
W15

Fagus sylvatica-*Deschampsia flexuosa* woodland

Synonymy

Chalk plateau beechwoods (c) Watt & Tansley 1930; Beechwoods on heath Watt & Tansley 1930; Beech associates, sere C Watt 1934*b*; Beech consociation, sere C Watt 1934*b*; *Fagetum arenicolum/ericetosum* Tansley 1939; Beech-Oak-Birch Association, types 1 & 2 *p.p.* McNeill 1961; Beech-oak-holly woods Peterken & Tubbs 1965 *p.p.*; Beechwood Rackham 1980 *p.p.*; Beech stand types 8A & 8B Peterken 1981; Woodland plot type 17 Bunce 1982 *p.p.*

Constant species

Fagus sylvatica (*Deschampsia flexuosa*, *Pteridium aquilinum*, *Dicranella heteromalla*, *Mnium hornum*).

Physiognomy

The *Fagus sylvatica*-*Deschampsia flexuosa* woodland is the third of the forest types in which beech attains great pre-eminence in Britain but, as in its counterpart at the opposite edaphic extreme, the *Fagus-Mercurialis* woodland, beech does not make such generally good growth here, nor is it so overwhelmingly dominant, as in the *Fagus-Rubus* woodland. Thus, though beech is the most frequent tree in this community as a whole and often the most abundant component of individual stands, the mean canopy height is usually less than 20 m and the trees are quite commonly of manifestly poor quality, sometimes growing crookedly and generally attaining no more than quality class III (Watt 1934*b*, Brown 1953, McNeill 1961, Rackham 1980). Coppiced stands are very rare (though they may have been more abundant in the past) and the usual structure is high forest, though signs of a variety of different treatments are widespread. Some tracts are obviously of planted origin, with morphologically-similar trees disposed in more or less even spacings (Watt 1934*b*, Brown 1953, 1964) and, in the Chilterns, where this community is represented among the plateau woodlands, a preponderance of smaller, poorly-grown individuals sometimes indicates long treatment under the selection system (Brown 1953, 1964,

Peterken 1981). Other stands have been treated as wood-pasture, as in Burnham Beeches (Tansley 1939), in Epping Forest (Paulson 1926, Tansley 1939) and parts of the New Forest (Peterken & Tubbs 1965, Tubbs 1968) and, in some of these places, magnificent pollard beeches survive. Even in stands which have been more actively managed, it is sometimes still possible to discern variation between individual trees and their groupings which can give some clue of the original development of the woodland by sub-spontaneous invasion with much-branched pioneers and unbranched followers (Watt 1934*b*) or clumped age-classes related to waves of colonisation (Peterken & Tubbs 1965, Tubbs 1968).

The most frequent canopy associate of beech in this community is again, as in the *Fagus-Rubus* woodland, oak. *Quercus robur* is much the more common of the two species within the natural range of beech, though *Q. petraea* is locally prominent in parts of the south (as in the New Forest, for example: Géhu 1975*b*) and it increases its representation towards south Wales (Peterken 1981); and, to the north of England, where planted stands occur widely, it is the more usual species. Where both oaks occur, hybrids can be frequent. Oak grows well here, often maintaining itself at constant, or near to constant, frequencies and commonly attaining the same height as *Fagus* or exceeding it: where it is less common, there is often the suspicion that it has been selected against. Generally, it has lower cover than beech, though it can be locally abundant and quite often the canopy presents the appearance of a mosaic of the two trees, a feature especially characteristic of the 'Ancient and Ornamental Woodlands' of the New Forest (Peterken & Tubbs 1965, Géhu 1975*b*), though also found on parts of the Chiltern plateau (Watt 1934*b*) and in Burnham Beeches (Tansley 1939). This means that spatial boundaries between this community and the *Quercus-Betula-Deschampsia* woodland, which grows in similar situations, are often somewhat unclear, a fact of some importance when considering the stability and successional status of both these communities.

Birch, too, is quite often a conspicuous feature in gaps and clearings and it can remain abundant for some time in newly-developing stands, with individuals surviving as a fairly frequent but low cover component of mature canopies. *Betula pendula* is by far the more frequent of the two species, with *B. pubescens* making only a very occasional contribution. *Acer pseudoplatanus* is much scarcer than birch, though it increases in frequency a little towards the wetter north-west, and *Fraxinus excelsior* is typically absent: even in regeneration cores, these species do not provide the early challenge to *Fagus* growth that is a feature of other kinds of beechwood. *Sorbus aria*, which has its best representation in the *Fagus-Mercurialis* woodland, and *Prunus avium*, a good occasional of the *Fagus-Rubus* woodland, are likewise very scarce here. *Pinus sylvestris*, on the other hand, can be locally prominent: it is sometimes planted as an ornamental here and can seed into young stands and gaps from nearby plantations.

The characteristically dense shade cast by the canopy of this kind of woodland is inimical to the development of rich understoreys, and in the very darkest stands there may be no smaller woody plants at all. The shade-tolerant *Ilex aquifolium* is, however, very frequent overall and, as in the *Fagus-Rubus* woodland it can thicken up to form an extensive second tier of trees beneath the beech, larger individuals, occasionally accompanied by *Taxus baccata*, almost breaking the canopy. *Ilex* becomes more frequent and abundant here outside drier areas like the Chilterns (Watt 1934b, Tansley 1939), though its prominence is very much related to the incidence of grazing and browsing, which hinder regeneration (Peterken 1965, 1966, Peterken & Lloyd 1967) and affect the physiognomy of any surviving trees. Holly is sometimes abundant in younger stands of the community that have sprung up in response to grazing relaxation (e.g. Peterken & Tubbs 1965, Tubbs 1968; also Géhu 1975b where such vegetation was included in a *Frangulo-Ilicetum*) and, being itself densely shading, can retain a local dominance, as in some parts of the New Forest (Peterken & Tubbs 1965, Peterken & Newbould 1966, Tubbs 1968).

Corylus avellana and *Crataegus monogyna* are excluded here, not by the shade but by the extreme edaphic conditions, and other associates of *Ilex* are few. Apart from occasional *Sorbus aucuparia* (and sometimes, in younger stands, *Frangula alnus*: e.g. Géhu 1975b), the most characteristic companions are saplings, especially of *Fagus* but also of *Betula pendula* and *Quercus robur*. Beech saplings can be found even under closed canopies, though their frequency and abundance depend ultimately on masting and predation of seed and seedlings and they are often checked under denser tree covers: a characteristic feature of many sites is an abundance of young beech, several years old but only

25–40 cm tall. Even around gaps, early growth may be hindered by the presence of dense bracken or prior occupation by thickly-set holly or birch (Watt 1923, 1925, 1934b). Oak saplings are generally confined to larger openings or newly-colonised ground (Jones 1959).

As in all beech-dominated woodlands, the field layer here is often reduced to very low cover by the dense shade of the *Fagus* and, if it is present, *Ilex*, younger stands which have not yet opened up by the natural death of the trees being especially impoverished. Then, the bulk of the ground may be bare of herbs, with great expanses of beech litter or, where this has been blown away, exposed patches of raw mor humus, among which the shallow roots of the beech can be seen winding. Even where the field layer is more extensive, its cover is often patchy and only continuous in areas of greater light penetration, as around the margins of stands or in gaps or, less luxuriantly, beneath the scattered oaks and birches, which cast a less dense shade than beech. A further feature of importance on the typically very free-draining soils here is that beech, being shallow-rooted, probably exerts considerable competition for water, conditions which are ameliorated under oak, the roots of which grow obliquely downwards. It should also be noted that, since the soils are also consistently base-poor, the potential vascular flora is considerably less rich than in other kinds of beechwood so, even in situations where shade and water shortage present less severe problems, cover and diversity are provided by variations in but a few species.

None of these attain constancy, though some would, were the shade not so habitually deep. The most frequent vascular plants are *Pteridium aquilinum* and *Deschampsia flexuosa*, the former very obviously limited by light penetration, often being represented by very sparse fronds and attaining real abundance and luxuriance only under more open canopies. In such places, its annual pattern of growth represents the only really obvious phenological change in the herbaceous component here. *D. flexuosa* is more shade-tolerant, though it, too, is rarely abundant and never forms the kind of continuous sward that can occur under the oak/birch-dominated canopies of the *Quercus-Betula-Deschampsia* woodland: quite frequently, it is reduced to widely-scattered plants with but a few lax leaves.

Other field-layer species are considerably less common overall. *Rubus fruticosus* agg. occurs occasionally throughout but it is often present as very weak sprawling shoots and, though it may present some check on beech regeneration in gaps (Watt 1934b), it does not here have the important role in suppressing the associated flora that it assumes in the *Fagus-Rubus* woodland. *Lonicera periclymenum*, which typically accompanies *Rubus* on more mesotrophic soils, is likewise only

occasional in this community and usually not abundant.

The grass component of the field layer is sometimes enriched by a variety of species, particularly in transitions to heaths or where grazing animals have access. *Agrostis capillaris* is the most consistent companion to *D. flexuosa* in such situations but *Holcus mollis* sometimes occurs and, less frequently, *Poa nemoralis*. In stands towards the south-west, most notably in the New Forest, *Molinia caerulea* may make a small contribution. *Melica uniflora* and *Milium effusum*, which are a very characteristic feature of beechwoods on less base-poor soils, are here rare. Among other monocotyledons, *Luzula pilosa* is quite a good indicator of this kind of beech woodland, though it is not very common. *L. sylvatica* is very much confined to ungrazed situations and, though scarce overall, it can attain local abundance. *Carex pilulifera* can also occur, again in ungrazed stands and transitions to open heath. That most characteristic species of British woodlands on more base-rich and moister soils, *Hyacinthoides non-scripta*, is hardly ever found, even where the shade is not too dense.

Other field-layer plants occurring with varying frequency, though never very commonly, include *Melampyrum pratense*, *Oxalis acetosella* and, particularly distinctive in the New Forest and locally elsewhere, *Ruscus aculeatus*. Ferns are typically sparse, though *Blechnum spicant* is sometimes found and, to the north, *Dryopteris dilatata*. Tree seedlings occur rather patchily, the exposed patches of the bare mor mat presenting an especially uncongenial substrate on which to gain a hold and herbivores often devouring the bulk of the more palatable plants. However, after good mast years, *Fagus* seedlings can be plentiful and less frequently, there can be some *S. aucuparia*, *Ilex* and, in gaps, *Q. robur* and birch. In western and northern stands, *A. pseudoplatanus* seedlings can also appear in considerable numbers but, even where shade or grazing are not a threat to survival, they rarely get away and often show severe signs of nutrient deficiency, probably of nitrogen.

Grazing and browsing also reduce the prominence of *Vaccinium myrtillus* which is strongly preferential to this kind of beech woodland, but very variable in its frequency of occurrence and its abundance. And, as in the *Quercus*-*Betula*-*Deschampsia* woodland, it tends to have a better potential representation outside drier areas, being very characteristic of ungrazed stands in the western Weald and the New Forest, where it occurs in both more open transitions to heath and under closed canopies with fairly dense shade. Much more strictly confined to the former situations and to gaps and rides is *Calluna vulgaris*. When either or both of these ericoids are present, they give this vegetation a heathy aspect never found in the *Fagus*-*Rubus* woodland.

Also very distinctive here is the bryophyte flora which, though not providing consistently high cover,

often gives the only touch of green to the ground beneath the densest stands of *Fagus* and includes a number of good preferentials against other kinds of beechwoods. The most frequent species overall are *Dicranella heteromalla* and *Mnium hornum* with *Hypnum cupressiforme* s.l. (often *H. mammilatum* over the beech roots), *Polytrichum formosum*, *Dicranum scoparium* and *Isopterygium elegans* somewhat less common and consistent; but the most striking species is *Leucobryum glaucum*, especially when it is present in abundance as pale green cushions set amongst a dark expanse of beech litter. Other species found more occasionally are *Lepidozia reptans*, *Calypogeia fissa/muellerana*, *Plagiothecium undulatum*, *Diplophyllum albicans*, *Rhytidadelphus loreus*, *Thuidium tamariscinum*, *Hylocomium splendens* or, in heavily-polluted stands in the Pennines, *Orthodontium lineare* and *Gymnocolea inflata*. There can also be some sparse patches of *Cladonia squamules* and, of course, this kind of woodland is renowned for its autumn fungi among which various species of *Boletus*, *Russula*, *Amanita* and chantarelles are especially distinctive.

Sub-communities

***Fagus sylvatica* sub-community.** Here, the vegetation is overwhelmingly dominated by beech in a canopy that is consistently closed and densely shading, with almost total exclusion of all other plants. Woody associates are very scarce with even *Q. robur* reduced to an occasional, generally low-cover, contribution; smaller trees and shrubs are virtually absent with only very sparse *Ilex* or a few *Fagus* saplings; the field layer is of negligible cover with even *D. flexuosa* eliminated and just beech seedlings occurring with any frequency or abundance (and, even then, varying very much with masting); and an impoverished ground layer comprises a few scattered tufts of *Mnium hornum*, *Dicranella heteromalla*, *Eurhynchium praelongum*, *Isopterygium elegans* and *Hypnum cupressiforme*.

***Deschampsia flexuosa* sub-community: *Rusco-Fagetum* Géhu 1975b p.p.** In this sub-community, there is a rather more varied canopy than in the above and all the other layers show at least some increase in cover and diversity. *Fagus* is still the most frequent tree and it is typically still the overwhelming dominant but oak (usually *Q. robur* but sometimes *Q. petraea* and hybrids) is quite frequent and it can be locally abundant; *A. pseudoplatanus* also makes an occasional contribution in stands to the west and north. Beneath, the prominence of smaller woody species is patchy and still generally of a low order but both *Ilex* and beech saplings are more common and abundant, *S. aucuparia* is sometimes found and, in more open places, there can be some

young birch. Much more obviously, there is a richer and more extensive herb cover, especially beneath the scattered oaks. *D. flexuosa* becomes constant and *Pteridium* occurs occasionally and there can be scattered plants of *Agrostis capillaris*, *Holcus mollis* and *Luzula pilosa*, sparse trailing shoots of *Rubus* or *Lonicera* and sometimes a little *Dryopteris dilatata*. *Holcus lanatus* and *Epilobium angustifolium* can occur in disturbed places, as in plantation stands. Bryophytes are also noticeably more varied and extensive: *Mnium hornum* and *Dicranella heteromalla* become frequent and *Polytrichum commune*, *Dicranum scoparium*, *Isoterygium elegans*, *Hypnum cupressiforme* and *Leucobryum glaucum* are occasional.

***Vaccinium myrtillus* sub-community:** *Rusco-Fagetum* Géhu 1975b p.p. Oak further increases its representation here, becoming as frequent as *Fagus* and quite often comprising 10–25% of the canopy. *B. pendula* is frequent, too, though its cover is usually low, and there can be occasional large *Ilex* or *Taxus*, but the main contribution of holly is to a second tier of trees which is here quite extensive and sometimes very dense. Beech saplings are frequent and *S. aucuparia* occurs occasionally.

The field layer is usually no more extensive than in the *Deschampsia* sub-community but it is a little richer in species and quite distinctive. Both *D. flexuosa* and *Pteridium* are constant but *Vaccinium myrtillus* is the most striking feature, sometimes growing up to half a metre tall and, in areas of less deep shade, attaining high cover values. Some herbs, such as *Carex pilulifera* and *Melampyrum pratense*, are preferentially frequent too and there can be a patchy ground cover of *Hedera*. The most numerous plants, however, are often tree seedlings with, as well as those of *Fagus*, many *Ilex* and *Q. robur* and occasionally some *S. aucuparia*. Bryophyte cover can be quite extensive though, apart from a slightly increased frequency for *Leucobryum* and an occasional preferential occurrence of *Calypogeia fissa/muellerana*, the species represented are very much as in the *Deschampsia* sub-community.

***Calluna vulgaris* sub-community:** *Frangulo-Ilicetum* Géhu 1975b p.p. The woody cover in this sub-community is not quite so continuous as elsewhere and, though *Fagus* remains constant and sometimes provides the bulk of the canopy, both *Q. robur* and *B. pendula* are common and patchily abundant and, quite often, mixtures of *Ilex* and young birch make up some of the cover. Beneath this more open canopy, the field layer is more extensive than usual in this kind of woodland, though it is largely made up of areas of *Pteridium*, occasional patches of *Vaccinium* and, especially distinctive here, *Calluna vulgaris*. Under the often quite tall growth of these species, casting a shade of their own and, in the

case of bracken, accumulating bulky litter, herbs, tree seedlings and bryophytes are all reduced. *D. flexuosa* and *Agrostis capillaris* can occasionally be found and there may be a few individuals of *Rubus*, *Lonicera* or *Luzula pilosa* but otherwise the ground is largely bare apart from sparse plants of *Dicranella heteromalla*, *Mnium hornum*, *Hypnum cupressiforme* and *Leucobryum*.

Habitat

The *Fagus-Deschampsia* woodland is confined to very base-poor, infertile soils in the southern lowlands of Britain. Within the native range of beech in this country, the community has some claim to be the climax forest type but it has developed widely in plantations, even in this region, and many stands bear signs of silvicultural treatment, being managed now as high forest for timber. In some places, it forms part of a wood-pasture landscape and grazing and browsing continue to be important in the floristics and regeneration of the community.

The *Fagus-Deschampsia* woodland is found over one extreme kind of afforested lowland soils, being limited to lime-free profiles with a superficial pH usually less than 4 and with mor humus (Watt 1934b, Rackham 1980, Peterken 1981). Among such soils, shallow humic rankers are quite rare here: they are not common anyway within the natural range of *Fagus* and where they are more abundant beyond this, as on Pennine sandstones and grits, they have been avoided in the planting of beech. Most often, then, the profiles are deeper and more mature, being brown earths with incipient podzolisation (frequently having discontinuous micropodzols in the top few centimetres) or podzols proper with prominent bleaching and humus iron pans. Typically, drainage is free to excessive, though some deep profiles are influenced by ground water below, when they are classified as stagno-podzols or stagnogley-podzols (Brown 1953, Avery 1958, 1964, 1980, Tubbs 1968).

Such soils are found under beech over a variety of parent materials. Arenaceous bedrocks are important substrates in the Weald where the community occurs on Cretaceous Ashdown and Tunbridge Wells beds with Poundgate stagnogley-podzols in the High Weald and on Folkestone and Hythe Beds with Shirrell Heath humo-ferric podzols around the western edge (Woolridge & Goldring 1953, Soil Survey 1983). Further north, plantations occur over podzolised soils derived from Triassic Keuper and Bunter sandstones and Carboniferous sandstones and grits, notably the Belmont stagno-podzols along the Pennine fringes (Carroll *et al.* 1979, Jarvis *et al.* 1984). Quite commonly, however, and especially in the south, the profiles are developed in part from coarse-textured superficials. In the New Forest, for example, Eocene Bagshot and Barton

sands and gravels overlain with Plateau Gravels carry extensive podzolised soils and similar mixtures of parent materials underlie stands in parts of Surrey and Essex, as in Epping Forest (Paulson 1926, Tansley 1939). North-west of here, running up the dip slope of the Chilterns, sandy remnants of Eocene Reading Beds, intermixed with Clay-with-Flints and thick Plateau Drift, have given rise to podzolised Batcombe and Berkhamsted soils, supporting this acidic extreme of the beechwood series described by Watt (1934b) and Avery (1958, 1964).

The general edaphic conditions here help define this community against its counterpart on somewhat less base-poor brown earths, the *Fagus-Rubus* woodland, though the very dense shade of beech often reduces the associates to such low levels of occurrence that visual differences between the two communities are not always very striking; and some species, such as *Ilex* and *Pteridium*, are common throughout both. Nonetheless, the lower frequency of *Rubus* here and its much less consistent abundance provide one good marker of the move towards more sharply draining and acidic conditions; the replacement of grasses like *Milium effusum*, *Melica uniflora*, *Poa trivialis* and *Deschampsia cespitosa* by *D. flexuosa* and *Agrostis capillaris* is another; then, there is the patchy prominence, where grazing and light permit, of the ericoid sub-shrubs and the preponderance, among the bryophytes, of markedly calcifuge species. And, overall, though *Fagus* remains generally dominant, there is an obvious reduction in the quality of the trees on these extreme soils (Brown 1953, 1964, McNeill 1961).

The general importance of this edaphic boundary can sometimes be clearly seen where both communities occur in close proximity in the kind of soil-vegetation series described from the Chiltern plateau (Watt 1934b, Avery 1958, 1964), the switch from the spongy mull of the *Fagus-Rubus* woodland to the firm mor mat of the *Fagus-Deschampsia* woodland often being felt underfoot. But small-scale variation within the kinds of soils that support both these communities is quite common, even over relatively short distances, being related in part to differences in superficials and in part to topography (exposed slopes blown free of litter being particularly likely to develop mor: Avery 1958, 1964). More accurately, then, the *Fagus-Deschampsia* woodland occupies soil mosaics in which podzolised profiles with mor predominate, the *Fagus-Rubus* woodland mosaics in which less strongly leached profiles with mull cover most of the ground. And it seems likely that temporal changes from one soil type to the other can also occur, partly as a consequence of natural replacement of beech by oak or *vice versa* at particular points in space, partly under the influence of certain kinds of treatment (see below). So small-scale edaphic and vegetational instability may be

a frequent, and in some respects quite normal, feature here.

Climate varies considerably across the range of the *Fagus-Deschampsia* woodland and plays some part in the exclusion of natural stands of the community from the drier parts of East Anglia and the cooler and wetter north and west (Godwin 1975, Rackham 1980), although planted beech grows well in this kind of woodland way beyond the limit which the tree was able to attain by natural spread. The effects of climatic differences on the associated flora are, however, not very obvious because of the striking ability of beech to create its own climate beneath the canopy, impoverishing the vegetation with its deep shade and through root competition, probably very severe again here, as on the rendzinas of the *Fagus-Mercurialis* woodland which are likewise very free-draining. Shade-tolerant species show the clearest response with *Ilex* and, to a lesser extent, *Hedera*, increasing in areas of more equable climate like the New Forest, as against the Chilterns. *Vaccinium* also is largely restricted to stands receiving more than 800 mm rainfall yr^{-1} and *Dryopteris dilatata* and *Acer pseudoplatanus* increase somewhat as annual precipitation approaches 1000 mm, though the former is not as common here as in north-western stands of the *Quercus-Betula-Deschampsia* woodland and both may be hindered by the way in which beech accentuates the natural dryness of the soils. The bryophyte component shows no marked enrichment in stands towards the more humid north-west, though atmospheric pollution may restrict their abundance in the southern Pennines: badly-affected *Fagus-Deschampsia* woods in this area can have very few species.

Such floristic differences of this kind as there are, are not a sufficient basis in this community for erecting subdivisions, but the influence of the local light climate is. At one extreme, the *Fagus* sub-community includes stands with the very deepest canopy shade where beech reigns supreme in a gap-free cover, typically associated with younger woodlands of natural origin where the trees have not yet begun to die or with unthinned plantations. In fact, so many of these beechwoods are under commercial forestry that natural gap formation can be quite rare, but where it does occur or where trees are extracted, the *Calluna* sub-community typically develops, with its abundance of heather and bracken and profusion of birch, holly and oak. Similar vegetation is characteristic of those places where beech is establishing itself on previously open heathland (Watt 1934b, Peterken & Tubbs 1965) and of stands of the community which occur in more heathy wood-pasture landscapes of some Forests and parks, where grazing helps maintain a mosaic of closed and open areas (Rackham 1980, Peterken 1981). In terms of their relationship with the degree of light penetration, the *Des-*

champsia and *Vaccinium* sub-communities lie between the two extremes, being associated with more or less intact canopies, though ones in which high frequencies and local abundance of oak and, to a lesser extent, birch, can provide some relief from the overwhelming shade of beech. In these kinds of *Fagus-Deschampsia* woodland, the field layer is often distributed rather patchily, thickening up most obviously beneath these other trees, which often occupy old gaps and which perhaps represent a stage in a slow cyclical replacement of the local dominants, one by the other.

The floristic differences between the *Deschampsia* and *Vaccinium* sub-communities illustrate very clearly the continuing importance of a further factor in these woods and that is grazing and browsing by stock and deer which influence not only the composition of the field layer but also the regeneration of the trees. *Vaccinium*, though its occurrence is limited to some extent by climate (it is sparse in drier regions and under very dense shade), only attains any prominence in the absence of herbivores which can reduce it to sparse and leafless shoots. Freedom from grazing also allows some herbs to increase their frequency and cover, but the most obvious response is often among tree seedlings. Regeneration of *Ilex* is under the close control of herbivores here (Peterken 1965, 1966, Peterken & Tubbs 1965, Peterken & Lloyd 1967) and its seedlings can become very common and plentiful in the *Vaccinium* sub-community. *S. aucuparia* is likewise very palatable and, though seed-parents are infrequent in the community, its seedlings too show an increase in this kind of *Fagus-Deschampsia* woodland. *Q. robur* is also well represented though it is less shade-tolerant than either holly or rowan and will only get away in gaps. And finally, seedlings of *Fagus* itself are more frequent here than in any other sub-community, subject, of course, to the vagaries of masting. No details of grazing history were available for the samples but the fact that well-grown holly and beech saplings are also abundant in the understorey of the *Vaccinium* sub-community here suggests that there has been some continuity in the exclusion of herbivores from these particular stands. Clearly, this need not always be the case because, where grazing has recently declined, it will take a considerable time for seedlings to progress and contribute to the taller tiers of the vegetation. Conversely, stands of the *Deschampsia* sub-community may be denuded of seedlings as each season progresses and yet have a dense understorey related to past periods of relative freedom from herbivores, as in the New Forest where waves of regeneration in woodlands to which this community contributes have been clearly related to grazing history (Peterken & Tubbs 1965, Tubbs 1968).

The regeneration of beech and oak here, though affected by grazing, is, however, rather more complex than that of holly. *Fagus* maintains its general domi-

nance, in the end, by the very considerable shade-tolerance of its own seedlings and saplings but it has difficulty in getting a hold if, either all litter is blown away leaving a bare mat of mor which sucks up water like a sponge, or the field layer is very densely-shading. It also fruits very erratically and the mast is not transported far, often just dropping straight down from the tree (Watt 1923, 1924, 1925). Conditions seem to be optimal where, after good mast years, fruit falls towards the edge of gaps which have not yet become clothed with dense *Pteridium* or *Calluna* or acquired a core of thickly-set *Ilex*, birch or oak, requirements whose importance is well illustrated here by the scarcity of beech seedlings in the *Calluna* sub-community. Oak is rather different: it, too, favours the presence of some loose litter to prevent desiccation but it can grow up through quite dense herbage (Jones 1959) and, more importantly, acorns can be transported considerable distances (Mellanby 1968) so, free of any challenge other than a previously-developed thick canopy of *Ilex*, it can gain the advantage over *Fagus* in the middle of gaps here and on open ground where new stands are developing. Where such an advantage prevails over substantial areas and/or for considerable lengths of time, the woodland cover can be seen as stabilising into the *Quercus-Betula-Deschampsia* woodland, the oak- (or birch-) dominated analogue of this community, but local and relatively short-term alternations of beech and oak are probably an integral part of canopy variation here and, as explained above, they can themselves affect the patterning of the field layer and perhaps alter the balance between mor and mull development in the soils.

The relative prominence of beech and oak in particular stretches of mature high forest has, however, been much affected by treatment. Even in the New Forest, where intimate mosaics are a prominent feature, the balance has been swung towards beech by preferential extraction of oak, often, in this case, for providing ship timber (Tubbs 1968). Elsewhere, *Fagus* has been favoured where the community has contributed to a local beech economy, either as semi-natural stands or, often, as plantations. Coppicing of beech is now defunct, though it was important in the Chilterns in medieval and later times (Mansfield 1952, Roden 1968), and stands are usually now treated on shelterwood or clear-felling systems for timber, restocking sometimes involving conifers (Brown 1953, 1964). However, there is still evidence in some stands in the Chilterns of the results of treatment on the selection system which depended on natural regeneration in gaps created artificially by extraction of individual trees. The unreliability of such regeneration, coupled with shifts in demand for beech, led eventually to the abandonment of this style of treatment but stretches of *Fagus-Deschampsia* woodland with a preponderance of densely-set, poorly-

grown trees bear witness to continued removal of better-quality timber. Such woodland seems especially likely to maintain mor soils and is perhaps more resistant to the kinds of vegetational and edaphic changes seen elsewhere in the community (Avery 1958).

Zonation and succession

Two kinds of zonation are commonly found within stands of the *Fagus-Deschampsia* woodland. The first relates to differences in canopy shade and it can be a direct reflection of the maturation of the vegetation, with the *Calluna* sub-community occupying recently-colonised ground, the *Fagus* sub-community forming dense woodland in the establishment phase, the *Deschampsia* or *Vaccinium* sub-community occurring where the canopy has begun to open up a little and the *Calluna* sub-community marking gaps. In fact, actively-colonising *Fagus-Deschampsia* woodlands are of rather restricted occurrence and, in commercial forests, natural gap formation is pre-empted, re-establishment is from planted stock and the resultant stands have trees of uniform age with a more homogeneous field layer. Here, then, the patterning of the different sub-communities is much more regular in both space and time with sharply-defined compartments of the *Fagus* sub-community before thinning, the *Deschampsia* or *Vaccinium* sub-community after, and the *Calluna* sub-community making only a brief appearance between rotations apart from along the edges of rides where it may mark a transition to a narrow strip of heath or bracken without trees. Characteristically, the outer margins of such treated stands are sharply defined with an abrupt switch to other types of forest (often conifer-dominated stands of the *Quercus-Betula-Deschampsia* woodland) or to surrounding agricultural land.

The other kind of zonation relates to the intensity of grazing or browsing. Sometimes differences in the present pattern of access by herbivores can be seen in a change from the *Deschampsia* to the *Vaccinium* sub-community at an artificial stock- and deer-proof boundary; in other cases, the structure of the vegetation itself may hinder access, creating protected enclaves (as in some stands surrounded by a ring of holly, a feature in parts of the New Forest: Tubbs 1968) or a diffuse mosaic of more- and less-grazed areas with these two sub-communities. Such patterns can be found in some ancient Forests and parks and they often also involve more open glades with the *Calluna* sub-community and stretches of heath where the establishment of a woody cover is held in check by the herbivores. Withdrawal of grazing in such situations (and the cessation of burning or the cutting of heather and bracken, once important on commons in the south) may allow more gradual zonations to develop in which light penetration through the canopy becomes the primary factor in determining

the distribution of the sub-communities. In fact, wood-pasture landscapes usually present complex patchworks of the various kinds of *Fagus-Deschampsia* woodland related to the interplay of grazing and shading, both at the present time and in the past, as Peterken & Tubbs (1965) showed in the New Forest.

Mosaics of this kind, developed over fairly uniform podzolised soils, also frequently involve tracts of woodland in which beech is so poorly represented in proportion to oak and birch that the vegetation is best considered part of the *Quercus-Betula-Deschampsia* woodland. The relative ease with which these trees outperform beech in the early colonisation of open ground means that this community often functions as a seral precursor to the *Fagus-Deschampsia* woodland, interposed between calcifugous grassland, heath and bracken on the one hand and mature beech forest on the other, both in time and in spatial zonations. The *Quercus-Betula-Deschampsia* woodland can also be a temporary replacement for the *Fagus-Deschampsia* woodland in larger gaps and clearings, before beech re-establishes by seeding in around the margins or is planted in; and, where *Quercus-Betula-Deschampsia* woodland seems more permanently ensconced, there is sometimes an assumption that it occupies ground that, had it not suffered gross disturbance, would naturally carry *Fagus-Deschampsia* woodland (e.g. Géhu 1975a). In fact, even within the native range of beech in Britain, this tree is rather slow to assert or reassert its dominance in these situations: on newly-colonised ground, the *Quercus-Betula-Deschampsia* woodland often seems to attain a stability of its own; and, even when beech is abundant in the immediate neighbourhood, it has some difficulty in getting away in larger gaps. It may therefore be too simplistic to regard the *Fagus-Deschampsia* woodland as the natural climax forest on more surface-leached soils in southern Britain: if anything, it is beech, with its unreliable fruiting and poor seed-dispersal, which requires a measure of assistance to succeed, a fact borne in on practitioners of the selection system of treatment (Brown 1953, 1964), and one invoked to explain the tardy and limited migration of this tree in the post-Glacial period in Britain (e.g. Godwin 1975). And, even where beech has become well established on such profiles, it may be more accurate to see its dominance as under a measure of threat from oak and birch, such that slowly-shifting patchworks of *Fagus-Deschampsia* and *Quercus-Betula-Deschampsia* woodlands are a quite natural feature, moved towards the former community by selection for beech, in favour of the latter wherever there is opportunity for expansion of the forest cover.

There may also be room for some reassessment of the status of the *Fagus-Deschampsia* woodland in relation to its counterpart on less base-poor brown earths, the *Fagus-Rubus* woodland. In general, the floristic distinc-

tions between these two communities are better defined than those between the *Fagus-Deschampsia* woodland and its oak-birch analogue, having a firm foundation in edaphic differences. Transitions from the one community to the other can sometimes be observed within individual stands, beech-dominance being maintained throughout, but the field and ground layers showing a marked change with the switch from leached brown earths with mull to podzols with mor, a zonation forming part of the soil-vegetation series described from the Chilterns (Watt 1934b, Avery 1958) but also seen in more complex mosaics in the New Forest (Tubbs 1968). As noted earlier, however, small-scale variation in topography and parent materials may make this kind of transition quite ill defined, so that again patchworks of the two communities are a fairly normal feature. It is also possible that, in more marginal situations, there is some measure of cyclical alternation in time between the *Fagus-Deschampsia* and *Fagus-Rubus* woodlands at any one place. Despite the fact that beech can encourage the formation of mor and thus favour the development of soil conditions inimical to the survival of some of its characteristic associates in the *Fagus-Rubus* woodland, this is not necessarily a progressive and irreversible process, indeed it seems to be best favoured by certain treatments of beech, rather than being a wholly natural development (Avery 1958). And, once again, it may be that, in less strictly-treated high forest, oak and birch play an important part here because with *Rubus* under-scrub, they can pre-empt beech in gaps, allow the spread of a more extensive field layer in their less dense shade and perhaps shift the edaphic and vegetational balance back to less extreme conditions. Along both its boundaries with other woodland types, the soil-related junction with the *Fagus-Rubus* woodland and the competitive/successional one with the *Quercus-Pteridium-Rubus*

woodland, the relationships of the *Fagus-Deschampsia* woodland are thus more complex than they seem at first sight.

Distribution

Within the natural British range of beech, this community is best represented in the Weald, the New Forest and on the Chiltern plateau with isolated sites elsewhere in the south. Planted stands, indistinguishable in their floristics, occur well beyond this limit, especially around the Pennine fringes.

Affinities

As defined here, the *Fagus-Deschampsia* woodland is the more or less exact equivalent of the most calcifugous beechwood in Watt's (1934b) Chiltern series, described by Tansley (1939) and referred to by Rackham (1980) as *Fagetum ericetosum* (or *arenicolum*). It includes the bulk of Peterken's (1981) 'acid oak-beechwoods', split in his scheme on the basis of whether the associated oak is *Q. petraea* (stand type 8A) or *Q. robur* (8B).

Apart from Watt's (1934b) original account and a phytosociological description provided from the New Forest by Géhu (1975b, where immature stands were treated as part of a separate community), systematic and complete treatments of this kind of woodland have not been published. Nonetheless, the parallels with similar communities in other parts of north-west Europe are very clear and the *Fagus-Deschampsia* woodland has obvious equivalents in such associations as the *Ilici-Fagetum*, the *Luzulo-Fagetum*, the *Deschampsio-Fagetum* and the *Fago-Quercetum* described from France, Belgium and the Netherlands (e.g. Durin *et al.* 1968, Westhoff & den Held 1969, Géhu 1975a). In phytosociological terms, then, this community represents the Luzulo-Fagion sub-alliance in Britain.

Floristic table W15

	a	b
<i>Fagus sylvatica</i>	V (7–10)	V (6–10)
<i>Quercus robur</i>	II (2–7)	III (1–4)
<i>Betula pendula</i>	I (3)	I (1)
<i>Ilex aquifolium</i>	I (3)	I (2–4)
<i>Quercus petraea</i>	I (4)	II (1–6)
<i>Taxus baccata</i>	I (3–5)	I (4)
<i>Acer pseudoplatanus</i>	I (2–4)	II (1–8)
<i>Pinus sylvestris</i>	I (2–4)	I (4)
<i>Quercus hybrids</i>		I (1–4)
<i>Betula pubescens</i>		I (3–4)
<i>Ilex aquifolium</i>	I (3)	III (1–2)
<i>Fagus sylvatica</i> sapling	I (1–2)	II (3–4)
<i>Sorbus aucuparia</i>		I (2–3)
<i>Quercus robur</i> sapling		I (1)
<i>Betula pendula</i> sapling		II (3–6)
<i>Rhododendron ponticum</i>		I (1)
<i>Fagus sylvatica</i> seedling	III (1–6)	III (1–4)
<i>Dicranella heteromalla</i>	II (1–3)	III (1–4)
<i>Pteridium aquilinum</i>	I (1–2)	II (2–7)
<i>Mnium hornum</i>	II (1–5)	IV (1–8)
<i>Deschampsia flexuosa</i>		V (2–8)
<i>Eurhynchium praelongum</i>	II (1–4)	
<i>Polytrichum formosum</i>		III (1–5)
<i>Dicranum scoparium</i>		II (2–5)
<i>Luzula pilosa</i>		II (1–3)
<i>Lepidozia reptans</i>		II (2–3)
<i>Isopterygium elegans</i>	I (2)	II (2–5)
<i>Cladonia fimbriata</i>		II (2–4)
<i>Dryopteris dilatata</i>		II (1–3)
<i>Holcus lanatus</i>		II (1–4)
<i>Epilobium angustifolium</i>		I (3–4)

c	d	15
V (6-9)	V (6-9)	V (6-10)
V (4-5)	III (3-4)	III (1-7)
III (1-4)	III (4-5)	II (1-5)
II (2-7)	I (3)	I (2-7)
II (1-4)		I (1-6)
I (4)		I (3-5)
		I (1-8)
		I (2-4)
I (1-4)		I (1-4)
		I (3-4)
IV (3-7)	IV (2-4)	III (1-7)
III (3-4)	I (4)	II (1-4)
I (1-2)		I (1-3)
I (7)	I (2-3)	I (1-7)
	III (3-6)	I (3-6)
	II (1-6)	I (1-6)
IV (1-3)	I (1-3)	III (1-6)
III (2-4)	III (2-4)	III (1-4)
V (3-8)	V (3-9)	III (1-9)
V (1-6)	III (2-3)	III (1-8)
V (1-5)	II (3-5)	III (1-8)
		I (1-4)
III (2-6)		II (1-6)
II (5-6)		I (2-6)
I (3)	I (3)	I (1-3)
	I (4)	I (2-4)
I (4)		I (2-5)
	I (3)	I (2-4)
I (3)		I (1-3)
		I (1-4)
		I (3-4)

Floristic table W15 (cont.)

	a	b
<i>Orthodontium lineare</i>		I (3–4)
<i>Gymnocolea inflata</i>		I (2–4)
<i>Quercus petraea</i> seedling		I (2–3)
<i>Hylocomium splendens</i>		I (5–6)
<i>Vaccinium myrtillus</i>		
<i>Ilex aquifolium</i> seedling		I (2)
<i>Leucobryum glaucum</i>		II (3–6)
<i>Quercus robur</i> seedling		I (2)
<i>Carex pilulifera</i>		I (3)
<i>Sorbus aucuparia</i> seedling		I (1–2)
<i>Calypogeia fissa/muellerana</i>		I (1–2)
<i>Melampyrum pratense</i>		I (1)
<i>Hedera helix</i>		I (3)
<i>Calluna vulgaris</i>		
<i>Hypnum cupressiforme</i>	I (3–4)	II (1–4)
<i>Rubus fruticosus</i> agg.	I (3–5)	II (3–6)
<i>Agrostis capillaris</i>		II (2–5)
<i>Lonicera periclymenum</i>	I (2)	II (1–4)
<i>Holcus mollis</i>	I (3)	I (3–8)
<i>Plagiothecium undulatum</i>	I (3–4)	I (1–3)
<i>Acer pseudoplatanus</i> seedling	I (2–3)	I (1–3)
<i>Poa nemoralis</i>	I (3–4)	I (1–3)
<i>Hyacinthoides non-scripta</i>	I (4)	I (1–2)
<i>Luzula sylvatica</i>	I (3)	I (1–7)
<i>Blechnum spicant</i>	I (3)	
<i>Oxalis acetosella</i>		I (1–3)
<i>Tetraphis pellucida</i>		I (2)
<i>Cladonia squamules</i>		I (1)
<i>Thuidium tamariscinum</i>		I (1)
<i>Rhytidiadelphus loreus</i>		I (1)
<i>Diplophyllum albicans</i>		I (3)

c	d	15
		I (3-4)
		I (2-4)
		I (2-3)
		I (5-6)
V (4-8)	II (4-7)	II (4-8)
IV (2-5)	I (3)	II (2-5)
III (4-6)	II (3-4)	II (3-6)
III (1-3)		I (1-3)
III (2-4)	I (3)	I (2-4)
II (2)		I (1-2)
II (2)		I (1-2)
II (3)		I (1-3)
II (3-4)		I (3-4)
	V (2-7)	I (2-7)
II (1-4)	II (2-3)	II (1-4)
II (3-4)	II (3-4)	II (3-6)
II (1-4)	II (2-3)	II (1-5)
II (2-3)	I (2)	I (1-4)
I (3-5)		I (3-8)
I (1-3)		I (1-4)
		I (1-3)
		I (1-4)
		I (1-4)
		I (1-7)
I (4)		I (3-4)
I (1-3)		I (1-3)
I (2)		I (2)
I (3)		I (1-3)
I (3)		I (1-3)
I (2)		I (1-2)
I (2)		I (2-3)

<i>Ruscus aculeatus</i>		I (1–3)
<i>Molinia caerulea</i>		I (1–3)
Number of samples	19	25
Number of species/sample	5 (1–15)	15 (8–23)
Tree height (m)	18 (15–25)	21 (15–25)
Tree cover (%)	98 (90–100)	92 (60–100)
Shrub height (m)	3 (1–6)	3 (1–5)
Shrub cover (%)	1 (0–5)	5 (0–50)
Herb height (cm)	11 (2–50)	19 (8–40)
Herb cover (%)	6 (0–30)	55 (10–90)
Ground height (mm)	10	17 (5–40)
Ground cover (%)	6 (0–30)	29 (0–90)
Altitude (m)	138 (61–270)	146 (75–380)
Slope (°)	11 (0–30)	11 (0–85)

- a *Fagus sylvatica* sub-community
- b *Deschampsia flexuosa* sub-community
- c *Vaccinium myrtillus* sub-community
- d *Calluna vulgaris* sub-community
- 15 *Fagus sylvatica*-*Deschampsia flexuosa* woodland (total)

I (1-3)		I (1-3)
I (1-3)	I (5)	I (1-5)
8	7	59
19 (10-32)	12 (9-14)	12 (1-32)
26 (10-35)	16 (9-30)	20 (9-35)
100	85 (50-100)	94 (50-100)
4 (2-5)	3 (1-4)	3 (1-6)
23 (1-60)	14 (0-40)	7 (0-60)
29 (15-50)	81 (20-120)	25 (2-120)
49 (10-100)	77 (40-100)	41 (0-100)
10	15 (10-30)	14 (5-40)
38 (1-90)	7 (1-15)	22 (0-90)
83 (25-122)	94 (20-152)	129 (20-380)
7 (0-30)	5 (0-10)	10 (0-85)

