of the New Forest (Tubbs 1968, Rackham 1980, Peterken 1981) and smaller parks like Staverton (Peterken 1969). Here, magnificent venerable oaks can survive with obstinate individuality among extensive lawns of the field layer of the community, providing historical continuity with an earlier kind of land use and invaluable habitats for invertebrates and lichens (e.g. Welch 1972, Rose 1974). Many of these ancient oaks were pollarded but coppiced oak underwood is quite common in older stands of the community too, with or without oak standards, and long-neglected moots can attain great size (Rackham 1980, Peterken 1981).

Birch can occur as an occasional in the canopy here but, throughout the community as a whole, it easily rivals oak in frequency and is quite commonly the more abundant tree, especially with the neglect of traditional treatments of coppice and wood-pasture and the abandonment of the grazing, cutting and burning of heathlands, over which the community has greatly increased its spread over the past century or so. The *Quercus-Betula-Deschampsia* woodland therefore includes many stands in which oak is sparse or absent, and where birch dominates as an open or patchy canopy or as dense thickets. In some existing schemes (e.g. Tansley 1911, Rackham 1980, Peterken 1981), such woodlands have been treated separately but, apart from the variation in the proportions of oak and birch, there is no floristic justification for this. Both species of birch (and intermediates) occur but their regional separation

is less well marked than that of the oaks: *Betula pubescens* is quite common here in the south-east among constant *B. pendula*; to the north-west, the latter species maintains itself at similar frequencies to *B. pubescens*.

No other larger woody species attains anything like the predominance of oak and birch here but, quite commonly, there is some *Pinus sylvestris*. This can be an abundant invader of heathlands, especially where, as is often the case, there are some plantations nearby, and it can persist as a prominent canopy component in sub-spontaneous stands, regenerating well in gaps, even where the woodlands are browsed and grazed (Tansley 1911, 1939, Wooldridge & Goldring 1953; Tubbs 1968). Plantations of pine themselves, where they occur on soils that would normally support this community, can be included within it. Denser stands are virtually bereft of any associates but margins, rides and clearings and older, more open tracts, which are very common in long-established plantations in the Weald and Breckland, have the characteristic field layer. Less commonly, *P. nigra* var. *maritima*, *Larix* spp., *Picea sitchensis*, *P. abies*, *Tsuga heterophylla* and *Pseudotsuga menziesii* can be found as canopy replacements.

One other tree which finds an occasional place in the canopy here is *Fagus sylvatica* but typically it is not abundant, and stands where more balanced mixtures of oak and beech occur over this kind of calcifugous field layer found in this community, a common feature in the New Forest and parts of the Chilterns, fall within the *Fagus-Deschampsia* woodland. *Castanea sativa* can sometimes be found (the community perhaps includes some of the more extreme 'chestnut-oak' woods of Rackham 1980) and, very occasionally, *Sorbus aria* and *Populus tremula*. *Acer pseudoplatanus* is typically scarce, even to the wetter north-west, and *Fraxinus excelsior* and *Ulmus* spp. are hardly ever found.

In some stands, the most characteristic of the smaller woody species of the community, *Sorbus aucuparia* and *Ilex aquifolium*, can also contribute to the main tier of trees. Neither of these is very frequent here, though *S. aucuparia* is markedly more common to the north-west, and, throughout, their occurrence is probably much affected by grazing and browsing, to which both are very sensitive. On ungrazed pasture and heath, both can be abundant invaders, *Ilex* especially having the facility to persist as a local dominant in this kind of woodland, as in some of the New Forest holms (Peterken & Tubbs 1965, Tubbs 1968, Géhu 1975b) and the remarkable Thicks at Staverton Park (Peterken 1969, Rackham 1980) where huge hollies, with a continuous range of descendants down to seedlings, prevail over many hectares. Both *S. aucuparia* and *Ilex* are shade-tolerant and will persist if overtopped by oak: in high-forest stands here, they usually comprise the bulk of the understorey, though generally as an open cover of scattered bushes.

Small woody associates are rare, with *Crataegus* spp. and *Corylus avellana* both being strikingly uncommon. The scarcity of the latter is especially noteworthy: in the southern lowlands of Britain, the frequency of *Corylus* provides a good separation among oak woodlands between this community and the *Quercus-Pteridium-Rubus* woodland, where it is very common, often abundant and has been widely favoured as a coppice crop. In the sub-montane analogues of these two communities, the same distinction does not hold true, *Corylus* transgressing a considerable way on to more surface-leached soils (cf. Peterken 1981).

Other species encountered occasionally are *Frangula alnus*, sometimes prominent too in young stands among invading trees (e.g. Géhu 1975b), *Sambucus nigra*, particularly in disturbed situations like plantations, and *Rhododendron ponticum*, widely planted as an ornamental in this kind of woodland and sometimes spreading to become an abundant and virtually ineradicable weed (Cross 1975).

Where there has been some relaxation of grazing or burning, saplings can be abundant in gaps and, in younger tracts of the community, can provide the bulk of the woody cover around pioneer trees and on expanding margins of more well-established stands. Along with smaller specimens of *Ilex* and *S. aucuparia*, young birch and oak can be plentiful, though the representation of these too is very dependent on the treatment history (e.g. Jones 1959, Pigott 1983). Saplings of *A. pseudoplatanus* can also sometimes be found, more often than canopy trees of this species, though much less commonly than seedlings.

The field layer here is characteristically species-poor but variations on its simple composition are quite wide. The two most consistent elements are *Deschampsia flexuosa* and *Pteridium aquilinum*. The high frequency of the former provides a good separation between this community and the *Quercus-Pteridium-Rubus* woodland, where *D. flexuosa* is uncommon and sparse, especially in the drier south-east. Here, it occurs very frequently and often in considerable abundance, particularly on the shallower soils where the community occurs over more massively bedded sandstones (a typical situation to the north-west) and where the vegetation is open to grazing. Then it can form a virtually continuous sward, close-cropped but rather hummocky, non-flowering in deep shade, and giving the field layer an unvarying dark green colour throughout the year, a very distinctive feature of Pennine woodlands of this kind that are open to sheep and deer (e.g. Moss 1911, 1913, Scurfield 1953, Pigott 1983). Where grazing is relaxed, *D. flexuosa* grows taller and flowers more prolifically but it also begins to trap tree leaf litter which was previously blown off its own short, fine foliage. This is of profound significance not only for its own survival (it tends to be

smothered and to die), but also for the subsequent establishment of birch (Pigott 1983: see below). In ungrazed stands, then, the cover of *D. flexuosa* becomes more patchy and confined to knolls and the surfaces of buried boulders standing proud of the slope.

Often, in stands with an uneven occurrence of soils of different depths, such patterning is accentuated by the inverse distribution of *Pteridium* but, where the soils are uniformly of moderate depth and the shade cast by the trees not too intense, bracken may be overwhelmingly dominant by mid-summer, forming a vigorous and dense canopy of fronds often more than a metre high and excluding virtually all other herbs with its own deep shade and thick, slowly-rotting litter. Under more densely shading covers of trees, whether in long-established oak high forest or coppice or beneath thick stands of birch, *Pteridium* may be more restricted, occurring in gaps and rides and along the margins, and continuing its cover into larger clearings, the lawns of wood-pasture areas or on to stretches of as yet uncolonised heathland. It can also come and go somewhat as trees fall or are cropped in coppices and then replaced by regeneration or regrowth, but rapid and extensive expansion of bracken can severely hinder the re-establishment of a woody cover. In stands with heavy amenity use (as on the commons of south-eastern England), the patterning in the *Pteridium* canopy, with its colour change through the year from fresh green to russet (virtually the only phenological variation shown by the field layer), provide a much-valued delight.

In contrast to the *Quercus-Pteridium-Rubus* woodland, *Pteridium* is not consistently accompanied here by an underscrub of *Rubus fruticosus* agg. and *Lonicera periclymenum*. *Rubus* occurs occasionally, *Lonicera* more rarely and, though they may thicken up somewhat when grazing is relaxed or after coppicing, they are typically present only as sparse, trailing shoots, providing little cover for small mammals, a feature of significance to the survival of tree seedlings (Pigott 1984). In some localities, as in parts of Surrey and Kent, *Gaultheria shallon*, an exotic undershrub used as pheasant cover, has become naturalised in this kind of woodland, spreading by seed and stolons.

Much more characteristic here, as bulkier components of the field layer, are ericoid sub-shrubs, particularly *Vaccinium myrtillus* and *Calluna vulgaris*, less commonly *Erica cinerea* and rarely, to the north-west, *V. vitis-idaea*. *V. myrtillus* is the most typical species of closed woodlands here, except where the shade is very dense, though it is more frequent in areas of higher rainfall (like the Weald, the north-west Midlands and more so the Pennines) and its prominence is very dependent on the intensity of grazing (Moss 1913, Scurfield 1953, Pigott 1983). Where the field layer is grazed, it is typically nibbled down to sparse shoots in a *Deschamp-*

sia sward, or to closely-browsed mats distributed over the surfaces of boulders, but it expands its cover and height substantially with enclosure, to the eventual detriment of *V. vitis-idaea* where both occur together, as in rockier Pennine woods (Pigott 1983). *Calluna* also occurs quite commonly, but it is very much a plant of more open places, surviving in colonised stretches of heathland until the canopy closes, after which it becomes leggy and eventually disappears, occurring thereafter largely in gaps or after coppicing (even in stands well away from heaths and then presumably surviving as buried seed: Rackham 1980). *E. cinerea* is likewise a species of more open mosaics of the community among heathland.

By and large, it is differences in the proportions of these elements, a *D. flexuosa* sward, a canopy of *Pteridium* and clumps of ericoids, which give the field layer of this kind of woodland its distinctive stamp and variety, whether on the wooded commons of south-eastern England, in oak coppices and the wood-pasture of ancient Forest or in the typical Pennine oakwood. But other species are quite characteristic at low frequencies and provide local enrichment and, when they are present in some abundance, a small measure of physiognomic variety. Quite commonly there are some other grasses along with *D. flexuosa*. *Agrostis capillaris* and *Anthoxanthum odoratum* occur occasionally and may attain prominence in more closely grazed field layers. *Holcus mollis* can also be found. This is more obviously a plant of the *Quercus-Pteridium-Rubus* woodland in southern Britain and its edaphic preferences as against those of *D. flexuosa*, which prefers and helps to maintain mor, are quite well marked (Jowett & Scurfield 1949, 1952). *H. mollis* can occur here wherever there is a slight shift towards mull conditions on moister and somewhat less acid soils, as where less freely draining drift occurs among sandy superficials or where head or downwashed soil has accumulated on gentler slopes or among boulders (e.g. Woodhead 1906, Moss 1913, Scurfield 1953). *H. mollis* also traps tree leaf litter better than does *D. flexuosa* even in grazed swards, and survives its blanketing effect more successfully, being more extensively rhizomatous, so it may encourage the local maintenance of mull conditions and, where it occurs in mosaics with *D. flexuosa*, expand its cover against it (Ovington 1953).

Other grasses occurring occasionally are *Holcus lanatus*, which is often associated with disturbed situations, as after coppicing or in plantations, and *Deschampsia cespitosa* and *Molinia caerulea*, both of which are generally scarce here but which sometimes mark areas with moister soils or transitions to flushes or wetter stretches of heath. Sedges are characteristically rare, but *Luzula pilosa* sometimes occurs and *L. sylvatica*, though uncommon, can show striking local abundance in

ungrazed stands, spreading over more inaccessible steeper slopes in valley-side woodlands, often to the exclusion of all other herbs.

One very marked and valuable distinction between this community and the *Quercus-Pteridium-Rubus* woodland is the great scarcity here of *Hyacinthoides non-scripta*: at most, this is of very local occurrence, usually marking out patches of mull, with *Holcus mollis*. In the absence of this plant and other spring-flowerers, the community typically has no vernal aspect to its field layer, though *Convallaria majalis* occurs locally, providing an attractive show of flowers in May and June. Other vascular associates are often limited to scattered individuals in areas free of substantial bracken or ericoid cover, nibbled down in grazed stands and often not flowering under more complete tree canopies. Among the more characteristic of these plants are *Galium saxatile*, *Potentilla erecta*, *Teucrium scorodonia*, *Corydalis claviculata*, *Digitalis purpurea*, *Solidago virgaurea* and *Rumex acetosella*. All of these may become more prominent in gaps and clearings or after coppicing, together with *Epilobium angustifolium*, persistent clumps of which may mark quite localised areas of disturbance or fire, a not uncommon occurrence in stands on heaths (e.g. Hopkinson 1927, Rackham 1980, Pigott 1983). *Ulex europaeus* and *Cytisus scoparius* can also figure in such situations.

One other occasional component of the field layer is *Hedera helix* but this is nothing like so common here as in the *Quercus-Pteridium-Rubus* woodland, in the range of which moister soils occur widely in areas of more equable climate. Edaphic and atmospheric dryness also restrict the occurrence of ferns in the community: *Blechnum spicant* occurs very sparsely throughout but *Dryopteris dilatata* is confined to north-western stands and more mesophytic dryopteroids and *Athyrium filix-femina* are typically absent.

Seedlings of all the major woody species of the community can also be found in the field layer, though their frequency and abundance, as well as their ultimate fate, are strongly influenced by the past and present treatment, the subtle effects of which on regeneration are discussed below. Seedlings of *A. pseudoplatanus* can also be found in small quantities though, even when there is no grazing, these do not get away here with anything like the facility this species shows on moister and more base-rich soils.

The dry character of the soils here and the low atmospheric humidity also play a part in limiting the contribution which bryophytes make to this vegetation over the more easterly parts of its range. And, though there is a clear increase in their variety and abundance to the wetter north-west, where they help define the *Vaccinium-Dryopteris* sub-community, many stands there are heavily affected by atmospheric pollution which res-

tricts the expression of this element. However, there are usually some small patches of a variety of species and cover may thicken up under the shelter of more open bushes of *Vaccinium* or *Calluna*, over tree bases and on the more open risers of terracettes which commonly develop on steeper slopes. Among the characteristic species are *Dicranum scoparium* and *Hypnum cupressiforme s.l.* (both of which can persist sparsely under dense bracken or in conifer plantation replacements), *Dicranella heteromalla*, *Isopterygium elegans*, *Mnium hornum*, *Campylopus paradoxus*, *Dicranoweissia cirrata*, *Pleurozium schreberi*, *Eurhynchium praelongum*, *Lophocolea bidentata s.l.* and the more pollution-tolerant *Orthodontium lineare* and *Pohlia nutans*. *Leucobryum glaucum* sometimes occurs but not so often as in the beech-dominated analogue of this community, the *Fagus-Deschampsia* woodland.

Sub-communities

***Quercus robur* sub-community:** Oak-birch-heath association Moss *et al.* 1910, Tansley 1911; *Quercetum arenosum roburis et sessiliflorae* Tansley 1911 *p.p.*; *Quercetum ericetosum* Tansley 1911, 1939; Dry oak-birchwood Hopkinson 1927 *p.p.*; *Querco-Betuletum* Klötzli 1970 *p.p.*; Oakwoods Rackham 1980 *p.p.*; Birchwoods Rackham 1980 *p.p.*; Birch-oak stand types 6Cb & 6Db Peterken 1981 *p.p.*; Woodland plot type 18 Bunce 1982 *p.p.* When oak occurs in the woodlands of this sub-community, which is more often than not, it is typically *Q. robur*, except in the *petraea* enclaves. Quite commonly, oak is the woody dominant, in high forest or neglected coppice, where it also provides such standards as are present, or is a long-established tree in wood-pasture where the individuals can be more widely spaced. In other stands, oak is frequent but of low abundance, as where younger woodlands are developing by invasion of open heath or where, with abandonment of traditional treatments, birch (or pine or, more locally, holly and rowan) have increased their proportion of the cover. In fact, stands dominated wholly by birch, usually *B. pendula* here with occasional *B. pubescens*, or by admixtures of birch and pine, to the exclusion of oak, are quite widespread. They may have been a long-standing feature in some places, like the striking landscape of Birklands in Sherwood Forest (Hopkinson 1927, Rackham 1980), but elsewhere are clearly related to a relaxation of the agricultural use of heaths, over which there characteristically develops a mosaic of stands of differing age and composition with intervening stretches of open ericoid vegetation, as on the commons of Surrey and the western Weald, where this patchwork of communities was early described as 'oak-birch-heath' (e.g. Moss *et al.* 1910, Tansley 1911, 1939, Wooldridge & Goldring 1953) and in the New

Forest (Peterken & Tubbs 1965, Tubbs 1968).

Apart from *Pinus sylvestris*, which is quite common here not only as an invader but as a canopy replacement in older plantations (it has fallen from favour somewhat in the south-east in more recent times) and *Fagus sylvatica*, which can become common in areas where beech figures prominently in semi-natural woodlands or plantations, other larger canopy trees are scarce. Smaller trees and shrubs are also infrequent here in well-established stands and, in high forest, the understorey is typically sparse with occasional *Ilex*, a little *Sorbus* and, in ungrazed situations, a few saplings of oak and birch in gaps.

Generally, however, the view beneath the trees is dominated by an abundance of *Pteridium* or, in areas of deeper shade, a sparser bracken cover over a *D. flexuosa* sward. In gaps, around margins and amongst newly-colonising stands on heaths, *Calluna* becomes common and there may also be some *E. cinerea* and *Ulex europaeus* and, in southerly stands, *U. gallii* or *U. minor*, sometimes with a little *Molinia*, the sequence of purple and golden flowers of these shrubs giving the patchwork of vegetation a delightful aspect. *Vaccinium* occurs here, too, surviving a quite dense shade, though it is restricted to stands in areas of higher rainfall, like the western Weald, the New Forest and the north-west Midlands, and its abundance is much affected by grazing.

The frequency of disturbance in many of these woodlands, whether through occasional fires on heaths or planting and felling, makes for a slightly preferential occurrence of species such as *Holcus lanatus*, *Festuca rubra*, *Agrostis stolonifera* and *Pseudoscleropodium purum* but, apart from these plants, the field and ground layers show no distinctive features.

Vaccinium myrtillus-Dryopteris dilatata sub-community:
Quercetum sessiliflorae, heathy sub-association Moss 1911, 1913; Southern Pennine oakwoods, *Deschampsia-Vaccinium* type Scurfield 1953; Oakwoods Pigott 1956*b p.p.*; Birch-oak stand type 6Ab Peterken 1981 *p.p.*; Woodland plot type 18 Bunce 1982 *p.p.* In contrast to the former sub-community, the oak here is almost invariably *Q. petraea* and commonly it is an overwhelming dominant in high forest with a well-defined, though not always very tall, canopy in which birch (both species and intermediates) is limited to more occasional occurrences in gaps or to margins (e.g. Moss 1911, 1913, Scurfield 1953, Pigott 1956*b*, 1983). Some stands are obviously of planted origin and may show ornamentation with *Pinus, Larix* spp. or *Fagus*, well beyond its natural range here. Other tracts show signs of coppicing for oak.

Many of these woodlands have a poorly-developed understorey, a reflection of the fact that they are often open to sheep and deer. However, *S. aucuparia* is preferentially frequent in this sub-community and *Ilex* occurs quite commonly too and these are the typical components of any second tier of trees, sometimes growing large enough to break the main canopy. In those situations where younger woodlands are developing, quite a rare occurrence in the region but sometimes to be seen on heaths which are no longer burned or grazed or in abandoned quarries, *S. aucuparia* can figure prominently alongside birch (and pine if seed-parents are close), with scattered oak, in low and patchy thickets.

The field layer here preserves the general picture in the community of mixtures of *D. flexuosa*, *Pteridium* and ericoids but often here these are disposed over the varied topography of valley sides with rock exposures and talus above, head and colluvium below, the distribution of which can produce distinctive patterns among these dominants. *Pteridium*, for example, is often limited largely to the deeper soils of the lower slopes, becoming sparse above and increasingly restricted to pockets between the scree fragments. *Vaccinium*, by contrast, though preferentially frequent in this sub-community is often much reduced by grazing on gentler slopes, where *D. flexuosa* forms a sward in unenclosed woods, and attains high and luxuriant cover only over more blocky talus, where it thrives on shallow rankers. Here, too, where the tree cover often thins out to smaller and more widely scattered individuals, *Calluna* can make a contribution.

One other species which frequently figures in the field layer is *Dryopteris dilatata*, a better preferential than *Vaccinium*, and a good indicator of the fact that the soils, though strongly leached, are kept moderately moist by the higher rainfall in the region. It can be very abundant, creating a rather stately impression where its crowns occur thickly scattered among a *D. flexuosa* sward. However, the soils are not so moist as to allow *Oxalis acetosella* to make more than a very occasional appearance here and never have that combination of moisture and somewhat greater fertility so favoured by *Viola riviniana*, its frequent associate in woods towards the north-west of Britain.

A further response to the moister climate, though one often offset in the southern Pennines by atmospheric pollution from the nearby industrial conurbations, is seen in the increased richness and abundance of the bryophyte flora here. *Hypnum cupressiforme s.l.*, *Mnium hornum*, *Isopterygium elegans*, *Dicranella heteromalla* and *Lepidozia reptans* are all preferential, and in more unpolluted and sheltered sites, especially where sandstone blocks provide a variety of niches, there can be records for a wide variety of other species including *Plagiothecium undulatum*, *Isothecium myosuroides*, *Dicranum majus*, *D. fuscescens*, *Polytrichum formosum* and *Rhytidiadelphus loreus* (e.g. Evans 1954, Pigott 1956*b*).

These, together with bulkier lichens, such as *Cladonia squamosa* and *C. polydactyla*, give a foretaste in such sites of the much greater diversity and importance of the cryptogam flora of the sub-montane analogue of this community, the *Quercus-Betula-Dicranum* woodland.

Habitat

The *Quercus-Betula-Deschampsia* woodland is confined to very acid and oligotrophic soils in the southern lowlands of Britain and the upland fringes of the Pennines. In some areas, long-established stands occur as high forest or old oak coppice or as components of ancient wood-pasture landscapes in Forests and parks, but to the south especially many stands are a relatively recent development on heathy commons whose traditional exploitation has fallen into disuse. Grazing continues to be important in some areas and afforestation with hardwoods and, more importantly, softwoods, has had a widespread influence on the composition and structure of the vegetation.

Edaphically, this community occupies one extreme among wooded lowland soils, being limited to lime-free profiles with a superficial pH that is rarely above 4 and with mor humus (Moss 1911, 1913, Tansley 1939, Rackham 1980, Peterken 1981). More lithomorphic soils are shallow humic rankers, sometimes amounting to little more than accumulations of organic remains and rock particles disposed fragmentarily over and among boulders, but deeper profiles are widespread, especially over superficials. Typically, however, the soils are free-draining, sometimes excessively so, being very commonly of a sandy texture and, when more mature, they characteristically show signs of strong eluviation, being of the brown podzolic type (sometimes with micropodzols) or humo-ferric podzols with marked bleaching and pan formation or, where there is some influence of ground water deep in the profile, stagnopodzols or stagnogley-podzols (Avery 1980: see also Tubbs 1968, Corbett 1973, Furness 1978, Carroll *et al.* 1979, Pigott 1983).

Within its range, the *Quercus-Betula-Deschampsia* woodland effectively serves to mark out the major areas of such soil types. In some places, their occurrence is related to the distribution of pervious arenaceous sedimentaries. In the Weald, for example, sands and sandstones of the Cretaceous sequence are important substrates, Ashdown and Tunbridge Wells Sands with Poundgate stagnogley-podzols occurring in Ashdown Forest on the High Weald, and Folkestone Sands and Hythe Beds carrying Shirrell Heath humo-ferric podzols running along the western rim (Wooldridge & Goldring 1953, Soil Survey 1983). The great frequency of the community in this area is carried over on to the Surrey commons where Eocene Bagshot sands and gravels have Holidays Hill stagnogley-podzols and a variety of pro-

files of this kind underlie stands on Bagshot and Barton beds in the New Forest (Tubbs 1968). In a great arc around the Midlands, running from Cheshire to Nottinghamshire, Triassic Keuper and Bunter sandstones provide localities with podzolised soils (Hopkinson 1927, Mackney 1961, Furness 1978) and, all around the Pennine fringes, a very characteristic sequence of Anglezarke humo-ferric podzols, Revidge humic rankers and Belmont stagno-podzols is disposed over the tops, freely-weathering faces and colluvial slopes of Carboniferous sandstones and grits carrying the *Vaccinium-Dryopteris* sub-community (Furness 1978, Carroll *et al.* 1979, Pigott 1983, Jarvis *et al.* 1984).

In other places, the *Quercus-Betula-Deschampsia* woodland occurs over more free-draining superficials, as in the New Forest where Pleistocene Plateau Gravels carry stagnogley-podzols (Tubbs 1968) and on the Cheshire Plain and in Breckland, down through Suffolk and into Essex, where extensive tracts of brown sands derived from fluvioglacial or aeolian material show patchy podzolisation (Corbett 1973, Furness 1978, Rackham 1980).

Variation in these kinds of profiles under individual stands of the community is often quite marked, even within very short distances (e.g. Mackney 1961, Pigott 1983), being related to differences in topography and in the character of the parent materials and perhaps also to developmental interactions between the vegetation and the soil (see below). As noted earlier, this can have some marked effects on the distribution and abundance of some of the important species here, notably *Pteridium*, *Vaccinium* and the bryophytes. But the general nature of the edaphic conditions is well marked in the overall floristic character of the community in both a negative and positive fashion. More calcicolous plants never find a place here and even more tolerant species like *Corylus*, *Crataegus* spp., *Rubus*, *Holcus mollis* and *Hyacinthoides*, which are so important on brown earths of low base-status, are largely excluded. By contrast, calcifuges, notably *D. flexuosa*, the ericoids, a variety of other low-frequency herbs and bryophytes, which are only very sparsely represented on such profiles, are strongly preferential. By and large, then, the soil-related boundary between this community and its counterpart on moister and less markedly leached profiles, the *Quercus-Pteridium-Rubus* woodland, is quite well defined, though transitional stands do occur, especially where the character of superficial deposits changes gradually; where the two communities are found contiguously, mosaics of their smaller herbs, sometimes overlain by an unbroken canopy of *Pteridium*, are fairly frequent. Coppicing for oak, extended over such transitions, may further blur their sharpness.

The floristic boundary with calcifuge woodlands of wetter, acid soils is generally a clear one. The free-

draining nature of the profiles here prevents any tendency to surface-water gleying and, though deeper soils are intermittently affected by the ground water-table (in the Weald, for example, and the New Forest), this never reaches high in the profile. Thus, though *Molinia caerulea* can occasionally be found in the community, this is more a reflection of the increasing prominence of this grass in fairly dry situations towards the south-west, rather than any obvious confusion of the junction between the *Quercus-Betula-Deschampsia* woodland and its counterpart on acid soils which show accumulation of surface peat, the *Betula-Molinia* woodland.

However, though the soils here are always free-draining, they are not necessarily kept exceedingly dry; and neither is atmospheric humidity consistently low. Indeed, there is quite a sharp difference in the value of these variables between stands in, say, East Anglia and the Pennines and this probably plays a considerable part in determining the floristic differences between the sub-communities. The effect of increasing rainfall and humidity can already be seen within the *Quercus* sub-community in the way in which *Vaccinium* appears in areas with a mean annual rainfall in excess of 800 mm but, with the further shift to precipitation levels approaching 1000 mm (*Climatological Atlas* 1952) and 140 wet days yr^{-1} (Ratcliffe 1968), the *Vaccinium-Dryopteris* sub-community becomes the characteristic type of *Quercus-Betula-Deschampsia* woodland with strongly preferential *D. dilatata* and a greater representation of bryophytes. Increasing richness among the latter component means that the ground flora of stands in this region begins to take on some of the character of the sub-montane *Quercus-Betula-Dicranum* woodland. Although, in their extreme forms, this community and the *Quercus-Betula-Deschampsia* woodland look very different, much of the contrast is provided by the bryophytes and, as rainfall and humidity rise progressively in moving to the north-western uplands, there is a fairly gradual switch from the one community to the other. Indeed, it is possible that, without such high levels of atmospheric pollution towards the northern fringes of the *Quercus-Betula-Deschampsia* woodland, some Pennine stands here would move over to the *Quercus-Betula-Dicranum* woodland, shifting the geographical boundary between the two communities. The demise of industrial activity in some Pennine valleys and an increasing attention to air-cleanliness could perhaps produce some change in this direction.

A further environmental variable affecting the *Quercus-Betula-Deschampsia* woodland is grazing and browsing by stock and deer which influence both the physiognomy and quantitative composition of the field layer (and of the bryophyte component in so far as it makes a contribution here) and the regenerative capa-

city of the major woody species. Even in such a floristically simple community as this, the ways in which larger herbivores, or their exclusion, operate are quite subtle though, in the long term, very striking. Thus, long-continued grazing and browsing play a major part in the appearance of this kind of woodland where it contributes, usually as the *Quercus* sub-community, to the wood-pasture landscape of some ancient Forests and parks, with a preponderance of older trees set amongst extensive grassy lawns and bracken (e.g. Hopkinson 1927, Rackham 1980, Peterken 1981). And in other situations where stock and deer have access, including many stands of the *Vaccinium-Dryopteris* sub-community which, in Pennine valleys, are often contiguous with open moorland, the striking scarcity of smaller trees and saplings can be directly attributed in many cases to the predation of herbivores (e.g. Pigott 1983). Conversely, where grazing and browsing have been reduced, there is often a clear response here among the more sensitive members of the field layer which increase in height and cover, in the bryophytes, which become more confined to rock outcrops and tree bases, and among the woody species which are able to regenerate more effectively. Such curtailment of grazing and browsing has occurred within stands of the community as a result of reduction in the numbers of particular herbivores (as in the New Forest: Peterken & Tubbs 1965, Tubbs 1968) or because of enclosure (as at Staverton Park: Peterken 1969, Rackham 1980) or as part of more widespread cultural changes (as on the Surrey and Wealden commons where grazing, and the burning and cutting of bracken and heather have all declined: Wooldridge & Goldring 1953, Hoskins & Stamp 1963). In many areas, there has been extensive renewed regeneration of this kind of woodland and a spread on to previously open ground in larger clearings within existing woods and on adjacent heath, and in some cases it is possible to trace the origin of individual stands to particular local events in the grazing history.

The intricacies involved in such events, and especially the different responses of oak and birch to the direct and indirect effects of grazing reduction, are well shown in the enclosure experiment which Pigott (1983) conducted in a Pennine stand of the *Vaccinium-Dryopteris* sub-community. Among all the woody species represented here, birch is the most consistent and prolific fruiter and wind-dispersal is very effective in producing a potentially widespread distribution of offspring. But birch is a great light demander, even at the germination stage, the largest numbers of seedlings being found in short turf or on patches of bare ground. Moreover, having small food reserves in the seed, it cannot get a hold on thicker deposits of loose litter. Grazing (or burning), which creates such close-cropped, litter-free conditions, thus tends to favour seedling establishment, though it can be

quite sufficient, even where canopy shade is not a problem, to eliminate each generation of offspring completely. When grazing was withdrawn in Pigott's experiment, some of the existing seedlings got away to form saplings in gaps but, as the *D. flexuosa* sward grew taller and began to trap litter, and *Vaccinium myrtillus* extended its cover, conditions became uncongenial for any further seedling establishment. The developing prominence of birch was thus related to a quite narrowly defined period of transition from the grazed to the ungrazed state. This kind of response, together with the fact that birch cannot regenerate under its own canopy, is probably responsible for the fact that, even where this species has become very abundant in stands on previously unwooded ground, it often occurs in patchy mosaics of more or less even-aged groups of trees.

Oak is rather different. It fruits less regularly and abundantly than birch but, after good summers, acorns can be plentiful. However, though it is one of the trees here that are less favoured by herbivores, and can be quite resistant to repeated damage even when very young (Jones 1959, Rackham 1980), seedlings are again often totally devoured where grazing continues. In Pigott's experiment, oak (*Q. petraea* in this case) got away only in the enclosure. In contrast to birch, however, seedlings continued to establish intermittently even in the ungrazed sward: in oak, germination is actually favoured by burial among taller herbage and litter, which affords protection against desiccation and predation, and, having bulky food reserves, fairly thick accumulations of unconsolidated material present no great barrier to radical growth down to the mineral horizons (Jones 1959). In the particular wood in which Pigott erected his enclosure, he considered that *Q. petraea* would come to outstrip birch as the eventual gap-filler. In *Quercus-Betula-Deschampsia* woods where *Q. robur* is the usual oak, as in most stands of the *Quercus* sub-community, oak regeneration under established canopies is more problematical. *Q. petraea* is about as shade-tolerant as *Vaccinium* but *Q. robur* is not and its great prominence in the *Quercus* sub-community (on soils which are not those most favoured by this species) may result from its greater ability to colonise new ground. Many stands in this sub-community are fairly young and tracts with *Q. petraea* are often long-established high forest or coppice. Though acorns are heavy, they can be transported considerable distances by small mammals and birds (Jones 1959, Mellanby 1968) and young saplings of *Q. robur* are a common feature among advancing birch here.

Grazing and browsing also have a marked effect on the smaller woody companions of oak and birch, *Ilex* and *S. aucuparia*. In Pigott's enclosure, the latter became quite plentiful, especially over block scree, and being shade-tolerant, grew well, even under more intact areas

of the canopy. *Ilex*, though rare in this particular wood, responds in the same way and is likewise shade-tolerant, even more so than *S. aucuparia* and, itself casting dense evergreen shade, can have a much more obvious effect on the accompanying flora where it becomes prominent (Peterken 1965, 1966). In stands in the New Forest (Peterken & Tubbs 1965) and in Staverton Park (Peterken 1969, Rackham 1980), local holly dominance in this community has been related to specific events in grazing reduction.

It is possible that grazing also has some effects on the soils under this community by helping maintain compact mor. Enclosure in Pigott's experiment did not disrupt the stability of the podzolised profiles but it did permit the development of more friable humus beneath the accumulations of decaying leaves and, within this, fine tree roots and fungal mycorrhizae became more profuse. Enhanced root growth may have been a response to decreased trampling by herbivores and the moister conditions developing beneath the leaf litter; mycorrhizal growth may have benefited by the decrease in *D. flexuosa* which seems to exert an inhibiting effect (Jarvis 1964). Whatever the particular causes, the scene seemed set for better tree growth within the enclosure and perhaps even reduced mortality (Pigott 1983). Local and temporary small-scale shifts in the character of the soils here, in response to grazing differences, may be quite widespread. They certainly seem to operate in edaphically transitional situations, as in mosaics with the *Quercus-Pteridium-Rubus* woodland, where litter accumulation, as a result of reduced grazing, can alter the balance in the field layer between *D. flexuosa* and *Holcus mollis* over soils that vary from brown earths with mull to podzols with mor (e.g. Ovington 1953).

Treatment of the *Quercus-Betula-Deschampsia* woodland as wood-pasture has sometimes been combined with pollarding of oak, and also in some places, of holly, in attempts to maintain a continuing balance of herbage and canopy. Other stands have been used as oak coppice and, locally, holly seems to have been cut as a supplement to winter fodder. Oak timber has also been widely extracted from this kind of woodland and some stands represent oak plantations. Where long established, these do not present a markedly different assemblage of species from semi-natural stands of the community, though they often have a sparse understorey and the trees lack individuality and great age. Older plantations of pine with some thinning can likewise conform in general terms to tracts with an oak and birch canopy, though recently-disturbed stands (and younger deciduous plantations) may show an abundance of herbs such as *Epilobium angustifolium*, *Holcus lanatus*, *Digitalis purpurea* and sub-shrubs like *Calluna, E. cinerea* and *Ulex* spp., an assemblage which probably approximates to the post-coppice flora here. Younger conifer plan-

tations on soils which could carry the *Quercus-Betula-Deschampsia* woodland look very different: here, in the very dark conditions beneath the canopy, the ground cover may be reduced to but a few sparse wefts of mosses over a carpet of needles.

Zonation and succession

Zonations from this community to other kinds of woodland are most frequently related to differences in soils. Quite often, these are complicated by the effects of sylvicultural treatments and the impact of larger herbivores, but grazing and browsing also mediate other kinds of transitions to grassland and heath which are a spatial expression of succession or its reversal. Burning is also a factor in these latter kinds of zonations. Although neglect of heathland exploitation has allowed extensive development of progressive successional change in some areas, many stands have artificially sharp boundaries with adjacent land converted to agricultural use.

Edaphically-related transitions usually reflect changes to soil parent materials that are not so markedly acidic or pervious (commonly both) as those which typically weather to the humic rankers and podzolised profiles characteristic here. Such changes are very common within whole woods in which this community is represented and they most often result in zonations to the *Quercus-Pteridium-Rubus* woodland, the forest type of base-poor brown earths, frequently with some drainage-impedence, in the British lowlands. Boundaries between the two communities are not always very sharp, especially where superficials provide the underlying substrate. Fluvioglacial deposits, for example, and aeolian material are commonly very heterogeneous, even over short distances, and, in parts of the Midlands, in Suffolk and Essex and in some areas of the New Forest, small-scale variation in the proportions of sand, silt and clay may be sufficient to produce mosaics of brown earths or brown sands and podzols which bear patchworks of these two kinds of woodlands, in these regions usually the Typical sub-community of the *Quercus-Pteridium-Rubus* woodland and the *Quercus* sub-community of the *Quercus-Betula-Deschampsia* woodland. The distribution of more mesophytic species characteristic of the former and the calcifuge herbs of the latter often provides a firm diagnosis of the components but, by mid-summer, when the vernal dominance of *Hyacinthoides* has faded from the *Quercus-Pteridium-Rubus* woodland and a dense canopy of bracken extends throughout, the distinctions may be masked. Uniform treatment as wood-pasture, which can eliminate most of the understorey, and pollarding throughout, can cause further confusion. Oak coppice sometimes extends over such boundaries, though the post-coppice floras in actively-treated stands of each of the two communities

can indicate the underlying soil differences afresh. Coppicing for hazel, largely confined to the *Quercus-Pteridium-Rubus* woodland, may actually highlight the transition.

Where these kinds of soil differences are related to changes in sedimentary rocks, the zonation between the two kinds of woodland can be a much sharper one. Interbedded clays are a characteristic feature among the Cretaceous sands and sandstones of the Weald and they occur, too, within the Eocene sequences of Essex and the New Forest. Similar alternations are found further north in the Triassic deposits of the Midlands. All of these can carry bands of the *Quercus* sub-community of the *Quercus-Betula-Deschampsia* woodland and the Typical sub-community of the *Quercus-Pteridium-Rubus* woodland, the former usually above the latter on the more resistant topography of the arenaceous rocks, giving way below to the more weathered argillaceous slopes. On the Pennine fringes this kind of geological and topographic contrast, reflected in the soils and woodland cover, is even more striking with Carboniferous sandstones and grits forming cliffs and screes with the *Vaccinium-Dryopteris* sub-community, giving way below to the *Acer-Oxalis* sub-community of the *Quercus-Pteridium-Rubus* woodland on shales. Edaphic variation over the extensive and varied grit exposures may also here introduce much more field-layer variation into the *Quercus-Betula-Deschampsia* woodland than is usual over the gentler topography of the southern lowlands. Quite a common complication, too, is for landslips to occur where incompetent shales collapse and spill down great blocks of the overlying grits on to the lower slopes: then perched fragments of the calcifuge flora of the community may occur among a ground of the *Quercus-Pteridium-Rubus* woodland, a striking sight in spring when a carpet of bluebells runs up between them.

Very often, on shedding slopes, these junctions between arenaceous and argillaceous sedimentaries are marked by flushing, as ground waters percolating through the sands, sandstones or grits hit the impervious clays or shales and emerge in springs or seepage lines. Then the transition from the *Quercus-Betula-Deschampsia* woodland to the *Quercus-Pteridium-Rubus* woodland can have some kind of interposed flush woodland, frequently of small extent, though often occurring repeatedly along the geological boundary. Where the flush waters are not too base-poor, the *Carex-Cirsium* sub-community of the *Alnus-Fraxinus-Lysimachia* woodland is typical in such situations, being a common feature in the western Weald and along Pennine valley sides; where they are more acid, frequently the case to the north where they drain from expanses of moorland, the *Juncus* sub-community of the *Betula-Molinia* woodland replaces it in analogous topographic situations.

Where flush waters emerge at such geological junctions within more level-bedded rocks and maintain the soils over the clays and shales in a more permanently waterlogged state, some surface peat may accumulate. Then, these kinds of flush woodland are replaced by their topogenous equivalents, the *Carex-Alnus* woodland in more base-rich sites (usually the *Chrysosplenium* sub-community), the *Sphagnum* sub-community of the *Betula-Molinia* woodland in the more base-poor. Often, the stands of these kinds of wet woodland are more extensive than their flush counterparts, sometimes wholly replacing the *Quercus-Pteridium-Rubus* woodland in its position below the *Quercus-Betula-Deschampsia* woodland. Again, the western Weald and the Pennine fringes have good examples of this kind of pattern.

The other very common kind of zonation in which this woodland can be found involves transitions to heaths, or to complexes of heath with calcifugous grasslands and stands of bracken. The type of heath occurring in association with the community varies considerably according to the region: over the range of the *Quercus-Betula-Deschampsia* woodland, heaths show wide phytogeographic differences. In East Anglia and down into parts of the Weald, the *Calluna-Festuca* heath is typical, then from there westwards the *Calluna-Ulex minor* and *Ulex minor-Agrostis curtisii* heaths and, in the north Midlands, the *Calluna-Ulex gallii* heath. In the Pennines, the *Calluna-Deschampsia* and *Calluna-Vaccinium* heaths are the usual companions. Sometimes the zonations from woodland to heath are well ordered and have some clear basis in topographic and edaphic variation, as where tree cover becomes very sparse over fragmentary humic rankers on grit boulders or cliffs in the Pennines (e.g. Moss 1913, Pigott 1956*b*), but very often such patterns are more complex and independent of substrates and soils. Frequently, here, fragments of heath occur within stretches of the woodland, confined to gaps or forming larger areas in the kind of landscape seen in some ancient wood-pastures (e.g. Hopkinson 1927, Mackney 1961, Rackham 1980, Peterken 1981), or stands of the woodland are distributed among extensive tracts of heath, as on the Wealden and Surrey commons and in parts of the New Forest (e.g. Tansley 1939, Wooldridge & Goldring 1953). And in such situations, it is usually abundantly clear that the zonations are an expression of seral progression to woodland or its reconversion to heath as a result of a variety of biotic activities.

Thus, heath sub-shrubs and *Pteridium* form the characteristic gap or coppice flora here, developing where trees fall or are extracted or cut as underwood. And these plants can spread at the expense of a tree cover in the immediate aftermath of destruction of the community by fire. Grazing and browsing may work more slowly, though to the same ultimate end: a very open canopy of trees can persist in wood-pasture stands of the *Quercus-Betula-Deschampsia* woodland for centuries, but with no hope of unaided regeneration if access to herbivores is maintained, a situation seen only too well in some old Forests and parks (Peterken & Tubbs 1965, Rackham 1980, Peterken 1981). Where the community has declined in extent or vigour, then, or where its expansion has been checked, it is these factors, working separately or often in complex combinations (e.g. Peterken & Tubbs 1965, Peterken 1969, 1981, Rackham 1980), that seem generally to blame, rather than any natural demise in the face of extreme edaphic conditions (cf. Tansley 1911, 1939) or a harsh climate (Pigott 1983). Moreover, the ability of the community to regenerate and colonise new ground has been observed with striking clarity wherever and whenever the incidence of these factors has declined, the neglect of the exploitation of heathy commons being especially important in the recent extensive spread of this kind of woodland in the south-east.

However, though the community seems to be a quite natural development from heaths at the present time, two questions arise over its status. The first is of long-term historical interest and concerns the possibility that, in many areas, heath vegetation has prepared the ground for the spread of the *Quercus-Betula-Deschampsia* woodland by enhancing podzolisation on land that was previously of higher fertility and perhaps bore more mesophytic forest but which was progressively exhausted by early agricultural activity (e.g. Dimbleby & Gill 1955, Dimbleby 1962, Gimingham 1972). This may well have been the case in some places but whether it has everywhere been a necessary precondition is another matter. The community can certainly maintain podzols in a stable state (Mackney 1961, Pigott 1983) and oak-birch forest of this kind may itself be able to promote podzolisation (Scheys *et al.* 1954, Munault 1959).

The second issue concerns the stability of the community in relation to its beech-dominated analogue, the *Fagus-Deschampsia* woodland, in particular the competitive ability of oak and beech on the markedly dry, acid soils characteristic of both communities. On moister soils of low base-status, *Fagus* is at some disadvantage against *Q. robur* (Watt 1924, 1934*b*), so the distinction between the *Quercus-Pteridium-Rubus* and the *Fagus-Rubus* woodlands often has a clear edaphic basis in semi-natural woods within the natural range of beech. Here, oak and beech are more closely matched in their potential ability to dominate, each is found in stands where the other is pre-eminent and, in those areas where both communities are well represented, as in the New Forest (Peterken & Tubbs 1965, Tubbs 1968) and parts of the Chilterns (Watt 1934*b*, Avery 1958), inti-

mate mosaics of the two are common. A number of factors are probably important in determining which species will come to prevail. First, though *Fagus* grows well way beyond its natural limit to the north, there may be some climatic restriction on its vigour towards the drier parts of East Anglia (Rackham 1980). Second, outside this area, *Fagus* is still a very erratic fruiter and oak, certainly *Q. robur*, though itself not very consistent in acorn production, has the advantage that its fruits can be transported over considerable distances, whereas beech mast generally drops straight down off the parent (Watt 1924, Jones 1959, Mellanby 1968). In larger gaps, therefore, and on previously open ground, colonisation by oak, as against beech, is more widespread and more regular, though grazing and browsing, which favour the latter, can offset this (Dengler 1930, Jones 1959). Third, under closed canopies, the advantage moves in the other direction (provided adult beech is present and has produced mast) because *Q. robur* regenerates badly under established woodland and beech seedlings and saplings are more shade-tolerant than those of *Q. petraea*. Here, then, beech may triumph eventually (Watt 1924, 1934*b*), even well outside its range (Pigott 1983).

The outcome of such conflicting factors may, in many places and at any given time, be a fairly even match so that the dominants, and their communities, form a mosaic, each coming and going, here and there, in a complex pattern of regenerative replacement. On the Continent, the consensus of opinion is that the equivalents of the *Fagus-Deschampsia* woodland represent the climax on the kinds of soil characteristic here, the counterparts of the *Quercus-Betula-Deschampsia* woodland, their seral precursors or degraded derivatives (e.g. Géhu 1975*a*) and, given ideal conditions for beech, this may well be the situation here. Often, however, conditions are not ideal so that the *Quercus-Betula-Deschampsia* woodland, though theoretically a sub-climax, attains a considerable measure of stability.

The other tree species which frequently complicates successions to this community is *Pinus sylvestris* which is widely distributed as an ornamental in this kind of woodland and extensively planted on lowland podzols. It fruits heavily, has light wind-dispersed seeds and does especially well, with birch, as a coloniser of open ground after fires have cleared a cover of bracken and heath (e.g. Tubbs 1968). Where its canopy remains open or where it is present in mixed covers of trees, the vegetation can retain the general character of the community but densely-shaded stands of pine quickly eliminate virtually all the field-layer species and bryophytes. The same poverty is characteristic of plantations of *P. sylvestris* and other conifers on the soils typical here, though thinning may restore some of the richness of the vegetation (such as it is). Often, now, in intensively afforested

areas, the *Quercus-Betula-Deschampsia* woodland is reduced to a fringe of birch, bracken and ericoids along the edges of rides and on recently-cleared compartments.

The generally poor quality of the soils under the community means that conversion of this kind of woodland to intensive agricultural land is exceptional. Quite commonly, stands have been reduced to isolated remnants but they usually persist, outside the heathland or wood-pasture context, in pastoral landscapes, marked off sharply from some kind of improved grassland, either various types of *Festuca-Agrostis* sward or more calcifugous sub-communities of mesotrophic grassland. Narrow strips of bracken, ericoids or *Ulex* spp. may occur as a compressed fringe around the woodland.

Distribution

The *Quercus-Betula-Deschampsia* woodland has a widespread but patchy distribution throughout the southern part of Britain, occurring in concentrations on areas of marginal land, notably in south-east England, the north-west Midlands and on the Pennine fringes and occasionally in other places where private parkland or common rights have afforded protection against clearance or favoured its advance.

Affinities

This kind of woodland has long been recognised as constituting a calcifugous extreme in the more southerly parts of Britain, though early descriptions tended to make distinctions within it according to whether it occurred as young stands in complexes with heath, where birch was often pre-eminent (e.g. Moss *et al.* 1910, Tansley 1911, 1939) or as more mature high forest where oak was the usual dominant (e.g. Moss 1911, 1913, Tansley 1939). Among the latter types of woodland, there has also been some hesitation as to whether stands should be separated on the basis of which oak species was the dominant. A distinction between birch- and oak-dominated woodlands persists in the scheme of Rackham (1980), where true acidophilous oak-woodland is consequently considered very rare in his lowland zone; separation on the basis of the oaks remains in Peterken's (1981) classification. Both these authors also include within their oak- and birchwoods vegetation which is, in this scheme, placed in the *Quercus-Pteridium-Rubus* woodland.

In phytosociological terms, the *Quercus-Betula-Deschampsia* woodland represents the Quercion roboripetraeae in the southern lowlands of Britain, the alliance which (with its beech analogue, the Luzulo-Fagion) replaces Carpinion woodlands on markedly-leached soils here and throughout the more temperate parts of Europe. It has clear counterparts in associations like the *Quercetum sessiliflorae* Lemée 1937, the *Betulo-Quer-*

cetum roboris Tüxen 1937, the *Querco petraeae-Betu-letum*, the *Luzulo luzuloidis-Quercetum* Noirfalise & Sougnez 1956 and the *Vaccinio-Quercetum sessiliflorae* Clement *et al.* 1975 described from France, Belgium and Germany (see also Dumont 1975, Duvigneaud 1975, Sougnez 1975, Frileux 1975, Tombal 1975). Some of these communities are considerably richer than the *Quercus-Betula-Deschampsia* woodland (being more akin to our sub-montane *Quercus-Betula-Oxalis* woodland) and they sometimes include wetter forms which are here placed in the *Betula-Molinia* woodland. But, in general floristics and in their edaphic and biotic relationships, they show a close similarity to their British counterpart.

Floristic table W16

	a	b	16
Betula pendula	V (4–10)	III (1–7)	IV (1–10)
Quercus robur	III (1–8)	I (1–8)	II (1–8)
Quercus petraea	II (1–9)	V (4–10)	II (1–10)
Betula pubescens	II (2–8)	III (1–7)	II (1–8)
Acer pseudoplatanus	I (1–4)	I (1–4)	I (1–4)
Castanea sativa	I (3–9)	I (6)	I (3–9)
Fagus sylvatica	I (3–7)	I (1–5)	I (1–7)
Ilex aquifolium	I (2–4)	I (1–4)	I (1–4)
Populus tremula	I (3–4)	I (3)	I (3–4)
Pinus sylvestris	II (3–8)	I (1–5)	I (1–8)
Frangula alnus	I (3–4)		I (3–4)
Sorbus aria	I (3)		I (3)
Ilex aquifolium	II (3–4)	II (2–4)	II (2–4)
Corylus avellana	I (5)	I (3)	I (3–5)
Crataegus monogyna	I (2)	I (1)	I (1–2)
Acer pseudoplatanus sapling	I (3–4)	I (1–2)	I (1–4)
Rhododendron ponticum	I (2–4)	I (1)	I (1–4)
Fagus sylvatica sapling	I (3)	I (1–3)	I (1–3)
Betula pendula sapling	I (4–5)	I (1–5)	I (1–5)
Quercus hybrids sapling	I (1–5)	I (1)	I (1–5)
Quercus robur sapling	I (1–4)		I (1–4)
Sorbus aucuparia	I (2–3)	III (2–4)	II (2–4)
Betula pubescens sapling	I (3–7)	II (1–5)	I (1–7)
Quercus petraea sapling	I (2–3)	II (2–6)	I (2–6)
Deschampsia flexuosa	IV (3–9)	V (1–9)	V (1–9)
Pteridium aquilinum	IV (1–10)	III (2–9)	IV (1–10)
Holcus lanatus	II (1–7)	I (4)	I (1–7)
Ulex europaeus	I (1–10)	I (2)	I (1–10)
Ulex gallii	I (6–10)		I (6–10)
Agrostis stolonifera	I (2–3)		I (2–3)
Festuca ovina	I (2–4)		I (2–4)
Festuca rubra	I (3–5)		I (3–5)
Pseudoscleropodium purum	I (3–5)		I (3–5)
Vaccinium myrtillus	II (2–7)	III (3–10)	II (2–10)
Dryopteris dilatata	I (1–6)	III (1–8)	II (1–8)
Dicranella heteromalla	I (2–5)	II (1–3)	I (1–5)

Hypnum cupressiforme	I (2–6)	II (1–4)	I (1–6)
Isopterygium elegans	I (2)	II (1–3)	I (1–3)
Mnium hornum	I (2–3)	II (1–5)	I (1–5)
Lepidozia reptans		II (1–5)	I (1–5)
Oxalis acetosella		I (2–3)	I (2–3)
Plagiothecium undulatum		I (1–4)	I (1–4)
Plagiothecium denticulatum		I (1–3)	I (1–3)
Tetraphis pellucida		I (1–3)	I (1–3)
Lophocolea heterophylla		I (1–2)	I (1–2)
Campylopus pyriformis		I (2)	I (2)
Dicranum fuscescens		I (6)	I (6)
Isothecium myosuroides		I (3)	I (3)
Plagiothecium succulentum		I (3)	I (3)
Plagiothecium sylvaticum		I (1)	I (1)
Rhytidiadelphus loreus		I (2)	I (2)
Rhytidiadelphus triquetrus		I (3)	I (3)
Thuidium tamariscinum		I (3)	I (3)
Barbilophozia attenuata		I (2)	I (2)
Calypogeia fissa		I (2)	I (2)
Cephalozia bicuspidata		I (1)	I (1)
Gymnocolea inflata		I (2)	I (2)
Cladonia coccifera		I (3)	I (3)
Cladonia coniocraea		I (1)	I (1)
Calypogeia trichomanis		I (3)	I (3)
Dicranodontium denudatum		I (3)	I (3)
Barbilophozia floerkei		I (5)	I (5)
Calluna vulgaris	II (2–6)	II (1–9)	II (1–9)
Rubus fruticosus agg.	II (1–7)	II (1–6)	II (1–7)
Agrostis capillaris	I (3–7)	I (4–5)	I (3–7)
Galium saxatile	I (1–5)	I (1–4)	I (1–5)
Epilobium angustifolium	I (1–3)	I (1–3)	I (1–3)
Hedera helix	I (3–7)	I (3–4)	I (3–7)
Holcus mollis	I (1–8)	I (4–8)	I (1–8)
Lonicera periclymenum	I (1–6)	I (3–4)	I (1–6)
Dicranum scoparium	I (1–4)	I (1–2)	I (1–4)
Potentilla erecta	I (1–4)	I (1–3)	I (1–4)
Teucrium scorodonia	I (1–5)	I (1–3)	I (1–5)
Corydalis claviculata	I (1–3)	I (1–3)	I (1–3)
Leucobryum glaucum	I (1–3)	I (3)	I (1–3)
Eurhynchium praelongum	I (1–3)	I (1–2)	I (1–3)
Hypnum jutlandicum	I (2–5)	I (1–4)	I (1–5)
Orthodontium lineare	I (1–2)	I (1–4)	I (1–4)
Lophocolea bidentata s.l.	I (1–3)	I (1–2)	I (1–3)
Sorbus aucuparia seedling	I (1–5)	I (1–3)	I (1–5)
Quercus petraea seedling	I (1–2)	I (1–2)	I (1–2)
Betula pubescens seedling	I (1–2)	I (1–2)	I (1–2)
Ilex aquifolium seedling	I (1–3)	I (1–2)	I (1–3)
Anthoxanthum odoratum	I (1–2)	I (4)	I (1–4)
Blechnum spicant	I (1–3)	I (1)	I (1–3)
Deschampsia cespitosa	I (1–3)	I (2)	I (1–3)

Floristic table W16 *(cont.)*

	a	b	16
Digitalis purpurea	I (2–3)	I (3)	I (2–3)
Hyacinthoides non-scripta	I (2–4)	I (4)	I (2–4)
Erica cinerea	I (2–7)	I (3)	I (2–7)
Luzula sylvatica	I (1–5)	I (4)	I (1–5)
Molinia caerulea	I (2–8)	I (1)	I (1–8)
Rumex acetosella	I (3–4)	I (3)	I (3–4)
Solidago virgaurea	I (2–6)	I (1)	I (1–6)
Campylopus paradoxus	I (3)	I (1–3)	I (1–3)
Dicranoweissia cirrata	I (1)	I (1–3)	I (1–3)
Pleurozium schreberi	I (2–5)	I (2)	I (2–5)
Pohlia nutans	I (2–3)	I (1)	I (1–3)
Cladonia fimbriata	I (2)	I (2)	I (2)
Cladonia polydactyla	I (1)	I (1–2)	I (1–2)
Cladonia squamosa	I (1–2)	I (1–3)	I (1–3)
Quercus robur seedling	I (2–3)	I (2)	I (2–3)
Fagus sylvatica seedling	I (2)	I (1)	I (1–2)
Acer pseudoplatanus seedling	I (1)	I (1–3)	I (1–3)
Betula pendula seedling	I (1)	I (2)	I (1–2)
Quercus hybrids seedling	I (1–5)	I (1)	I (1–5)
Number of samples	118	31	149
Number of species/sample	9 (3–26)	15 (8–29)	10 (3–29)
Tree height (m)	11 (3–17)	13 (3–23)	11 (3–23)
Tree cover (%)	77 (10–100)	81 (35–100)	78 (10–100)
Shrub height (m)	3 (1–6)	3 (2–8)	3 (1–8)
Shrub cover (%)	8 (0–80)	9 (0–60)	8 (0–80)
Herb height (cm)	71 (5–180)	40 (5–110)	65 (5–180)
Herb cover (%)	81 (1–100)	77 (10–100)	80 (1–100)
Ground height (mm)	2 (1–5)	11 (2–30)	4 (1–30)
Ground cover (%)	4 (0–75)	9 (1–40)	5 (0–75)
Altitude (m)	120 (5–335)	161 (30–230)	129 (5–335)
Slope (°)	13 (0–60)	22 (2–60)	15 (0–60)

a *Quercus robur* sub-community

b *Vaccinium myrtillus-Dryopteris dilatata* sub-community

16 *Quercus* spp.-*Betula* spp.-*Deschampsia flexuosa* woodland (total)

W16 *Quercus* spp.-*Betula* spp.-
Deschampsia flexuosa
woodland

W16 *Quercus* spp.-*Betula* spp.-
Deschampsia flexuosa
woodland

a *Quercus robur*
sub-community

W16 *Quercus* spp.-*Betula* spp.-
Deschampsia flexuosa
woodland

b *Vaccinium myrtillus-*
Dryopteris dilatata
sub-community