W17
Quercus petraea-Betula pubescens-Dicranum majus woodland

Synonymy

Caithness birchwoods Crampton 1911 *p.p.*; *Betuletum tomentosae* Moss 1911 *p.p.*; *Quercetum roboris* Tansley 1939 *p.p.*; *Quercetum petraeae/sessiliflorae* Tansley 1939 *p.p.*; *Betuletum Oxaleto-Vaccinetum* McVean & Ratcliffe 1962 *p.p.*; *Vaccinium*-rich birchwood association McVean 1964*a* *p.p.*; *Blechno-Quercetum* (Br.-Bl. & Tx. (1950) 1952) Klötzli 1970 *p.p.*; Loch Lomond oakwoods Tittensor & Steele 1971 *p.p.*; *Betula pubescens-Vaccinium myrtillus* Association Birks 1973 *p.p.*; Birch-oak woodland Peterken 1981 *p.p.*; Birch woodland Peterken 1981 *p.p.*; *Trientali-Betuletum pendulae* Birse 1982 *p.p.*; Woodland plot type 18 Bunce 1982 *p.p.*; *Blechno-Quercetum* (Br.-Bl. & Tx. (1950) 1952) Birse 1984 *p.p.*

Constant species

Betula pubescens, *Quercus petraea*, *Deschampsia flexuosa*, *Vaccinium myrtillus*, *Dicranum majus*, *Hylocomium splendens*, *Plagiothecium undulatum*, *Pleurozium schreberi*, *Polytrichum formosum*, *Rhytidiadelphus loreus*.

Rare species

Goodyera repens, *Adelanthus decipiens*, *Sematophyllum demissum*, *S. micans*.

Physiognomy

The *Quercus petraea-Betula pubescens-Dicranum majus* woodland, like its counterpart on less base-poor soils, the *Quercus-Betula-Oxalis* woodland, is almost always dominated by either oak or birch or various mixtures of the two trees, though in this community there is a more pronounced shift towards *Quercus petraea* and *Betula pubescens* as the characteristic species. *Q. petraea* is very common here and, in western Britain, where the bulk of the stands of this community are located, *Q. robur* makes only a very local, though sometimes conspicuous, contribution: it predominates, for example, in certain localities on Dartmoor, in Devon, notably at Wistman's Wood (Harris 1921, Christy & Worth 1922, Tansley 1939, Wigston 1974), and *robur* elements can also be detected elsewhere, as among the oaks at Keskadale in Cumbria and in some stands in Ross & Cromarty (Jones 1959, Gardiner 1974, Wigston 1974). However, it is only in eastern Scotland that there is any more widespread switch to *Q. robur* and hybrids, and here there seems a stronger likelihood of the oaks having originated from planted stock (Jones 1959, Gardiner 1974, Birse 1982, 1984).

Oak is often abundant in the canopy of this community though, even where it dominates, the tree cover is typically rather open and low, only rarely exceeding 20 m and generally being less than 15 m. In extreme situations, oak forms a very dwarfed canopy, as at Wistman's Wood (Harris 1921, Christy & Worth 1922) and Keskadale (Leach 1925), where many trees are less than 4 m and the most exposed individuals even shorter, their crowns wind-shaped into the contours of a rocky landscape. Elsewhere, in many stands in Wales, up through Cumbria and into south-west Scotland, the canopy presents an appearance of more orthodox high forest with well-grown oaks predominating though, moving further to the north-west of Scotland, oak becomes increasingly rare in the community and restricted to progressively lower altitudes: towards the limit of the range of this kind of woodland, it dominates up to only about 150 m (McVean 1964*a*) and is totally absent from many stands. It is likely that past treatment plays some part in the scarcity of oak in this region: there are strong suspicions that large timber has been widely removed from all kinds of woodland here (McVean & Ratcliffe 1962, McVean 1964*a*). Even where oak is dominant in this community, there is abundant evidence from throughout its range, that many stands have been treated as oak coppice. In western Britain, the *Quercus-Betula-Dicranum* woodland, together with the *Quercus-Betula-Oxalis* woodland, has been the major source of oak for charcoal and tan-bark, and tracts of multi-stemmed trees forming a fairly pure and structurally-even cover are widespread.

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It is in such stands that birch is generally most poorly represented, though it has often spread with the abandonment of coppicing and it was by no means always cleaned out as a weed, being itself cut to provide wood for bobbins or brushwood for besoms. Through the community as a whole, birch is very frequent, with *B. pubescens* being by far the more common species; *B. pendula* occurs only very occasionally overall though, like *Q. robur*, it tends to increase its representation in eastern Scotland. In high-forest stands, birch varies in abundance from occasional scattered trees growing amongst the oak to a much more prominent contribution, when the two trees form mosaics often, where the woodland is actively expanding, with a birch-dominated fringe around the margins. As oak decreases in frequency towards the north-west, birch becomes proportionately more obvious, just as it does in the *Quercus-Betula-Oxalis* woodland, until it provides the bulk of the woody cover. Towards higher latitudes, too, there is an increasing tendency for *B. pubescens* to be very obviously of ssp. *carpatica* with its distinct short and bushy habit (Walters 1964); elsewhere in this community, this taxon can be found in locally-exposed situations and at high altitudes.

Like oak, birch varies considerably in its physiognomy. In taller high forest, *B. pubescens* ssp. *pubescens* and *B. pendula* can readily keep pace with oak but birch-dominated stands often have a shorter canopy, especially where *B. pubescens* ssp. *carpatica* provides the cover. Dense thickets of birch can occur here, though the canopy is frequently more open with widely-spaced, and often rather sickly, individuals. Typically, stretches of birch have a rather uniform appearance: sometimes scattered pioneers are surrounded by younger trees but, more commonly, there is a single generation which shades out any offspring (McVean & Ratcliffe 1962).

As in the *Quercus-Betula-Oxalis* woodland, the most consistent woody associate of oak and birch is *Sorbus aucuparia*, though it is somewhat more frequent in this community than there. In high forest, it usually occurs as scattered trees, often of quite considerable size and breaking the canopy, though sometimes a little shorter than the oak and contributing to an ill-defined second tier of trees. However, it can be locally abundant (especially where there has been some relief from grazing: Anderson 1950, McVean 1964*a*) and, where oak becomes scarce towards the north-west it may share dominance with birch in a low, scrubby cover. The frequency and abundance of *Ilex aquifolium* are also affected by grazing and browsing: throughout this community, holly is rather uncommon, despite the favourable character of the climate.

Other tree species are scarce. *Fraxinus excelsior* and *Acer pseudoplatanus* occur very occasionally but they are rather strictly confined to pockets of more enriched soil. And, though *Tilia cordata* can sometimes be found growing on cliffs within Cumbrian stands of the community, it is very much a relic tree here, surviving at the extreme north-western limit of its British range (Pigott & Huntley 1978): such stands probably fall within Peterken's (1981) oak-lime stand type 5B, though the association of this species with the community is now essentially a topographic one, rather than of a vegetational kind. *Fagus sylvatica* occurs at very low frequencies, presumably having seeded in from introduced stock, and there are occasional records for conifers, extensive stands of which have been planted on soils that could support this community throughout the upland fringes of the north and west.

The contribution of smaller woody plants to the *Quercus-Betula-Dicranum* woodland is rather variable and only a few species, apart from saplings of those already mentioned, occur. In high-forest stands, there can be a discrete understorey, though its cover is somewhat patchy and usually low, sometimes negligible in old coppice or in woodlands which have been consistently grazed. In shorter canopies, stratification is indistinct and mature trees, shrubs and saplings merge into a single layer.

The most surprising feature among this element of the vegetation here, in sharp contrast to the lowland analogue of the community, the *Quercus-Betula-Deschampsia* woodland, is the continuing importance of *Corylus avellana*. In southern Britain, the frequency and abundance of this shrub provides a good floristic and ecological separation between the Carpinion 'bluebell woodland', where it is very common, and the Quercion 'bilberry woodland', from which it is virtually absent. The same is not true of the sub-montane north and west where, in the moister climate, it continues to be quite well represented even in those stands of the *Quercus-Betula-Dicranum* woodland which present a very calcifugous appearance (cf. Peterken 1981). However, there is no doubt that it does better on deeper and more fertile profiles, being confined to pockets of flushed soil in more bouldery woods and attaining its greatest cover where there is some accumulation of colluvium. And, although it has sometimes been selected for as a coppice crop here, it rarely forms a naturally dense understorey, occurring in high forest usually as scattered bushes. In the far north-west, it can contribute, with *B. pubescens* and *S. aucuparia*, to a scrubby cover over this community, though it is not so prominent in such mixtures here as it is in the canopy of *Quercus-Betula-Oxalis* woodlands of that region (e.g. Birks 1973).

Apart from *Corylus*, it is generally young trees and saplings of birch and rowan, together with occasional *Ilex*, that make up such understorey as there is in this kind of woodland. But the regeneration of all these is much affected by grazing, which is widespread in these woods, and also, in the case of birch, by canopy shade. Saplings of birch, then, are generally confined to gaps and margins and the usual picture beneath intact canopies where grazing and browsing are not severe is one of scattered and patchily dense rowan and holly. Young *Q. petraea* can also sometimes be found in ungrazed stands, even where the shade is quite deep (Jones 1959), and more occasionally there may be saplings of *Fraxinus* or *A. pseudoplatanus*. Hawthorn (always *Crataegus monogyna*) occurs very sparsely, even more confined to deeper, more fertile soils than *Corylus*, and there is sometimes a little *Salix caprea*. *Rhododendron ponticum* can occur, sometimes with local prominence: it has occasionally been planted into these woodlands and thrives on the acid soils in the moist climate (Cross 1975). In eastern Scotland, *Juniperus communis* may be found: in that region, the *Quercus-Betula-Dicranum* woodland can form mosaics with the more calcifugous stands of the *Juniperus-Oxalis* woodland, patchworks of birch and juniper extending over both.

Three components are especially important in giving the field layer of the *Quercus-Betula-Dicranum* woodland its distinctive stamp: grasses, bracken and ericoid sub-shrubs. However, the relative proportions of these elements varies considerably with a number of factors (notably topography and soils, shade and grazing) so that the gross physiognomy of the field layer is quite diverse; and bracken also provides a measure of phenological change. As in the *Quercus-Betula-Oxalis* woodland, grasses provide the background and they can be particularly prominent in grazed woods over more even topography when they show their flush of renewed growth in early summer. But, in contrast to that community, there is a shift among the species represented towards the more calcifugous. *Deschampsia flexuosa* is now the most consistently frequent grass throughout; it is quite often abundant and can maintain its cover even over very shallow soils extending over the tops of boulders. *Holcus mollis*, on the other hand, becomes less common and is more restricted to pockets of deeper moister soil, though it tends to increase its representation in consistently-grazed stands. *Anthoxanthum odoratum* and *Agrostis capillaris*, though somewhat more frequent overall than *H. mollis*, also become more common and abundant under grazing. Other grasses occurring occasionally throughout are *Agrostis canina* ssp. *montana* and *Festuca ovina* and, more obviously towards the far west, *Molinia caerulea*. Mesophytic species such as *Holcus lanatus* and *Deschampsia cespitosa* are, however, distinctly scarce.

The presence of *Pteridium aquilinum* in this community presents a further floristic similarity to the *Quercus-Betula-Oxalis* woodland, though its prominence here is rather more restricted by the frequent occurrence of rock exposures and boulders with, at most, a very thin capping of soil. In such situations, bracken is confined to deeper accumulations in larger crevices between the talus fragments, though it can be much more extensive wherever there is some downwash or creep and, over slope bases with much colluvium, it can provide a dense canopy by the time its fronds are fully unfolded in midsummer, severely restricting the richness of the associated flora with its heavy shade and thick litter. It is also itself influenced by the shade of the canopy, so that it tends to thin out under closely-set trees, thickening up in gaps and clearings; and it tends to become more prominent, too, where there has been some relief from grazing (e.g. Tittensor & Steele 1971). The two characteristic companions of bracken in woodlands of moister and less base-poor soils, *Rubus fruticosus* agg. and *Lonicera periclymenum*, are here not very frequent, though they can make some contribution to a patchy underscrub where edaphic conditions are less extreme than usual and they, too, can increase a little where grazing is relaxed. A very characteristic bramble in this community is *R. sprengelii*.

The plants which provide the major distinction between the field layer of this community and that of the *Quercus-Betula-Oxalis* woodland are, however, the ericoids which are generally of rather restricted occurrence there but which here attain quite high frequencies and often great abundance. The most common among them is *Vaccinium myrtillus*, which can tolerate quite dense shade and therefore continue to make a fairly prominent contribution here even under intact canopies. It is, though, very sensitive to grazing and browsing. The rougher, more inaccessible topography provided by large boulders may offer some protection against the attention of sheep and deer and, in such situations, *V. myrtillus* can grow vigorously, even on quite shallow soils, forming a patchy cover half a metre or more high. But, with continued grazing, it can be quickly reduced to sparse, leafless shoots or even eliminated altogether. Under such conditions, and with the attendant increase in such grasses as *Agrostis capillaris, Anthoxanthum odoratum* and *Holcus mollis*, it may be very difficult to separate the vegetation of the *Anthoxanthum-Agrostis* sub-community here from that of the *Blechnum* sub-community of the *Quercus-Betula-Oxalis* woodland: this is a reflection of the very real fact that, over less extreme soils in the north-western uplands, grazing produces a floristic convergence in these two kinds of woodland.

Calluna vulgaris, which is a little less common overall than *V. myrtillus* but equally characteristic, is also reduced by the presence of herbivores, though it is much more sensitive to shade than bilberry, and only attains abundance here in more open areas, as in gaps and around the margins of stands, where it can figure prominently in transitions to heaths. *Erica cinerea* also occurs occasionally, again mostly in places with less dense canopy shade and sometimes *V. vitis-idaea* is encountered, though where this grows among *V. myrtillus*, it can be shaded out by the more vigorous growth of the latter when grazing is relaxed (e.g. Pigott 1983). In this community, *V. vitis-idaea* is especially associated with transitions to the *Juniperus-Oxalis* woodland in which the *Calluna* sub-community is sometimes found in eastern Scotland (e.g. Birse 1982, 1984). *Erica tetralix* is rare, though it can be found on wetter, acid soils.

Apart from these three elements, two further groups of herbs can make a contribution to the field layer of the *Quercus-Betula-Dicranum* woodland. Smaller angiosperms are often not very prominent in terms of their cover but a number of species are characteristic. Among the most frequent are *Galium saxatile* (often increasing in abundance in grazed woods), *Potentilla erecta*, *Melampyrum pratense*, *Teucrium scorodonia*, *Succisa pratensis*, *Solidago virgaurea*, *Carex pilulifera*, *Luzula pilosa*, *L. multiflora* and *L. sylvatica* (the last sometimes becoming extremely abundant when grazing is withdrawn and over inaccessible ledges and cliff faces). In contrast to the southern *Quercus-Betula-Deschampsia* woodland, *Oxalis acetosella* is also very frequent here, a good indicator of the continual moistness of the soils (Packham 1978) and one of the plants best able to survive a thick cover of bracken, bilberry or *Luzula sylvatica* (Packham & Willis 1977). Its typical companion on moister and less base-poor profiles, *Viola riviniana*, is sometimes found too where there is gentle seepage. It is only in such situations that *Hyacinthoides non-scripta* makes an appearance here: the general scarcity of this species, and its replacement on very moist soils, *Anemone nemorosa*, provides a good separation between this community and the *Quercus-Betula-Oxalis* woodland (though, once again, grazing may blur the distinction by reducing the cover of *Hyacinthoides* in the latter). Flushed areas may also have a little *Lysimachia nemorum* but species characteristic of marked base-enrichment by flushing are typically absent.

Ferns (other than bracken) constitute a final element in the field layer. *Blechnum spicant*, though it is still somewhat preferential for one particular sub-community, is more frequent throughout this community than in the *Quercus-Betula-Oxalis* woodland and it can attain great abundance and luxuriance in the mild climate of the far west (where this kind of vegetation forms part of the *Blechno-Quercetum* Br.-Bl. & Tx. (1950) 1952 redefined by Klötzli (1970) and Birse (1982, 1984)). *Thelypteris limbosperma* also occurs, but it is much less frequent than *Blechnum* and, though it can attain local abundance, is less characteristic here than it is in the *Quercus-Betula-Oxalis* woodland. *Dryopteris dilatata* is found occasionally and, rather less commonly, *D. filix-mas* and *D. borreri*, *Athyrium filix-femina* and *Gymnocarpium dryopteris*. *Polypodium vulgare* (probably *s.s.*) is quite common as an epiphyte on oak. Then, among dripping mats of bryophytes, *Hymenophyllum tunbrigense* and *H. wilsonii* can sometimes be seen and, on the tops and shoulders of boulders or on ledges, *Dryopteris aemula* can occur. As in other sub-montane woodlands, this component of the field layer tends to attain maximum diversity and luxuriance where this community forms part of the vegetation mosaic of ravines: in such situations, a profusion of different niches in a very cool, humid environment can carry a spectacular fern-dominated cover beneath the overhanging trees.

Underlying this considerable variation in the part played by the different components of the vascular flora, there is a consistent and rich contribution from bryophytes. Six out of the eight field- and ground-layer constants of this kind of woodland are mosses; bryophytes often exceed vascular plants in their diversity and abundance in particular stands; and very frequently, they make an immediate visual impression, forming a mottled carpet which keeps its colours throughout the year and which, in rocky woods in the very wet far west, extends virtually everywhere, from more grassy swards, up over boulders, on to the faces and ledges of rock exposures and over the roots and bole bases of the trees. Different species tend to be prominent in different microhabitats over more diverse topographies but among the many species represented throughout the community are *Dicranum majus*, *Rhytidiadelphus loreus*, *Polytrichum formosum*, *Pleurozium schreberi*, *Plagiothecium undulatum* (the constancy of all of which helps separate the bryophyte element here from that in the *Quercus-Betula-Oxalis* woodland), *Hylocomium splendens*, *Dicranum scoparium*, *Mnium hornum*, *Thuidium tamariscinum*, *Isothecium myosuroides*, *Hypnum cupressiforme* (including *H. mammilatum*), *H. jutlandicum*, *Rhytidiadelphus squarrosus*, *R. triquetrus*, *Sphagnum quinquefarium*, *Pseudoscleropodium purum* and *Lophocolea bidentata s.l.* Less commonly, there are records among the community companions for *Dicranella heteromalla*, *Dicranum fuscescens*, *Eurhynchium praelongum*, *Rhizomnium punctatum*, *Polytrichum commune*, *Tetraphis pellucida*, *Sphagnum palustre*, *Ptilium crista-castrensis*, *Plagiochila asplenoides*, *Lophocolea cuspidata*, *Calypogeia fissa*, *C. muellerana*, *Cephalozia media*, *C. bicuspidata*, *Barbilophozia floerkii*, *Lepidozia pearsonii* and *Frullania tamarisci*. Against this general background, each of the sub-communities shows some peculiarities in its bryophyte flora. This is most marked in the *Isothecium-Diplophyllum* sub-community, where there is a further consistent enrichment and an occasional occurrence of a very large number of other species, including many of restricted distribution in Britain and some national rarities, which give this kind of *Quercus-Betula-Dicranum* woodland a unique character.

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Apart from these ground-growing bryophytes, there are often here specialised epiphytic floras of tree bases, branches and twigs, differing somewhat according to the woody species being colonised. Epiphytic lichens can also be very prominent. Each of these assemblages is mentioned below but, among the more widespread lichens of soil surfaces, rotting logs and rocks are *Cladonia impexa*, *C. squamosa*, *C. polydactyla*, *C. arbuscula*, *C. furcata*, *C. chlorophaea*, *Sphaerophorus globosus*, *S. fragilis* and *Parmelia saxatilis*.

Sub-communities

***Isothecium myosuroides-Diplophyllum albicans* sub-community:** *Betuletum Oxaleto-Vaccinietum* McVean & Ratcliffe 1962 *p.p.*; *Vaccinium*-rich birchwood association McVean 1964*a p.p.*; *Blechno-Quercetum typicum* Klötzli 1970 *p.p.*; *Betula pubescens-Vaccinium myrtillus* Association and associated *Hymenophyllum wilsonii-Isothecium myosuroides* Association Birks 1973; Birch-oak stand types 6Ab & 6Ac Peterken 1981 *p.p.*; Birch stand type 12A Peterken 1981 *p.p.*; *Blechno-Quercetum, Saccogyna viticulosa* Subassociation Birse 1984. This kind of *Quercus-Betula-Dicranum* woodland exhibits almost the full range of floristic and physiognomic variation found among the woody element of the community. In more southerly stands, in areas like Dartmoor, North Wales and the Lake District, oak-dominated high forest is the norm though, over the more rugged topographies which are characteristic here, the cover and stature of the trees are often reduced, sometimes to extremes. In more closed canopies, *B. pubescens* generally plays a minor role, occurring as occasional scattered trees with some *S. aucuparia* and a little *Ilex*, and only thickening up in gaps and around margins but, in ungrazed stands where the oak cover is less extensive, it can be co-dominant in mosaics of the two trees. And, increasingly to the far north-west of Scotland, oak becomes much scarcer so that, at the limits of this sub-community's range, lower, scrubby canopies of *B. pubescens* (usually now ssp. *carpatica*) and *S. aucuparia* usually provide the woody cover (e.g. McVean & Ratcliffe 1962, Birks 1973). Although this sub-community can be found within *Quercus-Betula-Dicranum* woodlands which have been coppiced, the often poor growth of the oak and the rough character of the ground have frequently limited this kind of treatment.

Corylus is rather infrequent here, probably because of the scarcity of pockets of deeper, moister soil, and it is usually found only as sparse, scattered bushes; to the north-west, it does not make the prominent contribution to the canopy that is typical of scrubby versions of the *Quercus-Betula-Oxalis* woodland. Smaller woody plants as there are, then, are usually saplings of *B. pubescens* and *S. aucuparia*, sometimes with a little *Q. petraea*.

The field layer here preserves the general features of the community as a whole and few vascular plants are preferential. The most prominent species are generally *Vaccinium myrtillus* and *Pteridium*, though the occurrence of both can be patchy. *Vaccinium* is restricted to some extent by the grazing of more accessible ground though it often gains some protection from herbivores over larger boulders and then can grow tall and bushy; over such areas, though, *Pteridium* can be sparse and confined to crevices with some downwashed soil, only growing really dense in less rocky ground. *Calluna* is found only occasionally in more open places and around the edges of stands.

Apart from *Deschampsia flexuosa*, which can extend its cover over the tops of more well-colonised boulders, the frequency and abundance of grasses in this sub-community is often restricted by the rough topography. On patches of soil, however, *Festuca ovina* (including *F. vivipara*), *Agrostis capillaris*, *A. canina* ssp. *montana* and *Anthoxanthum odoratum* can all occur, forming the basis of an open-textured sward. And, preferentially here, there may be some *Molinia caerulea*, occasionally in abundance. *Luzula sylvatica* can be prominent, too, sometimes becoming a local field-layer dominant in ungrazed stands. Then, there are scattered dicotyledons such as *Galium saxatile*, *Potentilla erecta*, *Melampyrum pratense* and, often most conspicuous of all, *Oxalis acetosella*. *Blechnum spicant* is rather more frequent here than in other sub-communities, often attaining majestic size, and there can be very occasional *Athyrium filix-femina*, *Thelypteris limbosperma*, *Dryopteris dilatata*, *D. filix-mas*, *D. borreri* and, in some localities, *D. aemula*. In sheltered ravines, this fern element can be very extensive and luxuriant.

Much more consistently obvious, however, and very distinctive of this kind of *Quercus-Betula-Dicranum* woodland, are the bryophytes. All the characteristic community species are very frequent and, as always, grazing may favour an abundance of more robust mosses among areas with a grassy turf. But, very commonly here, the bryophyte cover extends as a thick mat over the surfaces of boulders. Over flat or gently-sloping surfaces with a fairly substantial and more stable nidus, the community constants often provide the bulk of the cover, though even in such situations there may be some enrichment from mosses such as *Hylocomium brevirostre*, *Thuidium delicatulum* and *Isothecium myosuroides*. Some vascular species continue to be represented here, notably *D. flexuosa*, *Oxalis* and *P. erecta* and there may be a patchy cover of *Vaccinium* forming the kind of suite which Birks (1973) called the *Oxalis acetosella-Rhytidiadelphus loreus* Association.

More strikingly preferential in this sub-community, however, is a group of bryophytes characteristic of

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thinner and less stable humus and mineral mats which can extend down over the shoulders of boulders and hang over their steeper sides. Making a frequent appearance here are such species as *Isothecium myosuroides, Thuidium delicatulum, Diplophyllum albicans, Leucobryum glaucum, Campylopus paradoxus, Hylocomium umbratum, Lepidozia reptans, Plagiochila spinulosa, Scapania gracilis, Bazzania trilobata, Dicranodontium denudatum* and *Saccogyna viticulosa.* Where such mats are kept very moist, by the general shelter provided between the boulders and by dripping of condensation and rain, the filmy ferns *Hymenophyllum wilsonii* and *H. tunbrigense* can also be found constituting the vegetation which Birks (1973) characterised as the *Hymenophyllum wilsonii-Isothecium myosuroides* Association. Some of these species, notably *I. myosuroides, D. albicans* and *C. paradoxus,* can extend on to barer rock surfaces on the very steeply inclined sides of boulders and drier areas of this kind can provide a location for the Western Atlantic *Plagiochila punctata, P. tridenticulata* and *Dicranum scottianum.* Where there is periodic wetting in such situations, other western British species such as *Harpanthus scutatus, Scapania umbrosa, Jamesoniella autumnalis* and *Tritomaria exsecta* may be found and, in areas south of the north-west Highlands, the rare South Atlantic *Sematophyllum micans* and *S. demissum* (Ratcliffe 1968). More regular splashing with water, as by waterfalls and along stream sides, is often marked by an abundance of *Heterocladium heteropterum, Marsupella emarginata, Hyocomium flagellare* with some *Racomitrium aquaticum, R. fasciculare* and *Hypnum callichroum* (Birks' (1973) Open Boulder Association). Other interesting bryophytes recorded occasionally in this sub-community are the South Atlantic *Adelanthus decipiens,* the Western British *Bazzania tricrenata, Plagiochila killarniensis, P. atlantica, Anastrepta orcadensis* and *Jungermannia gracillima.*

Elements of the boulder bryophyte cover may run some considerable way up the trunks and branches of trees in this kind of woodland, with *Isothecium myosuroides, Dicranum scoparium, Hypnum mammilatum, Scapania gracilis, Plagiochila spinulosa, P. punctata* and *P. tridenticulata* often figuring in such assemblages, sometimes with filmy ferns (equivalent to the *Hymenophylleto-Isothecium myosuroidis* of Barkman 1958). Then, smaller branches of birch can have a rich epiphytic flora in which *Ulota crispa* (including var. *norvegica*) and *U. phyllantha* play a prominent part, together with *Lejeunea ulicina* and *Frullania tamarisci* (Ulotion crispae alliance: Barkman 1958). Rotting logs provide a further habitat: here *Nowellia curvifolia, Lophozia ventricosa, L. incisa, Cephalozia bicuspidata, C. connivens, C. media* and *Tetraphis pellucida* are best represented, together with *Tritomaria exsecta, Scapania gracilis, S. umbrosa, Plagiochila spinulosa* and some of the common community species such as *Dicranum scoparium, Hypnum cupressiforme s.l.* and *Isothecium myosuroides* (alliances Blepharostomion Barkman 1958 or Nowellion Philippi 1965).

Typical sub-community: *Betuletum Oxaleto-Vaccinietum* McVean & Ratcliffe 1962 *p.p.*; *Vaccinium*-rich birchwood association McVean 1964*a p.p.*; *Blechno-Quercetum typicum* Klötzli 1970 *p.p.*; Loch Lomond Community Types 1, 6 & 7 Tittensor & Steele 1971; *Betula pubescens-Vaccinium myrtillus* Association Birks 1973 *p.p.*; Birch-oak stand types 6Ab & 6Ac Peterken 1981 *p.p.*; Birch stand type 12A Peterken 1981 *p.p.*; *Blechno-Quercetum,* Typical Subassociation Birse 1984 *p.p.* Oak-dominated high forest and coppice are very common here and, in many such stands, *B. pubescens* is reduced to occasional occurrences in the canopy with patchy abundance in gaps and around margins. However, more balanced mosaics of oak and birch sometimes provide the woody cover and, though this sub-community does not extend to the far north-west of Britain, some stands have only occasional oaks in a scrubby canopy dominated by mixtures of *B. pubescens* (often ssp. *carpatica* in exposed situations) and *S. aucuparia. Corylus* is somewhat more frequent here than in the *Isothecium-Diplophyllum* sub-community, which is partly a reflection of the less bouldery character of this kind of *Quercus-Betula-Dicranum* woodland. It has sometimes clearly been coppiced in the past though, generally, scattered hazel bushes form part of an understorey, along with *S. aucuparia* and *Ilex,* and the cover of these smaller woody species can be quite extensive here because grazing and browsing are not consistent.

The field layer preserves the general character typical of the community as a whole with very few preferential species. However, apart from *D. flexuosa,* grasses are rather poorly represented here in terms of frequency and cover, whereas *Vaccinium,* and, in more open places, *Calluna* and occasionally *Erica cinerea,* can be abundant and vigorous. *Pteridium* is common, too, thickening up to a dense cover on deeper soils where the shade is not too deep, and *Dryopteris dilatata* is a little more frequent here than in other sub-communities. With the tall growth of these species, smaller dicotyledons tend to be rather uncommon and even the shade-tolerant *Oxalis* is scarce. With the lack of heavy grazing, seedlings of some trees increase a little: *Q. petraea* is especially noticeable in this respect and there can be some *S. aucuparia* and *Ilex.*

But it is among the bryophytes that the most obvious distinctions from the *Isothecium-Diplophyllum* sub-community are to be seen. All the general community species remain common here and they can be quite abundant in places where the cover of vascular plants is

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not so dense but, with the scarcity of more open bouldery areas, the numerous colonisers of thinner humus mats become markedly infrequent: even *Isothecium* and *Diplophyllum* themselves are recorded only occasionally and the rest are rare, just making an appearance in twos or threes where there are scattered outcrops. But these sites still experience very high rainfall and humidity, so the potential for enrichment with more Atlantic species is still present and the epiphytic floras of trunks and twigs can be profuse and varied.

***Anthoxanthum odoratum-Agrostis capillaris* sub-community:** *Betuletum Oxaleto-Vaccinietum* McVean & Ratcliffe 1962 *p.p.*; *Vaccinium*-rich birchwood association McVean 1964*a p.p.*; *Blechno-Quercetum coryletosum* Klötzli 1970 *p.p.*; Loch Lomond Community Type 2 Tittensor & Steele 1971 *p.p.*; Birch-oak stand types 6Ab & 6Ac Peterken 1981 *p.p.*; Birch stand type 12A Peterken 1981 *p.p.* Again, a variety of canopy compositions and structures can be found in this sub-community. Oak figures prominently and it often dominates in high forest or coppice but stands with much birch also occur. *S. aucuparia* and *Ilex*, however, are somewhat less frequent than in the Typical sub-community with saplings of these species being especially sparse. *Corylus* remains frequent and is often the most abundant member of an open or patchy understorey, occasionally accompanied by a little *Crataegus monogyna*.

In this sub-community, it is the field layer that provides most of the distinctive character of the vegetation. Ericoids are noticeably uncommon and of low cover, even in more open areas of canopy, with *Vaccinium* showing an especially striking reduction from the generally high levels that it attains in the *Quercus-Betula-Dicranum* woodland. And there is a corresponding increase in the number and abundance of grasses with, in addition to *D. flexuosa*, frequent records for *Anthoxanthum odoratum*, *Agrostis capillaris* and *Holcus mollis* and more occasional occurrences of *Agrostis canina* ssp. *montana*, *Festuca ovina*, *Holcus lanatus*, *Dactylis glomerata*, *Poa nemoralis* and *P. pratensis*. Typically, these species form considerable expanses of grassy turf which can be kept quite closely cropped where grazing is heavy.

Pteridium remains frequent, occurring as sparse fronds in more grassy areas and on shallower soils in denser shade, thickening up to a dense cover in glades and on deeper colluvium. And there is usually a fairly obvious contribution from dicotyledonous herbs with *Galium saxatile* and *Oxalis acetosella* both being especially common and often abundant, some *Digitalis purpurea* and *Rumex acetosa* (both weakly preferential here) and scattered plants of *Potentilla erecta*, *Melampyrum pratense*, *Teucrium scorodonia*, *Luzula pilosa* and *Viola riviniana*. Very occasionally, there may be some *Rubus fruticosus* agg. or *R. idaeus* and, in such stands, the vegetation approaches very closely to the more calcifugous forms of the *Quercus-Betula-Oxalis* woodland. In the north-western uplands, continuous variation in soil characteristics means that these two communities grade almost imperceptibly one into the other, and grazing often accentuates the floristic convergence over transitional profiles.

One element of the vegetation that can provide some guidance in separating the two kinds of woodland is the bryophytes. This sub-community has the less rich suite of mosses and liverworts characteristic of the Typical sub-community (bouldery ground again being rather scarce here) but more calcifugous mosses remain very frequent and can be abundant in the short-cropped sward, with bulky wefts of *Rhytidiadelphus loreus*, *Hylocomium splendens*, *Plagiothecium undulatum* and, a little less commonly here, *Pleurozium schreberi*, and tufts of *Dicranum majus*, *D. scoparium* and *Polytrichum formosum*.

***Rhytidiadelphus triquetrus* sub-community:** Birch-oak stand type 6Bb Peterken 1981 *p.p.*; Birch stand type 12A Peterken 1981 *p.p.*; *Trientali-Betuletum pendulae*, *Vaccinium vitis-idaea* Subassociation Birse 1984 *p.p.* In terms of its canopy composition, this is the most peculiar kind of *Quercus-Betula-Dicranum* woodland. Oak and birch remain the most frequent and characteristic trees but *Q. petraea* is now more consistently replaced by *Q. robur* and hybrids than in the other sub-communities; and, though *B. pubescens* is still very common, *B. pendula* increases to become occasional. The cover of the canopy is also frequently quite open with one or the other birch often predominating over oak. *S. aucuparia* is frequent, too, and, with smaller birch, but only very sparse *Corylus*, it usually forms the bulk of whatever understorey is present. Often here, though, stratification is indistinct and the canopy presents the appearance of a thicket-like cover. Very occasionally, *Juniperus communis* is present in more open places and this sub-community can occur in mosaics with the *Juniperus-Oxalis* woodland.

Ericoids are quite well represented here and, though their cover is patchy, they give an obvious heathy character to many stands. *Vaccinium myrtillus* is common, though more distinctive in the frequent open areas are *Calluna*, which is preferential to this sub-community, and, more occasionally, *Erica cinerea* and, especially in transitions to *Juniperus-Oxalis* woodland, *V. vitis-idaea*. *Pteridium* remains frequent and sometimes forms dense stands in glades.

Stretches of ground which do not have a thick cover of these taller species can be quite rich in herbs. *Oxalis*, *Melampyrum pratense*, *Potentilla erecta*, *Viola riviniana*

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and, especially common, *Galium saxatile*, all occur and, with slightly increased frequency here, *Luzula pilosa*. Also very distinctive, though no more than occasional, is *Trientalis europaea* which, as in other woodlands of eastern Scotland, from where most of the stands here originate, provides a Northern Montane feel to the vegetation. *Goodyera repens* has also been recorded in this sub-community and the Arctic-Subarctic *Cornus suecica*.

Bryophytes remain an important component here, though western or more strictly Atlantic species are very rare. Usually the bulk of the cover is provided by the common community species but a strong preferential in this kind of *Quercus-Betula-Dicranum* woodland, as again in other eastern Scottish woodland types, is *Rhytidiadelphus triquetrus*.

Habitat

The *Quercus-Betula-Dicranum* woodland is a community of very acid and often shallow and fragmentary soils in the cooler and wetter north-west of Britain. Local differences in climate and topography have an important influence on the vegetation and frequently interact with grazing to determine the distinctive floristics of the sub-communities and affect the pattern of regeneration of the woody species. Many stands have been treated as coppice and there is evidence of timber removal and planting.

This kind of woodland is largely confined to those parts of Britain where the annual rainfall exceeds 1600 mm (*Climatological Atlas* 1952) and where there are usually more than 180 wet days yr^{-1} (Ratcliffe 1968). And, typically, within this zone, it occurs only on the most acid soils, where the influence of underlying arenaceous bedrocks is not masked by drift or counteracted by flushing with base-rich waters, where there is a strong tendency to mor accumulation and where the high rainfall induces strong leaching in more mature profiles. The soils are thus typically lime-free with a surface pH generally below 4.

Such soils are widely distributed throughout north-western Britain, though they are strongly associated with the more rugged topographies produced by the weathering of harder rocks. Important substrates here are Pre-Cambrian Torridonian sandstones along the north-west seaboard of Scotland, Cambrian, Silurian and Ordovician rocks in Wales and deposits of the last two periods in the Lake District, Devonian Old Red Sandstone around the Moray Firth and in the south-central Highlands of Scotland, Carboniferous sandstones in the Pennines and around Dartmoor, intrusive igneous rocks, especially granitic rocks on Dartmoor and in various parts of Scotland, lavas like the Borrowdale Volcanics of the Lake District and also quartzites and gneisses in various localities. Stands on superficials are rare, though some occur over free-draining, coarse fluvioglacial deposits in Aberdeenshire. Pedogenesis over all these materials is typically slow and often repeatedly set back in more extreme situations by gross active weathering of the rocks, but the general trend is from very shallow accumulations of organic detritus and mineral fragments, which constitute humic rankers, through brown podzolic profiles to podzols proper with fully-developed humus and iron pans. The community occurs over the full range of these soils and, as detailed below, the degree of maturity of the profile is of considerable importance in determining the floristics of the different kinds of *Quercus-Betula-Dicranum* woodland.

At a more general level, however, the prevailing acid environment of these soils is reflected throughout the community and helps to define it floristically against its counterpart on less base-poor profiles in the north-west, the *Quercus-Betula-Oxalis* woodland. Transgression of less-demanding calcifuges into that kind of woodland is a major feature in the strongly-leaching environment of the sub-montane zone in Britain but, here, that element becomes much more obviously defined, with a marked increase in *Deschampsia flexuosa*, the ericoids and bryophytes like *Dicranum majus*, *Pleurozium schreberi*, *Polytrichum formosum*, *Rhytidiadelphus loreus* and *Plagiothecium undulatum*. Conversely, more mesophytic species, like *Rubus*, *Holcus mollis* and, especially, *Hyacinthoides non-scripta* (and its replacement in less oceanic areas, *Anemone nemorosa*) are much less important here. There is also a shift among the fern flora with dryopteroids, even *D. dilatata*, giving way to *Blechnum spicant* and, in some regions, *D. aemula*. However, it must be realised that such transitions among the various elements of the vegetation in these two communities are continuous, a reflection of gradual changes in the edaphic conditions and, frequently, of the impact of grazing and browsing which eliminate sensitive differentials from each and favour a spread of grasses through both.

Prominent among the shared species are plants which it would be very surprising to see in south-eastern calcifugous woodlands. *Corylus*, for example, though clearly associated with less extreme soils here, extends some way into the community and cannot readily be used to separate woodlands of more and less base-poor soils in the north-west (cf. Peterken 1981). *Oxalis* also remains very frequent (e.g. Packham 1978) and even *Viola riviniana* can be found very occasionally. All of these reflect the more consistently moist character of the soil surface here, in contrast to the typically parched upper horizons of rankers and podzols in the south-eastern lowlands. It should be noted, though, that this moisture is often provided by rain and condensation and that, where flushing occurs, it does not involve any enrichment in bases. Such a development would tend to favour the occurrence of either the *Quercus-Betula-*

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Oxalis woodland or, where there was more extreme enrichment, the *Fraxinus-Sorbus-Mercurialis* or *Alnus-Fraxinus-Lysimachia* woodlands.

A much more obvious effect of the higher rainfall and humidity here, though, is to be seen in the very striking increase in the bryophyte component of this kind of woodland, in both the greater abundance of the carpet of mosses and liverworts and in the higher frequency of a large number of species. By and large, it is this element which provides the best distinction between the *Quercus-Betula-Dicranum* and *Quercus-Betula-Deschampsia* woodlands, with the 1600 mm isohyet or 180 wet days yr^{-1} line showing a close correlation with the geographical boundary between the two communities. In only one region is this correlation broken and that is in the southern Pennines where the latter community occurs in places where the former might be expected on climatic grounds. This anomalous zone corresponds very well with one area of high atmospheric pollution in Britain (as measured by, for example, the SO_2 concentration: Seaward & Hitch 1982) and it is a noticeable feature of calcifugous woodlands in the area that they most closely approach the *Quercus-Betula-Dicranum* type in deeper valleys more remote from the great industrial conurbations. The boundary between the communities here may thus be artificially maintained.

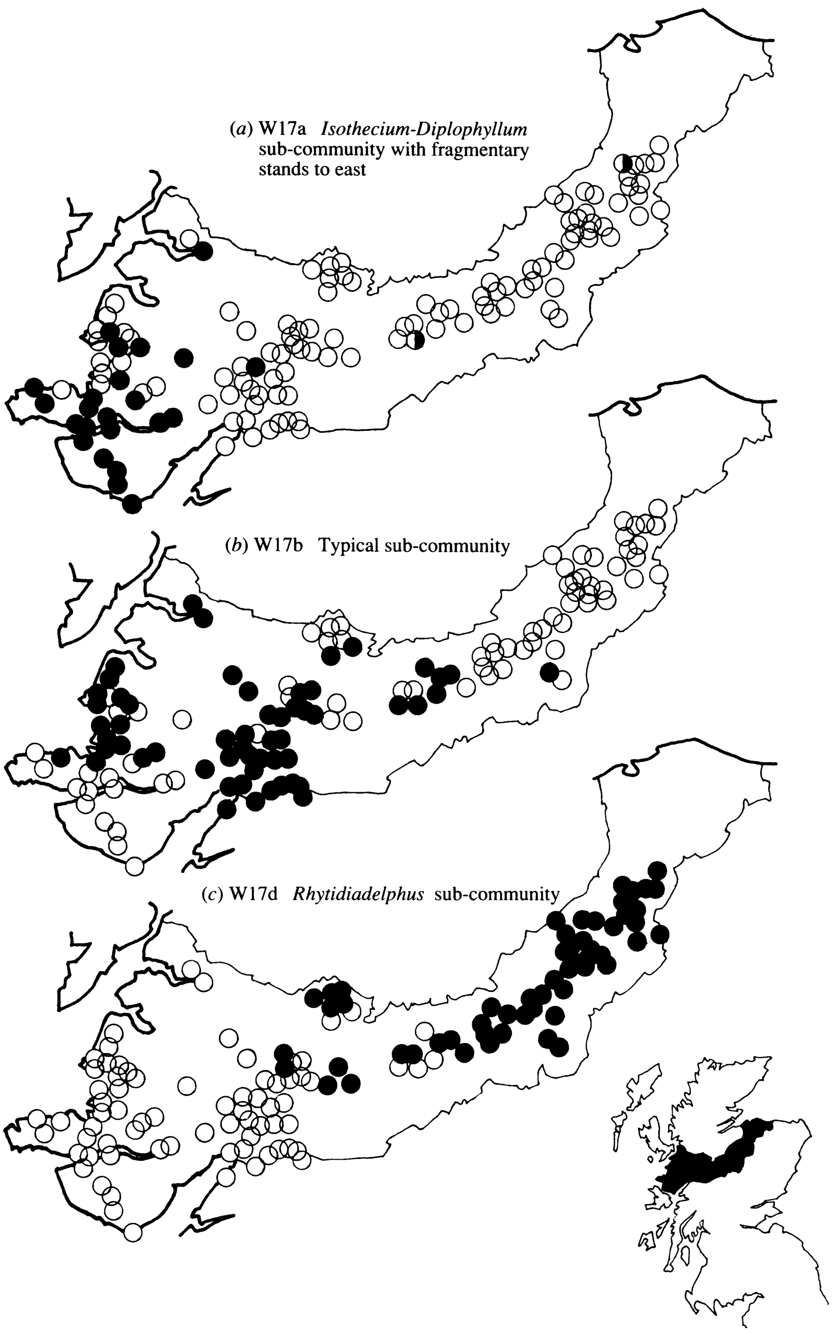
Within the community, there is a distinct association between the prominence and richness of the bryophyte element and the wetness of climate, as measured by the number of wet days yr^{-1} (a better index of the consistency of humidity than simple rainfall totals: Ratcliffe 1968). Lower levels of cover and smaller numbers of species characterise the *Rhytidiadelphus* and *Anthoxanthum-Agrostis* sub-communities where the number of wet days yr^{-1} either only just reaches 180 or, in parts of eastern Scotland, falls below this figure. In the area bounded by the 180–200 wet days yr^{-1} contour, the Typical sub-community is the usual type of *Quercus-Betula-Dicranum* woodland where abundance and variety of bryophytes are greater, but the most striking enrichment is seen in the *Isothecium-Diplophyllum* sub-community, most of the stands of which fall within the 200+ wet days yr^{-1} line, the richest of all occurring in the far north-west of Scotland where the figure exceeds 220 (Ratcliffe 1968). A considerable proportion of the wealth of bryophytes involved in this gradient consists of quite common and widespread species: here the difference is one of increased frequency of occurrence and abundance, such that these plants come to form the basis of an extensive and luxuriant mat. But superimposed on this, there is also a rise to prominence of mosses and liverworts with a more obvious western bias to their British distribution, either fairly widespread European sub-montane plants whose range in Britain reflects the predominance of higher ground towards the west (Ratcliffe's (1968) Western British group including *Bazzania trilobata*, *Dicranodontium denudatum*, *Hypnum callichroum*, *Scapania umbrosa*, *Tritomaria exsecta*, *Harpanthus scutatus*, *Sphagnum quinquefarium*) or more strictly Atlantic species (including the Widespread Atlantic *Saccogyna viticulosa*, *Plagiochila punctata*, *P. tridenticulata* and *Dicranum scottianum* and the Southern Atlantic *Sematophyllum micans*, *S. demissum* and *Adelanthus decipiens*, which do not penetrate quite so far to the north). Exactly the same pattern of a general increase in abundance and a rising prominence of a western component is seen among the epiphytic species, with trees in the Typical and especially the *Isothecium-Diplophyllum* sub-communities having their trunks and branches festooned with rich and luxuriant assemblages. And, among the vascular plants, there is a preferential occurrence of ferns like *Hymenophyllum tunbrigense*, *H. wilsonii* and *Dryopteris aemula*, the first two typically in close spatial association with bryophyte mats.

Atmospheric humidity, as measured by the annual number of rain days provides only a crude index of the increasing oceanicity of the climate towards the west and other climatic factors are undoubtedly important in encouraging the bryophyte richness found in the *Isothecium-Diplophyllum* sub-community, such as a fairly equable range of temperature variation, with moderately cool summers and largely frost-free winters (Ratcliffe 1968). The region where the sharpest gradients in all these variables can be seen is in northern Scotland where, in running from west to east, from say Skye to Aberdeenshire, the climate becomes markedly more continental. And it is here that the most striking contrasts in the bryophyte component of the *Quercus-Betula-Dicranum* woodland can be seen, with an obvious loss of more western species and an increasing prominence of *Rhytidiadelphus triquetrus* (a difference seen also in the *Pinus-Hylocomium* woodland which spans the same geographical range). The appearance of *Trientalis* marks the same climatic shift and, perhaps also, the partial switch from *Betula pubescens* to *B. pendula* (Figure 24).

Topography plays an important part in the climatic features characteristic of the area where the *Quercus-Betula-Dicranum* woodland occurs. This can be seen on a large scale in the orographic influence of the high ranges of hills of more resistant rocks that typify the western parts of Britain, which force the wet westerly winds upwards with a release of rain. But there are other small-scale effects which produce local modifications to the general distribution pattern of the sub-communities in relation to annual patterns of rainfall. This can sometimes be seen as an effect of aspect, north-facing slopes preserving more consistently the cool, humid conditions favouring the bryophyte richness of the *Isothecium-Diplophyllum* sub-community and it is visible, too, in the preferential occurrence of this kind of *Quercus-Betula-Dicranum* woodland in damp, shady ravines. Even on the level of individual large boulders, there can be a marked difference in the bryophyte flora of more sheltered and more exposed faces.

Various physical characteristics of the rocks over which this community is typically found are important in this respect (e.g. Ratcliffe 1968). Not only are they generally hard and resistant but, when they do weather and are eroded, many of them produce very angular landscapes, at all scales. Glacial erosion and freeze-thaw have resulted in rugged cliffs and crags, and streams have cut steep-sided ravines; great tumbles of often huge

Figure 24. Distribution of sub-communities of W17 *Quercus-Betula-Dicranum* woodland through Lochaber and Strathspey (after NCC reports).



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boulders present a great diversity of surfaces with complex patterns of crevices between. All of these features enhance local interactions with climate of the kind noted above. And they have a direct effect, too, in presenting a large and often continually renewed rock surface for colonisation by the bryophyte flora. The difference between the *Isothecium-Diplophyllum* sub-community and the other kinds of *Quercus-Betula-Dicranum* woodland is thus partly an index of rockiness of the environment (Kelly & Moore 1975). Here, immature rock-dominant soils are characteristic and vascular plants are often largely confined to crevices and more stable boulder tops and ledges. In particular, the habitat of this sub-community provides an abundance of gently-sloping to steep faces on the sides of large boulders and over crags where the distinctive suite of bryophytes which Birks (1973) termed the *Isothecium-Hymenophyllum* Association can gain a hold on fragmentary accumulations of humus and mineral particles (see also Ratcliffe 1968). It is probable that, even within stands of this woodland which are stable on a large scale, there is a small-scale successional turnover among the bryophyte element, species of more open boulders giving way to mosses and liverworts of thin rankers (the *Isothecium-Diplophyllum* suite) and finally to the more stable mats of bulky bryophytes characteristic of intact swards over more mature profiles (the community constants) (Richards 1938, Evans 1954). In fact, on steeper faces, the effect of gravity often slows or repeatedly sets back colonisation, as fragments of the hanging bryophyte mat drop off (Lye 1967, Ratcliffe 1968, Birks 1973). Certain lithological features of the rocks may also encourage colonisation by bryophytes: Ratcliffe (1968) noted that the best substrates were those which presented a coarse-grained and somewhat porous surface, like granites and grits. Such deposits figure prominently throughout the community and they may be more frequent in the *Isothecium-Diplophyllum* sub-community.

The rockiness of the environment interacts with a further factor of importance in the *Quercus-Betula-Dicranum* woodland, grazing and browsing, the influence of which is seen not only among the bryophytes but in all other layers of the vegetation. Very often, stands of this community are open to stock, usually sheep, and deer, frequently backing on to open moorland which forms part of the grazing land of upland farms, and providing a valuable bite and shelter, especially in winter. Where there are large boulders, though, or generally precipitous and rocky ground, access is more limited, so even where there is a potentially large influence of herbivores, the actual effects may be much reduced. The impact of this, and of variation in actual herbivore numbers in more accessible stands, can be seen in all kinds of *Quercus-Betula-Dicranum* woodland but are of particular importance in helping define some of the sub-communities.

The most obvious visual effect of grazing and browsing is usually to be seen in the proportions of ericoids to grasses. The former, especially *Vaccinium myrtillus*, the most generally common sub-shrub of this kind of woodland, are much reduced, indeed can be totally eliminated, by the predations of sheep and deer; whereas the latter, particularly species like *Anthoxanthum odoratum* and *Agrostis capillaris* and, to a lesser extent on these very acid soils, *Holcus mollis*, thrive under continuous cropping. Variations in other herbs also reflect the impact of herbivores: the very palatable *Luzula sylvatica*, for example, is only prominent where there is no grazing (as on cliff ledges or on islands: well seen in Tittensor & Steele's (1971) Loch Lomond stands), whereas other low-growing and less palatable plants like *Oxalis acetosella* and *Galium saxatile* can thrive in a close-grazed sward. These contrasts are very well seen in the differences between the *Anthoxanthum-Agrostis* sub-community, which is more consistently grazed, and the other kinds of *Quercus-Betula-Dicranum* woodland, especially the Typical sub-community, which is characteristic of similar, slightly rocky ground.

Grazing also favours the abundance of bryophytes by keeping down the cover of larger vascular plants and, even where there are no boulders, the cover of bulkier mosses is usually high, though the species involved are generally common ones. Increased rockiness restricts the impact of grazing, though the species which respond are only those which can tolerate the shallower soils. *Vaccinium* typically increases, though its cover can be patchy and restricted to more stable accumulations of soil; *Luzula sylvatica*, too, can form great hanging sheets in quite precarious situations. But, in the *Isothecium-Diplophyllum* sub-community, the great preponderance of boulders restricts the lushness of the vascular flora that might be expected with the limitation of grazing. Response from this element is better seen, though even there not very clearly, in the Typical and *Rhytidiadelphus* sub-communities.

The other important influence of herbivores is seen in the regeneration pattern of the woody species. In the *Quercus-Betula-Dicranum* woodland, younger individuals of the trees are often sparse and very much restricted to less heavily grazed or ungrazed stands. All the major species of the community are affected but the interactions between factors like frequency of fruiting, dispersal, food reserves in the seed and germination patterns on the one hand, and release from or imposition of grazing and browsing on the other, are complex; they sometimes work indirectly through features like the increased frequency with which ungrazed swards trap and hold litter; and they are compounded by the character of the canopy shade (e.g. Jones 1959, Peterken 1966, Pigott 1983). In any particular stand, then, the prominence of saplings and seedlings often reflects rather particular combinations of past and present

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conditions. Among the available data, the best illustration of the general affects of herbivore predation on regeneration is seen in the contrasts between the Typical and *Anthoxanthum-Agrostis* sub-communities. In the former, which is less consistently grazed, the understorey is not generally denser, but saplings, especially of *S. aucuparia* and *Ilex*, the two most palatable trees here, are much commoner than in the latter: a rise in the abundance of these species, especially of the less cold-sensitive *S. aucuparia*, is often a marked feature of island stands of this kind of woodland (e.g. Anderson 1950, McVean 1964*a*, Tittensor & Steele 1971). And there is a slight increase in the occurrence of seedlings, including those of *Q. petraea*, which is able to regenerate under its own canopy given freedom from grazing (Jones 1959). Birch is more complex in its response: it is more light-demanding than any of the above and has smaller seed reserves so its progression from the seedling stage may depend on a more precise combination of freedom from canopy shade, from a blanket of leaf litter and from grazing. As Pigott (1983) demonstrated in the closely-related *Quercus-Betula-Deschampsia* woodland, such a coincidence of favourable conditions may be very short-lived which is perhaps one reason why more extensive stands of birch here (as elsewhere) are often more or less even-aged.

Again, it should be noted that, though the rocky terrain of the *Isothecium-Diplophyllum* sub-community offers the kinds of protection from herbivore predation that favours the active regeneration of trees, actual growth of the plants beyond the seedling stage is often prevented by the thin and sponge-like character of the bryophyte mat and the absence of any substantial amounts of mineral material. Soil can accumulate in crevices though, in deeper clefts, heavy shade becomes a problem for seedling survival.

Usually, now, if stands of the *Quercus-Betula-Dicranum* woodland are grazed, there is little interest in exercising any control over access to stock and, in many places, the community is regenerating only slowly or sporadically, so that we can see the kind of agriculturally-related decline that has played such a large role in the disappearance of this kind of woodland over many centuries (e.g. McVean & Ratcliffe 1962, McVean 1964*a*, Pearsall 1968, Pearsall & Pennington 1973). In certain periods in the past, however, control of grazing has been important because many stands of the community bear testimony to use as coppice. Sometimes, hazel has been the crop, or birch (both trees yielding wood for bobbins: e.g. Pearsall & Pennington 1973) but much more widespread has been coppicing for oak. Towards the north-west of Britain, this community and its less calcifugous counterpart, the *Quercus-Betula-Oxalis* woodland, have been the mainstay of woodland industries yielding charcoal, tan-bark and pit- and constructional timber (e.g. Tittensor 1970*a*, *b*, Tittensor & Steele 1971, Pearsall & Pennington 1973, Linnard 1982). Remains of such activities can often be seen here in stands with regularly-disposed oak moots among which other tree species still play only a minor role; and there are frequently physical features such as disused charcoal pit-steads and interconnecting burners' pathways over the slopes (e.g. Pigott & Huntley 1978, Barker 1985).

Although oak shows some climatically related reduction in its growth in this community at high altitudes and latitudes, treatment has also probably played an important part in the scarcity of this species towards north-west Scotland where much of the good timber has been removed over the centuries (McVean & Ratcliffe 1962, McVean 1964*a*). There has also been a progressive rundown of many stands of the *Rhytidiadelphus* sub-community in eastern Scotland, where birch-dominated thickets are prominent (Birse 1984). Preferential planting of *Q. robur* in this region may also account for the scarcity of *Q. petraea* in such stands as are still oak-dominated (Jones 1959, Gardiner 1974), though other local occurrences of *Q. robur* in other sub-communities are not so easily explained. The striking prominence of this species in virtually pure populations in places like Wistman's Wood may be due in part to patterns of early migration in the post-Glacial and partly to geological preferences: in Devon, there is a rather well defined association between the occurrence of *Q. robur* on granite and *Q. petraea* on other rocks like the Culm Measures (Wigston 1974).

Zonation and succession

Zonations between the different types of *Quercus-Betula-Dicranum* woodland and from this community to other vegetation types are most commonly related to differences in microclimate, topography and soils and grazing and, as explained above, all these factors can interact in complex fashion, often in an inter-dependent way, so it is quite rare to find simply-explicable transitions.

The edaphic trend within the community is essentially one of soil maturity, running from lithomorphic rankers, such as are typical of the *Isothecium-Diplophyllum* sub-community, to the deeper, more stable and mature brown podzolic soils and podzols characteristic of the other sub-communities. To the west, such a trend is often visible in terms of a zonation from the former over the rocky ground of crags and screes to either the Typical sub-community (in less heavily grazed woods) or the *Anthoxanthum-Agrostis* sub-community (in heavily-grazed woods) on downwash soils over the gentler slopes below. And, on a smaller scale, the pattern may be repeated over the variably-sloping surfaces of every large boulder in differences in the stability and composition of the bryophyte mat. Between the two zones, there can be very complex mosaics as stretches of deeper soil run up between boulders and become fragmented

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into pockets between and atop the rocks; and, in the other direction, as boulders become progressively more isolated and sunken into the body of the creep soils. And such zonations are frequently complicated by climatically-related responses in the vegetation, so that shifts towards a more southerly, sunnier aspect may increase the proportion of ground occupied by either the Typical or *Anthoxanthum-Agrostis* sub-communities (especially perhaps the latter as lack of cool shade may depress *Vaccinium* and enhance the grass cover); or, conversely, a move towards more northerly aspects may produce a greater contribution from the *Isothecium-Diplophyllum* sub-community. Especially complex patterns may be found in landscapes cleft by repeated ravines, where alternating zones may lie side by side along a slope and where, within each gorge, there is a small-scale and almost unfathomable jumble of vegetation disposed over cliffs, ledges, tumbled blocks and slips of soil.

Quite commonly in the situations where the *Quercus-Betula-Dicranum* woodland is found, edaphic zonations continue to less base-poor profiles, usually strongly-leached brown earths. Such a transition can be related to a change in the underlying bedrock from more coarse-grained arenaceous sedimentaries or igneous or metamorphic rocks to more fine-grained ones which weather to a less readily leached mantle: this kind of switch is a fairly common feature in Silurian and Ordovician sequences in Wales and the Lake District and among volcanic rocks in the Lakes and parts of Scotland (e.g. Pearsall 1968, Pearsall & Pennington 1973). In such cases, the associated edaphic and vegetational changes can be sudden and clearly marked but, very often, it is the presence of superficials, like glacial drift or head, or the effect of flushing, that shifts the direction of soil development by masking the effect of the underlying acidic rocks and then the edaphic and vegetational gradient is much more gradual and ill defined. Typically, though, in all these situations, the *Quercus-Betula-Dicranum* woodland gives way, with varying degrees of sharpness, to the *Quercus-Betula-Oxalis* woodland, with a decline in ericoids and more calcifugous herbs and bryophytes and an increase in *Hyacinthoides*, *Rubus* and *Holcus mollis*. But uniformly intense grazing over these boundaries may soften the transition and, even where there is no grazing, very much the same kind of tree canopy extends over both communities with even *Corylus* providing no sure guide as to the move from one to the other (Figure 21).

The juxtaposition of highly acidic and markedly basic rocks, or the presence of very calcareous drift over siliceous substrates, or strong flushing with very base-rich waters, all of which can occur locally within the range of the *Quercus-Betula-Dicranum* woodland, result in a sharper shift from the community to either the *Fraxinus-Sorbus-Mercurialis* woodland or, in very wet situations, the *Alnus-Fraxinus-Lysimachia* woodland. Then there is often a much more obvious floristic difference among all elements of the vegetation with calcicolous species replacing the calcifugous. In some areas though, extreme climatic conditions produce a convergence among certain components: this is well seen in the Suardal area of Skye where stands of all three of these communities, and of the *Quercus-Betula-Oxalis* woodland on intermediate soils, occur under scrubby canopies of *B. pubescens*, *S. aucuparia* and *Corylus* and with a prominent western element among the bryophytes (Birks 1973).

As well as confounding the simplicity of these kinds of zonations, grazing and browsing also produce transitions of their own which are essentially a reflection of the successional development of the community or, very commonly, its reversal. Burning is also frequently involved as a factor in such zonations. Seral progressions to the *Quercus-Betula-Dicranum* woodland have not been followed (they are rare, of course, and now often seen only in fenced sections of reserves or in forestry or reservoir enclosures) but the most obvious natural precursors to the community are probably the *Luzula sylvatica-Vaccinium myrtillus* tall-herb vegetation and certain kinds of *Calluna-Vaccinium* heath. Both of these show considerable overlap with the *Quercus-Betula-Dicranum* woodland in their edaphic and climatic requirements and essentially reproduce elements of its field and ground layers: McVean & Ratcliffe (1962) included stands of the *Luzula-Vaccinium* community as a 'treeless facies' of the woodland. Small stands of these rich vegetation types can sometimes be found in close spatial association with the community and, like it, survive as fragments within much-modified landscapes. They also extend the typical sub-shrub, herb and bryophyte cover characteristic of the community to considerably higher altitudes than those at which the woodland itself is found.

In fact, much more widespread are zonations to more species-poor kinds of *Calluna-Vaccinium* heath (in which bryophytes in particular are ill-represented), various types of calcifugous grasslands (notably less-improved *Festuca-Agrostis-Galium* swards) and stands of the *Pteridium-Galium saxatile* community, in landscapes which bear obvious signs of a long history of woodland clearance, grazing, burning and agricultural neglect. Quite often, the sequence of such vegetation types reflects the kind of underlying edaphic variation, running down from crags and screes over thin soils to colluvium, that can be seen picked out in the surviving woodland by the spatial sorting of *Vaccinium myrtillus*, grasses and bracken, though the proportional contribution of the last is often much greater with freedom from canopy shade on the open slopes. Fragments of the bryophyte-richness of the *Quercus-Betula-Dicranum* woodland may persist in derived *Calluna-Vaccinium* heath, though burning is very deleterious, and, among the sward of the plagioclimax *Festuca-Agrostis-Galium* grassland, continuous grazing and increased exposure to sun and wind can eliminate all but the more robust mosses; less intractable slopes may also have been improved by fertiliser application. Dense bracken stands, too, are usually impoverished: ericoids and herbs may persist patchily but the bryophytes are rapidly reduced by the combination of deep shade and thick litter. Finally, one very common additional element of these altered landscapes is coniferous forest which has been widely planted in the north-western uplands on soils which could otherwise support this community. Such woodlands have not been extensively sampled, though more open stands could probably be incorporated here as impoverished variants.

In some parts of Scotland, there is the further problem of the relationship between the *Quercus-Betula-Dicranum* woodland and what seems, from palynological evidence, to be the natural forest cover of the region, the *Pinus-Hylocomium* woodland (e.g. McVean & Ratcliffe 1962, Birks 1970, Gunson 1975, O'Sullivan 1977). There is a considerable floristic overlap between the associated species of these two woodland types and what may have happened here, with the destruction of the original, and apparently fairly mixed, woody cover of the pine forest is that birch and oak, especially the former, have now come to dominate in the *Quercus-Betula-Dicranum* woodland on the more acidic mineral soils that could naturally support pine.

Distribution

The community is widely distributed through the upland fringes of western and northern Britain from Dartmoor to Sutherland with especially good stands in mid and north Wales, the Lake District and along the north-western seaboard of Scotland. The sub-communities show a fairly clear climatically-related pattern of occurrence with the *Isothecium-Diplophyllum* type in the most oceanic areas, the Typical and *Anthoxanthum-Agrostis* sub-communities in somewhat less extreme situations and the *Rhytidiadelphus* sub-community in the more continental parts of eastern Scotland.

Affinities

The *Quercus-Betula-Dicranum* woodland unites more calcifugous and heathy woodlands which have sometimes been described within a general *Quercetum petraeae* where the stress has been on oak-dominance (e.g. Tansley 1939), or diagnosed as birch-dominated communities from higher latitudes (e.g. McVean & Ratcliffe 1962, Birks 1973, Birse 1982). Although the proportion of oak here does have some climatic basis, it is, in part, a treatment-related phenomenon which has little effect on the associated flora (e.g. McVean & Ratcliffe 1962, McVean 1964*a*, Tittensor & Steele 1971, Birks 1973). Neither is it fruitful to make any distinction according to which of the oaks or birches is predominant: early (e.g. Tansley 1939) and later (e.g. Peterken 1981) schemes have sometimes used the oak species as diagnostic in this respect but, again, there are no directly-related differences in the other layers of the vegetation. Furthermore, the ecological significance of the representation of the two species varies according to the locality: sometimes it appears to have a geological basis (as in Dartmoor), in other cases preferential planting seems to have been largely responsible (in eastern Scotland).

Uniting all such woodlands within a single community has the advantage that it is possible to make some integrated assessment of national variation. The most obvious trend is the increasing contribution from the bryophytes, in particular a more Atlantic element, in moving from the comparatively drier east and south to the very wet west and north. We can thus now see the context of more extreme versions of this community described from Scotland (McVean & Ratcliffe 1962, Klötzli 1970, Birks 1973, Birse 1980, 1982, 1984) and generally related to the *Blechno-Quercetum*, the association in which Braun-Blanquet & Tüxen (1952) placed the very distinctive Irish oakwoods first described from Killarney (e.g. Rübel 1912, Richards 1938, Turner & Watt 1939, Tansley 1939). Reanalysis of old and new data from this kind of woodland in Ireland (Kelly 1981; see also Kelly & Moore 1975) has confirmed Braun-Blanquet & Tüxen's original recognition of two sub-types, the *scapanietosum* (originally called *isothecietosum*), significantly associated with wetter regions and rockier situations and very similar to the *Isothecium-Diplophyllum* sub-community here, and a *typicum*, including vegetation here split into the Typical and *Anthoxanthum-Agrostis* sub-communities. Kelly & Moore's (1975) *coryletosum*, significantly correlated with richer and less humic soils of higher pH, would here be placed in the oceanic *Blechnum* sub-community of the *Quercus-Betula-Oxalis* woodland.

The *Quercus-Betula-Dicranum* woodland thus incorporates some of the most oceanic Quercion forest in Western Europe, linking through the less extreme stands of the Typical and *Anthoxanthum-Agrostis* sub-communities with more mainstream associations like the *Vaccinio-Quercetum sessiliflorae* Clement *et al.* 1975, and through the *Isothecium-Diplophyllum* sub-community with the *Blechno-Quercetum scapanietosum* Kelly & Moore 1975 of western Ireland (Géhu 1975*a*). The *Rhytidiadelphus* sub-community of eastern Scotland provides a floristic connection in a different direction, to the Scandinavian calcifuge birchwoods in such associations as the *Betuletum myrtillo-hylocomiosum* (Nordhagen 1928, 1943), where species such as *Trientalis europaea, Cornus suecica* and *Linnaea borealis* become much more frequent.

Floristic table W17

	a	b
Quercus petraea	V (1–10)	V (3–10)
Betula pubescens	III (1–9)	III (1–7)
Sorbus aucuparia	II (1–5)	I (1–2)
Fraxinus excelsior	I (2–6)	I (1–3)
Acer pseudoplatanus	I (1–4)	I (1–2)
Ilex aquifolium	I (1–4)	
Fagus sylvatica		I (1–2)
Betula pendula	I (2–5)	I (2–4)
Quercus robur		I (6)
Quercus hybrids		
Corylus avellana	II (1–7)	III (1–7)
Sorbus aucuparia	I (1–5)	III (1–4)
Betula pubescens sapling	I (1–4)	II (1–4)
Quercus petraea sapling	I (1–2)	II (1–4)
Ilex aquifolium	I (1–2)	II (1–5)
Crataegus monogyna	I (1–4)	I (1–2)
Fraxinus excelsior sapling	I (1)	I (1–3)
Fagus sylvatica sapling	I (1–4)	I (1–2)
Acer pseudoplatanus sapling	I (2)	I (1)
Rhododendron ponticum	I (1)	I (1–4)
Betula pendula sapling	I (2)	
Salix caprea		I (2)
Juniperus communis communis		
Deschampsia flexuosa	IV (2–7)	V (1–8)
Rhytidiadelphus loreus	V (1–9)	IV (1–6)
Polytrichum formosum	V (1–5)	IV (1–6)
Dicranum majus	V (1–6)	V (1–7)
Hylocomium splendens	IV (1–6)	III (2–5)
Pleurozium schreberi	IV (1–5)	IV (1–6)
Vaccinium myrtillus	III (1–7)	IV (1–9)
Plagiothecium undulatum	IV (1–5)	III (1–5)

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c	d	17
V (4–10)	I (8–9)	IV (1–10)
III (3–7)	IV (1–9)	III (1–9)
II (1–5)	III (1–4)	II (1–5)
I (1–7)	I (4)	I (1–7)
I (2–5)	I (1)	I (1–5)
	I (1–2)	I (1–4)
I (1–5)	I (3–4)	I (1–5)
I (1–3)	II (2–8)	I (1–8)
I (5–10)	II (2–8)	I (2–10)
	I (4–9)	I (4–9)
III (1–6)	I (1–5)	II (1–7)
I (1–4)		II (1–5)
I (2–4)		I (1–4)
I (1–2)		I (1–4)
I (1–3)		I (1–5)
II (1–5)		I (1–5)
I (1–2)		I (1–3)
I (4)		I (1–4)
I (2)		I (1–2)
I (1)		I (1–4)
	I (1)	I (1–2)
	I (2–3)	I (2–3)
	I (1–5)	I (1–5)
III (1–8)	V (1–9)	V (1–9)
V (1–7)	III (1–6)	IV (1–9)
V (1–5)	III (1–4)	V (1–6)
III (1–5)	III (1–6)	IV (1–7)
III (1–5)	V (1–9)	IV (1–9)
II (1–5)	V (1–8)	IV (1–8)
I (1–5)	V (1–9)	IV (1–9)
IV (1–5)	II (1–4)	IV (1–5)

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Isothecium myosuroides	IV (1–6)	II (1–4)
Diplophyllum albicans	IV (1–4)	II (1–4)
Hypnum cupressiforme	III (1–5)	II (1–5)
Blechnum spicant	III (1–5)	II (1–5)
Lepidozia reptans	III (1–4)	I (1–4)
Thuidium delicatulum	III (1–5)	I (1)
Leucobryum glaucum	III (1–6)	I (1–6)
Campylopus paradoxus	III (1–4)	I (1–2)
Plagiochila spinulosa	III (1–4)	I (1–2)
Scapania gracilis	III (1–5)	I (1–3)
Bazzania trilobata	III (1–6)	I (1–5)
Molinia caerulea	II (1–7)	I (1–5)
Dicranodontium denudatum	II (1–5)	I (1–3)
Saccogyna viticulosa	II (1–5)	I (1–5)
Hylocomium umbratum	II (1–3)	
Isopterygium elegans	II (1–4)	I (1–4)
Parmelia saxatilis	II (1–4)	I (1)
Hymenophyllum wilsonii	II (1–5)	
Heterocladium heteropterum	II (1–4)	
Racomitrium heterostichum	II (1–3)	I (2–4)
Lophozia ventricosa	I (1–2)	
Marsupella emarginata	I (1–3)	
Barbilophozia attenuata	I (1–3)	I (1–2)
Jamesoniella autumnalis	I (1–4)	I (1)
Hypnum callichroum	I (1–4)	I (1)
Racomitrium fasciculare	I (1–4)	I (1–2)
Racomitrium lanuginosum	I (1–3)	I (4)
Plagiochila asplenoides major	I (1–3)	I (1)
Scapania nemorosa	I (1–2)	
Blepharostoma trichophyllum	I (1–2)	
Lejeunea ulicina	I (1–2)	
Plagiochila punctata	I (1–3)	
Sematophyllum micans	I (2–7)	
Hyocomium armoricum	I (1–3)	
Scapania umbrosa	I (1–2)	
Andreaea rupestris	I (1–2)	

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II (1–6)	I (1–2)	II (1–6)
I (1–4)		II (1–4)
I (1–3)	I (1–4)	II (1–5)
I (1–2)	II (1–5)	II (1–5)
I (2–3)	I (1–2)	I (1–4)
I (1)	I (3)	I (1–5)
I (1)	I (2)	I (1–6)
I (1–3)	I (1)	I (1–4)
I (2–3)		I (1–4)
I (1–2)		I (1–5)
I (3)		I (1–6)
I (1–6)	I (5–8)	I (1–8)
I (1–2)		I (1–5)
I (1–2)		I (1–5)
I (4)	I (4)	I (1–4)
I (1–4)		I (1–4)
	I (2)	I (1–4)
I (1)		I (1–5)
I (1–2)		I (1–4)
		I (1–4)
	I (1)	I (1–2)
I (1)		I (1–3)
		I (1–3)
		I (1–4)
		I (1–4)
		I (1–4)
		I (1–4)
		I (1–3)
		I (1–2)
		I (1–2)
		I (1–2)
		I (1–3)
		I (2–7)
		I (1–3)
		I (1–2)
		I (1–2)

Floristic table W17 *(cont.)*

	a	b
Tritomaria quinquedentata	I (1–2)	
Jungermannia gracilima	I (1)	
Adelanthus decipiens	I (1–4)	
Sematophyllum demissum	I (1–2)	
Hymenophyllum tunbrigense	I (1–2)	
Tritomaria exsecta	I (1–2)	
Nowellia curvifolia	I (1–3)	
Plagiochila killarniensis	I (1–5)	
Sphaerophorus fragilis	I (1–3)	
Sphagnum fimbriatum	I (1–3)	
Dicranum scottianum	I (1–2)	
Plagiochila atlantica	I (1–3)	
Primula vulgaris	I (1–2)	
Dryopteris aemula	I (1–4)	
Anastrepta orcadensis	I (1–2)	
Cladonia subcervicornis	I (1–2)	
Harpanthus scutatus	I (2)	
Plagiochila corniculata	I (1)	
Dryopteris dilatata	I (1–6)	II (1–4)
Quercus petraea seedling	I (1–3)	II (1–2)
Cladonia squamosa	I (1–3)	II (1–2)
Quercus sp. seedling		I (1–2)
Cladonia digitata		I (1–3)
Eurhynchium striatum		I (1–2)
Hypericum pulchrum		I (1–2)
Galium saxatile	II (1–5)	II (1–4)
Anthoxanthum odoratum	II (1–6)	II (1–4)
Agrostis capillaris	II (1–6)	I (1–5)
Holcus mollis	II (1–6)	I (1–5)
Rubus fruticosus agg.	I (1–5)	I (1–7)
Eurhynchium praelongum	I (1–2)	I (4)
Dicranella heteromalla	I (1–2)	I (1–3)

c	d	17
		I (1–2)
		I (1)
		I (1–4)
		I (1–2)
		I (1–2)
		I (1–2)
		I (1–3)
		I (1–5)
		I (1–3)
		I (1–3)
		I (1–2)
		I (1–3)
		I (1–2)
		I (1–4)
		I (1–2)
		I (1–2)
		I (2)
		I (1)
I (1–4)	I (1–5)	I (1–6)
I (1–3)		I (1–3)
I (1–2)		I (1–3)
		I (1–2)
		I (1–3)
		I (1–2)
		I (1–2)
IV (1–6)	IV (1–4)	III (1–6)
IV (1–8)	II (1–4)	II (1–8)
IV (1–7)	I (1–4)	II (1–7)
III (2–8)	I (1–3)	II (1–8)
II (1–9)	I (5)	I (1–9)
II (1–3)	I (1)	I (1–4)
II (1–4)	I (1)	I (1–4)

Digitalis purpurea		I (1)	II (1–5)		I (1–5)
Dactylis glomerata			I (2–3)		I (2–3)
Rumex acetosa			I (1–3)		I (1–3)
Poa nemoralis			I (1–3)		I (1–3)
Poa pratensis			I (2–3)		I (2–3)
Calluna vulgaris	II (1–6)	III (1–6)	I (1)	IV (1–9)	III (1–9)
Pseudoscleropodium purum	I (1–4)	I (1–4)	II (1–9)	III (1–4)	II (1–4)
Rhytidiadelphus triquetrus	I (1–5)	I (1–2)	I (1–4)	III (1–5)	I (1–5)
Luzula pilosa	I (1–3)	I (1–4)	I (1–3)	II (1–4)	I (1–4)
Trientalis europaea				II (1–5)	I (1–5)
Goodyera repens				I (1)	I (1)
Cornus suecica				I (2)	I (2)
Dicranum scoparium	IV (1–5)	III (1–6)	III (1–4)	III (1–4)	III (1–6)
Mnium hornum	IV (1–4)	IV (1–4)	III (1–5)	I (1–3)	III (1–5)
Pteridium aquilinum	III (1–7)	III (1–7)	IV (1–8)	III (1–8)	III (1–8)
Thuidium tamariscinum	III (1–7)	III (1–5)	III (1–7)	II (1–8)	III (1–8)
Oxalis acetosella	III (1–5)	I (1–4)	IV (1–7)	III (1–5)	III (1–7)
Lophocolea bidentata s.l.	I (1–2)	III (1–4)	II (1–3)	III (1–6)	II (1–6)
Agrostis canina montana	II (1–6)	I (1–5)	II (1–6)	II (1–6)	II (1–6)
Festuca ovina	III (1–5)	I (2–3)	II (2–6)	II (1–6)	II (1–6)
Hypnum jutlandicum	I (1–4)	III (2–5)	II (1–5)	II (1–6)	II (1–6)
Rhytidiadelphus squarrosus	I (1–4)	I (1–4)	II (1–7)	II (1–4)	II (1–7)
Lonicera periclymenum	I (1–5)	II (1–6)	I (1–3)	I (1–4)	I (1–6)
Sorbus aucuparia seedling	I (1–4)	II (1–3)	I (1–3)	II (1–4)	I (1–4)
Sphagnum quinquefarium	II (1–7)	II (1–7)	I (3–4)	I (2–6)	I (1–7)
Potentilla erecta	II (1–7)	I (1–3)	I (1–4)	II (1–5)	I (1–7)
Melampyrum pratense	II (1–7)	I (3–8)	I (2–5)	II (1–6)	I (1–8)
Dryopteris filix-mas	I (1–4)	I (4)	I (1–5)	I (2)	I (1–5)
Dryopteris borreri	I (1–2)	I (1–2)	I (1–5)	I (2)	I (1–5)
Ilex aquifolium seedling	I (1–3)	I (1–2)	I (1–3)	I (1)	I (1–3)
Viola riviniana	I (1–4)	I (1–3)	I (2–3)	I (1–5)	I (1–5)
Holcus lanatus	I (1–4)	I (1)	I (1–4)	I (2)	I (1–4)
Rubus idaeus	I (3–4)	I (1)	I (2–3)	I (2)	I (1–4)
Thelypteris limbosperma	I (1–4)	I (2)	I (1–6)	I (1)	I (1–6)
Calypogeia fissa	I (1–2)	I (1–3)	I (1)	I (1)	I (1–3)

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Floristic table W17 *(cont.)*

	a	b
Betula pubescens seedling	I (1–3)	I (1–2)
Tetraphis pellucida	I (1–3)	I (1–2)
Teucrium scorodonia	I (2–3)	I (1–4)
Luzula sylvatica	I (1–7)	I (4)
Hyacinthoides non-scripta	I (1–5)	I (1–2)
Sphagnum palustre	I (2–8)	I (2–6)
Carex pilulifera	I (2–3)	I (3)
Erica cinerea	I (4)	I (1–5)
Anemone nemorosa	I (1–2)	I (1–2)
Athyrium filix-femina	I (1–4)	
Cladonia impexa	I (1–2)	I (1–5)
Succisa pratensis	I (1–4)	I (1)
Quercus hybrids sapling	I (1)	I (1)
Lophocolea cuspidata	I (1–2)	I (3)
Rhizomnium punctatum	I (1)	I (1)
Calypogeia muellerana	I (1–2)	I (1)
Cladonia polydactyla	I (1–2)	I (1)
Barbilophozia floerkei	I (1–3)	I (1–2)
Cephalozia media	I (1)	I (1)
Bazzania tricrenata	I (1–3)	I (2)
Hedera helix	I (1–4)	I (1–4)
Lepidozia pearsonii	I (1–3)	I (1–3)
Solidago virgaurea	I (1–2)	I (1)
Deschampsia cespitosa	I (5)	I (4)
Ptilidium ciliare	I (1)	I (1)
Cladonia chlorophaea	I (1)	I (1–2)
Polytrichum commune	I (2–4)	I (1–6)
Dicranum fuscescens		I (2–3)
Plagiochila asplenoides		I (1)
Luzula multiflora		I (2)
Mylia taylori	I (1–3)	I (3)
Sphaerophorus globosus	I (1–2)	I (1–2)
Cladonia arbuscula	I (1–3)	I (1–4)

c	d	17
I (1–3)	I (1–4)	I (1–4)
I (1–3)	I (1)	I (1–3)
I (1–4)	I (5)	I (1–5)
I (4–9)	I (1–9)	I (1–9)
I (2–5)	I (1–3)	I (1–5)
I (2–6)	I (6)	I (2–8)
I (1)	I (1)	I (1–3)
I (1)	I (1–7)	I (1–7)
I (1)	I (1)	I (1–2)
I (1–5)	I (1)	I (1–5)
	I (1)	I (1–5)
	I (1–2)	I (1–4)
	I (1–3)	I (1–3)
I (1)		I (1–3)
I (1–2)		I (1–2)
I (1)		I (1–2)
I (1–3)		I (1–3)
I (1–2)		I (1–3)
I (1)		I (1)
I (2)		I (1–3)
I (1–4)		I (1–4)
I (1–3)		I (1–3)
I (1)		I (1–2)
I (1–5)		I (1–5)
	I (1)	I (1)
	I (1)	I (1–2)
	I (1–8)	I (1–8)
I (1)	I (1–3)	I (1–3)
I (1–2)	I (2–4)	I (1–4)
I (1)	I (1–3)	I (1–3)
		I (1–3)
		I (1–2)
		I (1–4)

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Sphagnum russowii	I (2–3)	I (3)
Cladonia furcata	I (1–2)	I (1–3)
Ptychomitrium polyphyllum	I (1)	I (2)
Cephalozia bicuspidata	I (1–2)	
Fraxinus excelsior seedling	I (1–3)	
Cladonia squamules	I (1–2)	
Frullania tamarisci	I (1–3)	
Lysimachia nemorum	I (1–3)	
Hylocomium brevirostre	I (1–4)	
Sphagnum subnitens	I (2)	
Ptilium crista-castrensis	I (1–4)	
Plagiothecium denticulatum	I (1–5)	
Polypodium vulgare	I (2–3)	
Erica tetralix	I (4)	
Agrostis stolonifera		
Lophocolea heterophylla		
Quercus robur seedling		
Number of samples	131	48
Number of species/sample	32 (15–55)	29 (17–48)
Tree height (m)	12 (7–22)	14 (5–24)
Tree cover (%)	74 (10–100)	87 (60–100)
Shrub height (m)	3 (1–5)	3 (1–5)
Shrub cover (%)	19 (0–90)	12 (0–60)
Herb height (cm)	30 (4–120)	28 (10–80)
Herb cover (%)	42 (2–90)	53 (4–100)
Ground height (mm)	44 (10–100)	40 (10–100)
Ground cover (%)	62 (10–100)	54 (10–90)
Altitude (m)	144 (12–280)	160 (30–290)
Slope (°)	22 (2–80)	29 (0–80)

a *Isothecium myosuroides-Diplophyllum albicans* sub-community
b Typical sub-community
c *Anthoxanthum odoratum-Agrostis capillaris* sub-community
d *Rhytidiadelphus triquetrus* sub-community
17 *Quercus petraea-Betula pubescens-Dicranum majus* woodland (total)

		I (2–3)
		I (1–3)
		I (1–2)
I (1–2)		I (1–2)
I (1–2)		I (1–3)
I (1)		I (1–2)
I (2)		I (1–3)
I (3)		I (1–3)
I (1–4)		I (1–4)
	I (1–4)	I (1–4)
	I (2–4)	I (1–4)
	I (1–3)	I (1–5)
	I (2)	I (2–3)
	I (1–4)	I (1–4)
I (1–4)	I (2)	I (1–4)
I (1–2)	I (1)	I (1–2)
I (1–2)	I (1)	I (1–2)
69	55	303
23 (15–50)	22 (13–31)	28 (13–55)
16 (8–26)	14 (6–30)	14 (5–30)
86 (70–100)	56 (15–90)	76 (10–100)
3 (1–5)	3 (2–6)	3 (1–6)
12 (0–50)	1 (0–4)	13 (0–90)
26 (3–62)	31 (10–70)	29 (3–120)
60 (5–100)	80 (40–100)	55 (4–100)
30 (10–90)	35 (30–50)	39 (10–100)
47 (7–90)	51 (2–95)	55 (2–100)
175 (75–300)	159 (40–519)	162 (12–519)
25 (4–50)	10 (0–28)	22 (0–80)

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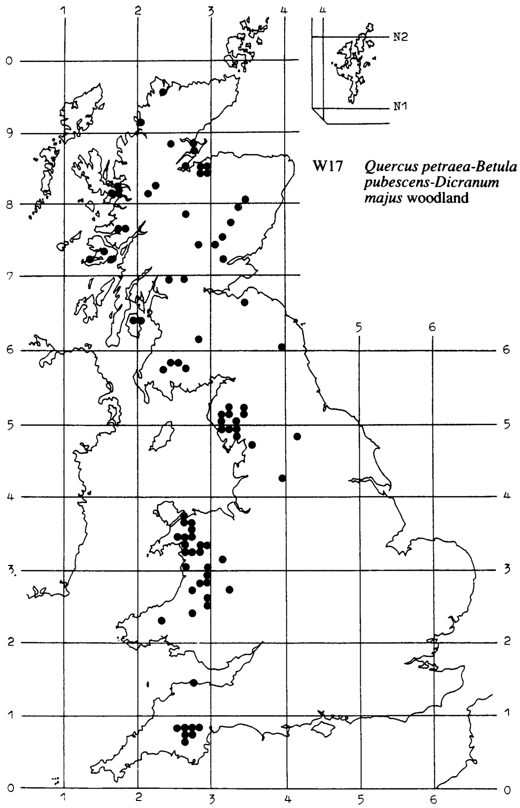
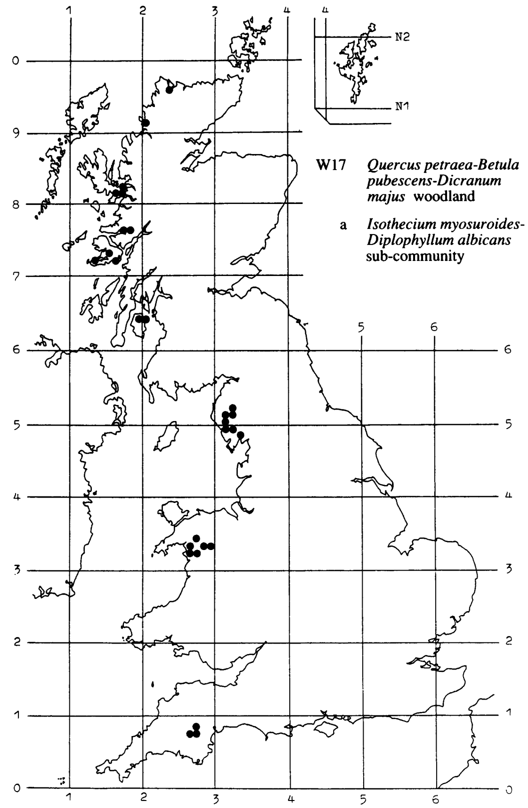
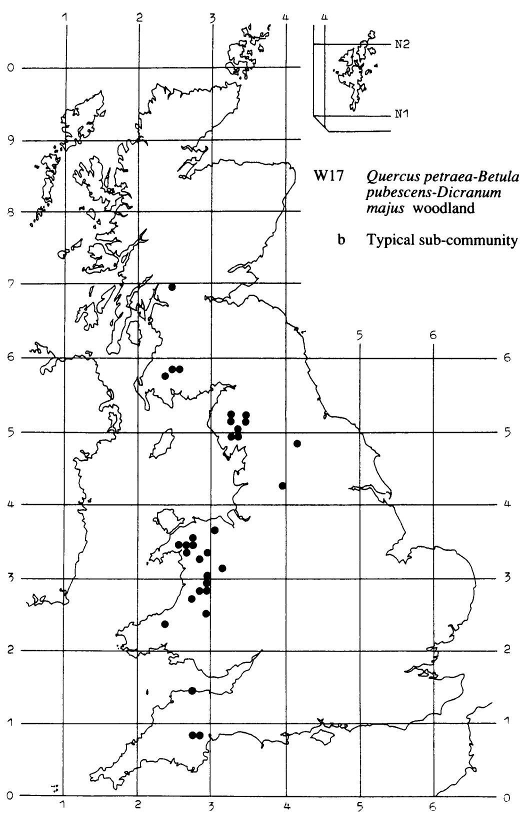


W17 *Quercus petraea-Betula pubescens-Dicranum majus* woodland



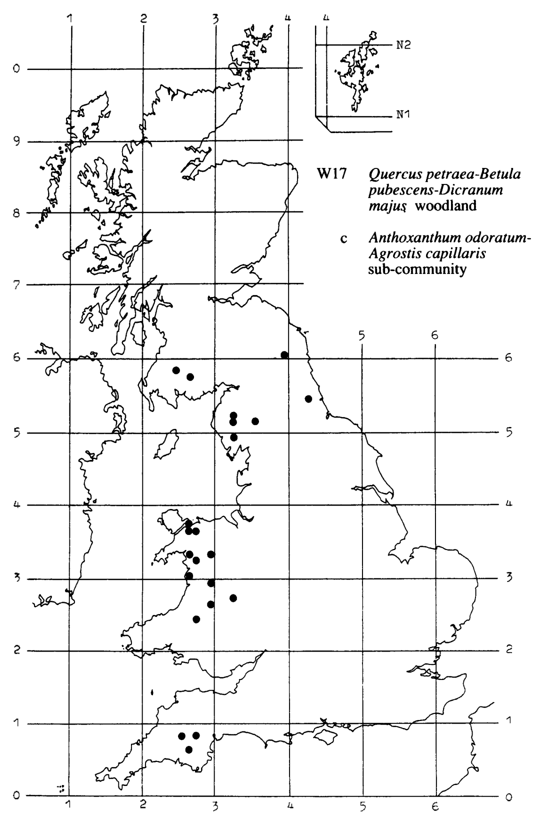
W17 *Quercus petraea-Betula pubescens-Dicranum majus* woodland

a *Isothecium myosuroides-Diplophyllum albicans* sub-community



W17 *Quercus petraea-Betula pubescens-Dicranum majus* woodland

b Typical sub-community



W17 *Quercus petraea-Betula pubescens-Dicranum majus* woodland

c *Anthoxanthum odoratum-Agrostis capillaris* sub-community

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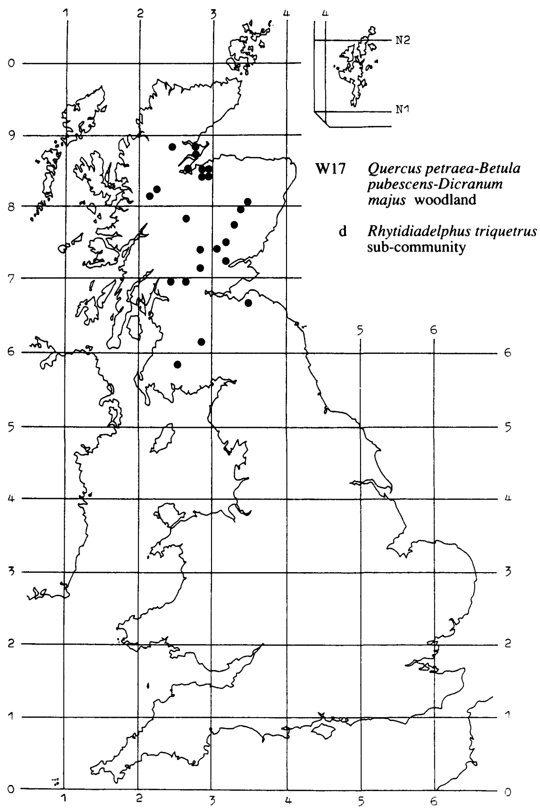

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