W18
Pinus sylvestris-Hylocomium splendens woodland

Synonymy
Scottish *Pinetum sylvestris* Tansley 1911; Highland Pine Forest Tansley 1939; Pinewood communities Steven & Carlisle 1959 *p.p.*; *Pinetum Hylocomieto-Vaccinietum* McVean & Ratcliffe 1962; Pinewood *Vaccinium*-moss association McVean 1964*a*; Pinewood *Vaccinium-Calluna* association McVean 1964a; Pinewood plot types 1–8 Bunce 1977; *Erica cinerea-Pinus sylvestris* Plantation Birse & Robertson 1976 *emend.* Birse 1980; Pine woodland Peterken 1981; *Pinetum scoticae* (Steven & Carlisle 1959) Birse 1980, 1982; Woodland plot type 28 Bunce 1982.

Constant species
Pinus sylvestris, Calluna vulgaris, Deschampsia flexuosa, Vaccinium myrtillus, V. vitis-idaea, Dicranum scoparium, Hylocomium splendens, Plagiothecium undulatum, Pleurozium schreberi, Rhytidiadelphus loreus.

Rare species
Arctostaphylos uva-ursi, Goodyera repens, Linnaea borealis, Moneses uniflora, Orthilia secunda, Pyrola media, P. rotundifolia, Mastigophora woodsii.

Physiognomy
The *Pinus sylvestris-Hylocomium splendens* woodland always has *Pinus sylvestris* as the most abundant tree. Indigenous Scots pine is generally referred to *P. sylvestris* var. *scotica* (Willd.) Schott (Gaussen *et al.* 1964), though populations show considerable and continuous variation in characters like crown shape, foliage colour and bark textures (Carlisle 1958, Steven & Carlisle 1959) and many of the distinctive morphological traits recognised in Scotland occur in populations elsewhere in the range of the species (Carlisle & Brown 1968). Moreover, up until about 1950, there had been extensive introduction of *P. sylvestris* of unknown or uncertain origin into or adjacent to stands of the native tree (Carlisle 1977, Faulkner 1977). Some earlier schemes have concentrated on the classification of apparently native woodlands (e.g. Steven & Carlisle 1959) and others have recognised distinct communities from either semi-natural or planted stands (e.g. Birse & Robertson 1976, Birse 1980, 1982, 1984). As defined here, the *Pinus-Hylocomium* woodland includes more natural pine forest, modified stands and plantations (as in McVean & Ratcliffe 1962 and McVean 1964*a*), though treatment is recognised as one of the factors important in controlling variation in the associated flora.

Although pine predominates here, the stocking density of stands is very variable. In many tracts, the canopy is very open, creating the impression of heath with trees, a kind of landscape that has long had great aesthetic appeal, organised on a large scale, allowing the trees to be seen in their often great individuality, and permitting glimpses of the surrounding scenery, which is frequently grand (e.g. Ratcliffe 1974, Thom 1977). A sensible lower limit of pine cover for defining this kind of woodland (in the absence of other canopy trees) is perhaps 25%, which may amount to no more than two large or several small specimens in a 50×50 m quadrat, but which makes an effective separation from more open ericoid vegetation with very widely-scattered pines which, in this scheme, is treated separately (cf. McVean & Ratcliffe (1962) where a treeless facies is incorporated into the community). At the other extreme are fully-stocked stands with a virtually complete canopy. Between the two, there is a continuous range of tree covers, though most semi-natural stands have a canopy of less than 70%. There is also a distinct tendency for a geographical separation with denser covers prevailing in eastern Scotland, more open ones being commoner in the west (Steven & Carlisle 1959, McVean & Ratcliffe 1962, Goodier & Bunce 1977); and there is an obvious association between this pattern of canopy structure and the distribution of the sub-communities, though not all their preferential features are directly related to the degree of closure.

Although stands with scattered trees are quite common here, *P. sylvestris* is essentially a gregarious

species (Carlisle & Brown 1968) and it is a very characteristic feature of stretches of this kind of woodland that they are made up of a mosaic of quite well segregated age-classes, rather than being an intimate mixture of trees of all ages as in other kinds of semi-natural high forest. McVean & Ratcliffe (1962) noted three major arrangements at the time of their survey: more or less even-aged stands, 80–150 years old, sometimes with suppressed individuals of the same age; two-generation mixtures of pioneers, 150–200 years old, embedded in a matrix of straight-stemmed offspring, 80–100 years old; and pine-heath stands of varying densities but composed exclusively of broad-crowned pioneers, 150–200 years old. The proportions of these different kinds of groupings varies within the individual tracts of pine forest (Steven & Carlisle 1959), but a recent survey (Goodier & Bunce 1977) has confirmed the great predominance of older trees in semi-natural stands. Dead specimens, however, seem to be rather rare: in Scotland the maximum age of *P. sylvestris* is probably in excess of 300 years (Steven & Carlisle 1959). The implications of these types of structural arrangements for the natural regeneration of the community are taken up below but, again, it should be noted that there is some relationship between the canopy age-structure, in both these semi-natural stands and in younger even-aged plantations included here, and the floristics of the field and ground layers.

The age and size of the pine in this community are not always closely correlated and small, stunted trees towards the upper limit of woods can exceed 200 years of age (Steven & Carlisle 1959). Even in more favourable situations, the canopy is usually only 13–15 m high, exceptionally reaching more than 20 m on better soils in sheltered sites, though it should always be remembered that bigger specimens may have been extracted, especially from stands where growth is generally better and where access is easier. Despite this generally small stature and the often low cover of the canopy, *P. sylvestris* always dominates here in terms of proportional abundance and height: within stands of the community, associated trees and shrubs are rare and typically shorter than the pine. Birch is the commonest companion, with *B. pubescens* (often ssp. *carpatica*) more characteristic of western stands, *B. pendula* of those towards the east, and *Sorbus aucuparia* occurs occasionally. These species can be found either as scattered individuals under moderately close pine canopies or in thicker patches where the cover is more open. Strictly speaking, however, denser groups with a very low proportion of pine would, in this scheme, be considered as part of mosaics between the *Pinus-Hylocomium* woodland and either the *Quercus-Betula-Dicranum* woodland or, on somewhat more fertile soils, the *Quercus-Betula-Oxalis* woodland. Such mosaics are a very common feature of Scottish pine forest and they usually involve birch- (occasionally rowan-) dominated stands of these other communities, though oak can figure at lower altitudes, *Quercus petraea* being typical to the west, *Q. robur* and hybrids becoming more frequent in the east. It is in this kind of situation that *Ilex aquifolium* is found in close association with pine, especially in the milder west, though it is often nibbled to a low undershrub by sheep and deer. In other cases, *Juniperus communis* can be found as scattered bushes or in small patches within the *Pinus-Hylocomium* woodland but, again, where it thickens up in the local absence of pine, such stands are best seen as mosaics with the *Juniperus-Oxalis* woodland, a characteristic feature of more high-altitude situations in eastern Scotland. Quite commonly, this kind of variegation in the vegetation cover within pine forests also takes in stands of wetter woodland on valley and basin mires: this is why such species as *Alnus glutinosa*, *Salix cinerea*, *S. aurita*, *S. pentandra* and *Populus tremula* sometimes figure in descriptions of *P. sylvestris* woodland which have a broader basis of definition (e.g. Steven & Carlisle 1959). Finally, there may be occasional records for other exotic conifers seeding in from nearby plantations.

The associated flora of the *Pinus-Hylocomium* woodland has three major elements, *Deschampsia flexuosa*, ericoid sub-shrubs and bryophytes. As in other of our more calcifugous woodlands, *D. flexuosa* forms a fairly consistent grassy background to the field layer here and it can be especially prominent in more heavily grazed stands or under denser shade where the ericoids are reduced: it may dominate, for example, in pine plantations at the thicket stage (Birse 1980). Generally, though, it is variation among the two other elements that is more important here, both in general visual terms and in the particular definition of the different sub-communities. Among the ericoids, *Vaccinium myrtillus*, *V. vitis-idaea* and *Calluna vulgaris* are all more consistently frequent here than in any other kind of woodland, even the most floristically-similar *Juniperus-Oxalis* woodland where the same combination of highly acid soils and open canopies can occur. But the abundance of these species is very variable, being affected not only by canopy shade and grazing but also by such factors as their relative speed of colonisation when there is some change in the intensity of these variables or after burning (a frequent occurrence here) and inter-specific competition. *Calluna*, especially, is very sensitive to shade, and is much more prominent in sub-communities with a more open canopy, but *V. vitis-idaea* can suffer against *V. myrtillus* where the latter is growing very vigorously or where the trees are more closely set and, in very dense pine, all three can be eliminated, leaving bryophytes and *D. flexuosa* as effective dominants. When the canopy is opened up, a change which can precipitate a seral

development from one sub-community to another, all the ericoids can expand or colonise, though the eventual prominence of the Vaccinia is very dependent on how much of them survived the period of denser shade, because *Calluna* is the most rapid invader and it may come to dominate, restricting the growth of the other species with a cover of leggy bushes more than half a metre high (McVean & Ratcliffe 1962). Grazing and browsing can also effect a marked reduction in the abundance of *V. myrtillus* and *Calluna*, both of which are readily eaten by stock and deer (the latter also by grouse), or alter the balance between them and favour a prominence of *V. vitis-idaea*, which is less palatable (Ritchie 1955).

Other sub-shrubs which can play a prominent, though less consistent, role here are *Empetrum nigrum* ssp. *nigrum*, *Erica tetralix*, which is very characteristic of moister, peatier soils, especially in the wetter west and in local transitions to mires, and *E. cinerea*, particularly distinctive of earlier and thinned stages in plantations though also occurring occasionally in more open, semi-natural stands. *E. nigrum* ssp. *hermaphroditum* and *V. uliginosum*, both of which are important species in certain types of Scandinavian pine associations (e.g. Aune 1977), are rare, as is *Arctostaphylos uva-ursi*.

The third important element of the flora here is the bryophytes, particularly bulkier mosses. Some of the species occur at consistently high frequencies throughout, being found even in denser stands of pine, where, with the reduction in ericoids, they can comprise the most prominent component of the ground vegetation: these species are *Hylocomium splendens*, *Dicranum scoparium* and *Pleurozium schreberi*. Two further species, *Plagiothecium undulatum* and *Rhytidiadelphus loreus*, are much less common under more closed canopies but they are so frequent elsewhere in the community that they attain constancy overall. This suite of more calcifugous mosses is very characteristic of a number of north-western woodland types on strongly acidic soils but one further species, not quite constant but very frequent under all but the densest canopies, is particularly distinctive of the *Pinus-Hylocomium* woodland and that is *Ptilium crista-castrensis*, a moss which maintains this important role in Scandinavian pine forests (e.g. Aune 1977). Other bryophytes occurring commonly throughout are *Hypnum jutlandicum* and *Lophocolea bidentata* *s.l.* and, more occasionally, *Hypnum cupressiforme s.l.*, *Polytrichum commune* (less frequent here than in calcifuge oak-birch woodlands of the north-west), *P. formosum*, *P. juniperinum*, *Campylopus paradoxus* and *Aulacomnium palustre*.

Then, there are further species which, though not common throughout, are preferentially frequent in different groups of sub-communities. *Rhytidiadelphus triquetrus*, *Pseudoscleropodium purum* and *Dicranum fuscescens* provide an important part of the definition of *Pinus-Hylocomium* woodlands with more closed and younger canopies, especially in the drier east. By contrast, *Sphagnum capillifolium/quinquefarium* (not consistently distinguished in the data), *Dicranum majus* and *Scapania gracilis* are more characteristic of stands with more open and older covers of pine, particularly in the wetter west, where they may be accompanied by various less frequent species including other Sphagna of the Acutifolia group, like *S. russowii* and *S. girgensohnii*, *S. palustre*, *Leucobryum glaucum*, *Calypogeia trichomanis/muellerana* and some western or more strictly Atlantic bryophytes. The floristic distinction between these two groups is essentially that used by McVean & Ratcliffe (1962) in their definition of two pine associations and by Birse (1984) in his recognition of eastern and western races among semi-natural stands.

Among the bryophyte mat, there may be some sparsely-scattered *Cladonia* spp., including *C. cornuta*, *C. pyxidata*, *C. digitata*, *C. macilenta*, *C. impexa* and *C. arbuscula*, but these never attain the high frequencies and covers which mark many Scandinavian pine woods (Aune 1977).

Generally speaking, additional elements of the flora of the *Pinus-Hylocomium* woodland are either infrequent throughout or rather unevenly represented in the different sub-communities. *Pteridium aquilinum*, despite the often open cover of trees, is nothing like so common here as in the more calcifuge oak-birch woods of the region and, though *Blechnum spicant* becomes frequent in certain kinds of *Pinus-Hylocomium* woodland, ferns as a group are poorly represented. Other grasses, apart from *Deschampsia flexuosa*, are few in number, too. *Molinia caerulea* becomes more common towards the west and it can figure locally elsewhere in transitions to mires and, on somewhat less extreme soils or where there is consistent grazing, *Agrostis capillaris*, *A. canina* ssp. *montana*, *Anthoxanthum odoratum* and *Festuca ovina* can become prominent. Apart from *Melampyrum pratense*, which is frequent in all but the densest stands of pine, other herbaceous associates are usually sparse. There is sometimes a little *Potentilla erecta* and, in eastern Scotland, *Trientalis europaea* can be recorded; then, on rather more fertile soils, *Luzula pilosa*, *Oxalis acetosella* and *Galium saxatile* often appear together, a development which is sometimes accompanied by a rather more prolific representation of birch and rowan or, to the east, juniper, and which may mark transitions to woodlands dominated by these trees.

Finally, there is a group of herbs which, though generally infrequent, are especially characterisitic of the *Pinus-Hylocomium* woodland. The most uniformly distributed of these is *Listera cordata* which Steven & Carlisle (1959) found to be best represented in the south-

eastern woodlands from Rannoch to Speyside, usually growing among hypnaceous mosses under tall *Calluna* beneath rather irregular pine covers; but other species occasionally found are the various wintergreens, *Pyrola minor* and the nationally rare *P. media*, *P. rotundifolia*, *Moneses uniflora* and *Orthilia secunda*, all of them plants with a strong Continental Northern distribution through Europe. The Northern Montane *Linnaea borealis* also occurs at a few sites. More common than any of these, though strongly associated with denser covers of pine, especially in eastern Scotland, and often found in plantations, is *Goodyera repens*.

Sub-communities

Erica cinerea-Goodyera repens **sub-community:** Pinewood community 1   Steven & Carlisle 1959; *Pinetum Hylocomieto-Vaccinietum triquetrosum* McVean & Ratcliffe 1962; Pinewood *Vaccinium*-moss association, *Hylocomium-Rhytidiadelphus* facies McVean 1964*a*; *Erica cinerea-Pinus sylvestris* Plantation, Typical sub-community, typical variant   Birse & Robertson 1976 *emend.* Birse 1980. This sub-community is characteristic of stands with a closer, even-aged and younger cover of pine and it is often found in plantations where there may be some admixtures of other conifers (like *Larix* and *Picea* spp.) and patchy colonisation, in the early stages or after thinning, by birch (generally *B. pendula*), rowan or even oak (Steven & Carlisle 1959, McVean & Ratcliffe 1962, Birse 1980).

The most obvious feature of the field layer here is generally the scarcity and low cover of the characteristic sub-shrubs of the community, particularly in the period after canopy closure and before thinning. Indeed, this feature may persist for some considerable time after the tree cover has been opened up, though *Calluna* is a fairly early invader (McVean & Ratcliffe 1962) and it is often accompanied here by *Erica cinerea*, so high frequencies (but usually low covers) of these two ericoids are characteristic. Vaccinia, by contrast, are very sparse and *Empetrum nigrum* ssp. *nigrum* is absent: a little *V. myrtillus* may persist through the period of deeper shade but it is slow to re-invade after thinning. In the absence of the sub-shrubs, the most prominent vascular plant is usually *Deschampsia flexuosa* and, in some stands, this may dominate the field layer, though it, too, can become very thin and is quite often eliminated completely as the canopy closes. Most of the other herbaceous associates of the community are also very sparse but a very good preferential for this kind of *Pinus-Hylocomium* woodland is *Goodyera repens*. This orchid is very frequent here, though it is generally found as scattered individuals or in small clumps, its rhizomes and runners ramifying the moss carpet. It can persist in quite dense shade, probably being strongly dependent on a mycorr-

hizal fungus, but it flowers best after the canopy has been thinned.

By and large, with this poor representation of vascular plants, the most prominent element of the flora here consists of bryophytes. Some of the characteristic mosses of the community are rather sparse here, notably *Rhytidiadelphus loreus*, *Ptilium crista-castrensis* and, a little less so, *Plagiothecium undulatum*, but others are very common: *Hylocomium splendens*, *Pleurozium schreberi*, *Dicranum scoparium*, *Hypnum jutlandicum* and *Lophocolea bidentata s.l.* And, in addition, *Rhytidiadelphus triquetrus* and *Pseudoscleropodium purum* are frequent. Among these, *R. triquetrus* and *H. splendens* are usually the most abundant, forming the bulk of a bryophyte carpet that can cover most of the ground or, in the very deepest shade, be reduced to patches amongst a covering of pine needles and areas of exposed mor humus.

Vaccinium myrtillus-V. vitis-idaea **sub-community:** Pinewood community 3   Steven & Carlisle 1959 *p.p.*; *Pinetum Hylocomieto-Vaccinietum myrtillosum* McVean & Ratcliffe 1962; Pinewood *Vaccinium*-moss association, *Vaccinium* facies   McVean 1964*a*; Pinewood plot types 1 & 2   Bunce 1977; *Erica cinerea-Pinus sylvestris* Plantation, *Polytrichum commune* sub-community   Birse & Robertson 1976 *emend.* Birse 1980; *Pinetum scoticae*, Typical subassociation, typical variant, eastern race   Birse 1984. The pine canopy here is typically a little less dense than in the *Erica-Goodyera* sub-community, though there is a considerable overlap in the ranges of tree cover and these two kinds of *Pinus-Hylocomium* woodland are often found in close spatial association in mosaics.

The essential difference between the two sub-communities lies in the relative prominence of the sub-shrubs and the bryophytes. Here the former are more varied and abundant, frequently covering up to 75% of the ground. *Vaccinium myrtillus* and *V. vitis-idaea* are generally the most extensive species, dominating in various proportions, but there is usually some *Calluna* and, quite often, some *Empetrum*. *Erica cinerea*, by contrast, is now infrequent. In more open places among the bushes, *Deschampsia flexuosa* can form a patchy carpet, sometimes, in more westerly stands, with a little *Molinia caerulea*, and, in the less intense shade of the canopy, some herbs flourish: *Melampyrum pratense* occurs frequently and there can be scattered plants of *Potentilla erecta* and *Galium saxatile*. *Goodyera* is occasionally found.

The bryophyte carpet is still extensive here, though usually not so well seen with the abundance of sub-shrubs. Indeed, it is a little more varied than in the *Erica-Goodyera* sub-community with *Plagiothecium undulatum*, *Rhytidiadelphus loreus* and *Ptilium crista-castrensis*

becoming constant and *Dicranum fuscescens* joining *R. triquetrus* and *Pseudoscleropodium purum* as a preferential. Each of these can be abundant in particular stands, though *Hylocomium splendens* is the most consistent dominant. In more westerly stands, *Sphagnum capillifolium/quinquefarium* or *Dicranum majus* may make an occasional appearance but typically these mosses are not represented here.

Luzula pilosa sub-community: Pinewood communities 3, 4 & 5   Steven & Carlisle 1959; Pinewood plot types 3 & 4   Bunce 1977; *Erica cinerea-Pinus sylvestris* Plantation, Typical and *Polytrichum commune* sub-communities, *Oxalis acetosella* variants   Birse & Robertson 1976 *emend.* Birse 1980; *Pinetum scoticae*, Typical subassociation, *Oxalis acetosella* variant   Birse 1984. The general features of the vegetation here are very much as in the *Vaccinium* sub-community with a moderately close cover of pine, a field layer dominated by the Vaccinia with a little *Calluna* (usually only sparse *Empetrum*) and a rich and extensive bryophyte carpet in which the trio *R. triquetrus, P. purum* and *D. fuscescens* continue to be well represented in the general absence of Sphagna. But, among the herbs, there are some clear preferentials with *Luzula pilosa, Oxalis acetosella* and *Galium saxatile* all becoming frequent and grasses such as *Anthoxanthum odoratum, Agrostis capillaris, A. canina* ssp. *montana* and *Festuca ovina* occurring occasionally. Among eastern stands represented here, *Blechnum spicant* is a little commoner than usual in the region.

Sphagnum capillifolium/quinquefarium-Erica tetralix sub-community: Pinewood communities 2, 6, 8 & 9   Steven & Carlisle 1959; *Pinetum Vaccineto-Callunetum*   McVean & Ratcliffe 1962 *p.p.*; Pinewood *Vaccinium-Calluna* association McVean 1964*a* *p.p.*; Pinewood plot types 5–8   Bunce 1977 *p.p.*; Woodland plot type 28   Bunce 1982; *Pinetum scoticae*, Typical subassociation, *Molinia* variant   Birse 1984. In this sub-community, there is a distinct shift towards a more consistently open cover of pine, with denser plantations rarely represented and many stands having the kind of open heath structure or two-generation mixes that McVean & Ratcliffe (1962) detected. Among this less dense canopy, there can be some birch (usually *B. pubescens* in this predominantly western sub-community) and *S. aucuparia* and, in more southerly stands, a little *Juniperus*.

Sub-shrubs continue to be an important element in the field layer here, though there is a rather different balance among the common species of the community. *Calluna* is very frequent and is now the usual dominant with *V. myrtillus* often playing a subsidiary role and *V. vitis-idaea* and *Empetrum nigrum* ssp. *nigrum* very common but typically of low cover. *Erica cinerea* is sometimes found but much more characteristic here are small amounts of *E. tetralix*.

Deschampsia flexuosa maintains its high frequency in this sub-community but generally it is not abundant and, quite often, a more prominent grass is *Molinia caerulea*. In drier places, there is occasionally some *Pteridium*, though its cover is usually low, and there can be scattered plants of *Blechnum spicant, Melampyrum pratense* and *Listera cordata*.

All the characteristic bryophytes of the community are well represented here with *H. splendens* and *P. crista-castrensis* often being especially abundant, but the really distinctive feature of the ground layer is the prominence of deep tussocks of Acutifolia Sphagna, especially *S. capillifolium* and *S. quinquefarium. Dicranum majus* also becomes frequent while *R. triquetrus, P. purum* and *D. fuscescens* are only rarely recorded. Other bryophytes sometimes found here include *Leucobryum glaucum, Calypogeia trichomanis/muellerana, Aulacomnium palustre, Barbilophozia floerkii,* the Sub-Atlantic *Scapania gracilis,* the Western British *Bazzania trilobata* and *Hylocomium umbratum* and the Northern Atlantic *Mastigophora woodsii* and *Herberta adunca* (Ratcliffe 1968).

Quite frequently, these various components are disposed over very uneven topography in this sub-community with the ground thrown into hummocks by bryophyte-covered pine stumps and boulders and with hollows where the *Pinus-Hylocomium* woodland gives way to mire forest or herbaceous bog vegetation.

Scapania gracilis sub-community: Pinewood community 2   Steven & Carlisle 1959 *p.p.*; *Pinetum Vaccinieto-Callunetum*   McVean & Ratcliffe 1962 *p.p.*; Pinewood *Vaccinium-Calluna* association   McVean 1964*a* *p.p.*; Pinewood plot types 5–8   Bunce 1977 *p.p.*; *Pinetum scoticae*, Typical subassociation, typical variant, western race   Birse 1984. The general characteristics of the vegetation here are very similar to those of the *Sphagnum-Erica* sub-community with a more open pine canopy, a mixed cover of sub-shrubs and a hummocky bryophyte carpet in which Sphagna continue to play a prominent part. Here, however, *Erica tetralix* and *Molinia caerulea* are usually absent and there is a further enrichment of the bryophyte element. *Thuidium tamariscinum,* generally speaking a rare moss in the *Pinus-Hylocomium* woodland, becomes frequent but more striking is the common occurrence of *Scapania gracilis* and *Diplophyllum albicans* and the occasional appearance of the Sub-Atlantic *Anastrepta orcadensis,* a hepatic usually associated with bryophyte mats in vegetation above the forest zone (Ratcliffe 1968).

Habitat

The *Pinus-Hylocomium* woodland is characteristic of strongly-leached soils in the cooler parts of the north-

western sub-montane zone in Britain. Floristic variation within the community is closely related to the density and age of the pine canopy but other factors, such as climatic and edaphic differences and the incidence of grazing and browsing and burning, also play an important role and make it difficult to attribute the character of the different sub-communities unequivocally to the antiquity or naturalness of the vegetation.

Two climatic variables, temperature and rainfall, have a major influence here. By and large, the *Pinus-Hylocomium* woodland is confined to those parts of Britain where the mean annual maximum temperature is 23 °C or less (Conolly & Dahl 1970), the annual accumulated temperature between 280 and 550 °C (500–1000°F: Page 1982), with most stands occurring in the central and north-west Highlands of Scotland. And the prevailing cool character of the climate is reflected in the occurrence in the community of Northern Montane plants like *Goodyera repens, Listera cordata, Trientalis europaea* and *Linnaea borealis* and the Continental Northern wintergreens. Apart from *Goodyera*, none of these is very common here but most of them are preferentially frequent and their British distributions roughly coincide with or are included within that of the *Pinus-Hylocomium* woodland. *Empetrum nigrum* ssp. *nigrum*, which has a wide range in Britain but has an Arctic-Alpine distribution through Europe as a whole, is also much better represented here than in any other calcifugous north-western woodland. The only major absentees among this group are the two other Arctic-Alpine sub-shrubs, *E. nigrum* ssp. *hermaphroditum* and *Vaccinium uliginosum*, which are important species in some Scandinavian pinewoods but very scarce here. As always in this community, it is possible that the great reduction in its extent has resulted in a floristic impoverishment, though the rarity of these two quite widely distributed species is very consistent throughout the range of the woodland.

Within this cooler zone, the community can be found from almost sea-level up to more than 600 m, extending noticeably higher in the east where, on Creag Fhiaclach in the north-west Cairngorms, it probably attains a natural altitudinal limit, with the pines becoming increasingly stunted and sparse beyond 640 m (McVean & Ratcliffe 1962: Plate 6, Ratcliffe 1977). In such situations, cold and exposure to wind probably restrict growth and reproduction, though this is not known for certain (Carlisle & Brown 1968). What is clear is that, though *P. sylvestris* can ascend to higher levels than oak, the *Pinus-Hylocomium* woodland is not an altitudinal replacement for the *Quercus-Betula-Dicranum* woodland: birch-dominated stands of the latter extend to roughly the same altitudes as the former and zonations from oak- to pine-dominance (they are actually rather uncommon despite Tansley's (1939) supposition) gener-

ally reflect edaphic transitions (McVean 1964a: see below). More accurately, the remaining distribution of the *Pinus-Hylocomium* woodland reflects a regional prominence of pine in the cooler parts of Scotland that is probably a direct inheritance of its prevalence there through the post-Glacial period (McVean & Ratcliffe 1962, O'Sullivan 1977). However, within this zone, its natural extent has been much reduced with widespread replacement by planted stands of pine and by subspontaneous development of the *Quercus-Betula-Dicranum* woodland; and outside this zone, planting of pine has extended the range of the *Pinus-Hylocomium* woodland into areas where the *Quercus-Betula-Dicranum* woodland might be expected as the natural climax forest. Many stands of the latter kind can be found around the Moray Firth and in central Scotland (e.g. Birse & Robertson 1976, Birse 1980, 1982, 1984, Blaxter 1983) and there may be others beyond these regions where acid soils under pine experience sufficiently high rainfall to acquire the distinctive bryophyte flora of this community.

It is this related combination of a generally wet climate and high soil acidity that gives the *Pinus-Hylocomium* woodland much of its remaining floristic character. In fact, *P. sylvestris* will grow on quite calcareous soils: calcicolous pinewoods are a feature of various parts of Europe (e.g. Aune 1977, Ellenberg 1978) and they may have occurred in Britain in the past. But, at the present time, our pine woodlands are found, for the most part, on very strongly leached, lime-free profiles and the characteristic soil type under the *Pinus-Hylocomium* woodland is the podzol (e.g. Steven & Carlisle 1959, Manley 1961, McVean & Ratcliffe 1962, Carlisle & Brown 1968, Fitzpatrick 1977). Typically, raw litter overlies a mat of mor humus, with slow integration of organic matter through fungal decay and arthropod activity. The surface pH is consistently low, generally 3.5–4.5, and there is marked leaching with a prominent E_b and deposition horizons with humus and iron. The texture throughout the mineral layers is generally sandy and the structure very poor, often single-grain with but minimal deposition of any clay coatings. In Scotland, such soils are very widespread over a variety of pervious siliceous substrates: especially important here are the extensive sandy and gravelly fluvioglacial deposits laid down over Dalradian and Moine schists and granites in the east and south, where the community occupies a very distinctive habitat over undulating terraces; elsewhere, podzols are developed directly from quartzites and sedimentaries like the Torridonian sandstone and Devonian Old Red Sandstone.

The highly acidic and impoverished soil conditions here are reflected in the *Pinus-Hylocomium* woodland as a whole by the great predominance of calcifuges in its flora, among the sub-shrubs, the herbs and the bryo-

phytes, many of which it shares with other acidophilous woodlands of the north-western part of Britain. Some of these, of course, help maintain the mor humus regime and encourage podzolisation, by the provision of acidic litter. Pine itself produces large quantities of litter (Bray & Gorham 1964, Carlisle & Brown 1968), mainly leaves, small branches and bark, which decays very slowly (Kendrick & Burges 1962), but the sub-shrubs are also important, particularly *Calluna*, which can also acidify its root environment (e.g. Gimingham 1972). This is a more frequent and abundant plant in this community than under the often closed canopies of the *Quercus-Betula-Dicranum* woodland and it is a noticeable feature of the soils here that they are most strongly podzolised, with the development of a thin iron pan, in the open heathy vegetation of the *Sphagnum-Erica* and *Scapania* sub-communities where *Calluna* is frequently the field-layer dominant (Fitzpatrick 1977).

These two kinds of *Pinus-Hylocomium* woodland are also characteristic of the wetter areas in which the community is found, at lower altitudes towards the west and at higher altitudes in the east, where the annual rainfall is usually more than 1600 mm (*Climatological Atlas* 1952) with at least 180 wet days yr^{-1} (Ratcliffe 1968), in some places rising to 2000 mm and 200 wet days or beyond. This index of climate provides quite a good separation between the two groups of sub-communities, the *Sphagnum-Erica* and *Scapania* types on the one hand and the *Erica-Goodyera*, *Vaccinium* and *Luzula* types on the other, with acutifolia Sphagna and *Dicranum majus* diagnostic of the former, *Rhytidiadelphus triquetrus*, *Pseudoscleropodium purum* and *Dicranum fuscescens* preferential for the latter. Not only do the soils of the former show a somewhat stronger tendency towards podzolisation but they are generally noticeably moister, with thicker accumulations of litter, sometimes reaching 30 cm and forming what is in effect a layer of peat, constantly replenished by the decay of the *Sphagnum* tussocks. In the hummocky topography characteristic of the *Sphagnum-Erica* and *Scapania* sub-communities, there may also be some local impedence of drainage in the lower horizons. Here, then, the vegetation takes on some of the character of a mire forest with *Erica tetralix* and *Molinia caerulea* becoming prominent on profiles which approach peaty podzols or gley-podzols though, with very marked waterlogging, pine growth becomes severely hindered (Carlisle & Brown 1968) and there is a transition to other kinds of woodlands in very wet hollows (see below).

The increased surface moisture of the soils in the *Sphagnum-Erica* and *Scapania* sub-communities is also part of the complex of factors that imparts a more oceanic feel to their flora. The floristic element involved is not a large one and the two main species (*Sphagnum quinquefarium* and *Scapania gracilis*) are only of rather broadly Atlantic nature (Ratcliffe 1968) but, where they become especially prominent in the *Scapania* sub-community, with *Diplophyllum albicans* and *Anastrepta orcadensis*, in Wester Ross pinewoods with an annual rainfall over 3000 mm (220 wet days yr^{-1}), the vegetation begins to take on some of the character of the strongly oceanic *Quercus-Betula-Dicranum* woodlands of that region.

The other soil-related trend visible in the community has to do with fertility. By and large, the podzols under the *Pinus-Hylocomium* woodland are very infertile and perhaps only able to maintain a forest cover by the constant, though slow, cycling of nutrients derived from the litter (Carlisle & Brown 1968, Fitzpatrick 1977). But, in some situations, conditions are not so extreme, where, for example, there is some heterogeneity among the parent materials, with less siliceous strata interposed or a variety of superficials admixed, or where there is some flushing with less base-poor waters, a feature well seen in the Loch Maree woodlands where there is seepage from calcareous mudstones (Ratcliffe 1977). Then the effects of leaching are offset a little and the profile tends towards a brown podzolic soil or even a brown earth with a somewhat milder humus regime (Fitzpatrick 1977, Birse 1980, 1984). Among the different kinds of *Pinus-Hylocomium* woodland, there is a clear association between such conditions and the *Luzula* sub-community. This is quite a widely distributed vegetation type, being related to local edaphic variation rather than any regional pattern of soil differences, but it seems to be more frequent in the drier east, so its general affiliations are with the *Erica-Goodyera* and *Vaccinium* sub-communities.

As noted above, the tendency towards more pronounced leaching in soils under the *Pinus-Hylocomium* woodland is associated with and perhaps favoured by the openness of the pine canopy. The density of the tree cover certainly has a marked effect on the field and ground layers of the community by altering the balance between the more shade-tolerant bryophytes and the more light-demanding sub-shrubs. This can be seen within individual sub-communities, as when *Erica-Goodyera* plantations close over and are later thinned (Birse 1980, 1984), and in the general contrast between this sub-community and the *Vaccinium* type where canopies are usually rather more open (McVean & Ratcliffe 1962). And, within the community as a whole, there is a broad shift towards a prominence of sub-shrubs under the more consistently open canopies of the *Sphagnum-Erica* and *Scapania* sub-communities. But, apart from the effect on *Calluna*, the coincidence between the major contrast in canopy density and the most obvious difference in soil conditions within the *Pinus-Hylocomium* woodlands may be largely accidental. Vagaries of treatment history could have left us with

the predominance of more open stands of pine that we now see in the wetter regions; extensive planting in the drier areas has certainly increased the proportion of denser stands there. By its effect on sub-shrub abundance, variation in canopy closure thus reinforces differences between the sub-communities, seen best among the species of bryophytes, that are directly related to regional variations in soil development.

The potential dominance of sub-shrubs in the field layer which increased penetration of light permits is often moderated here by the influence of herbivores; and these play an important role in controlling the ultimate density of trees by their effect on regeneration. Many stands of the community, particularly the more semi-natural remnants, occur within tracts of unenclosed upland, with the vegetation freely open to stock and deer. Before the mid-eighteenth century, mixed pasturing of these woodlands seems to have been common with cattle, sheep, goats and ponies all involved, though apparently all in fairly small numbers (Steven & Carlisle 1959). After that time, there was a switch to sheep and an increase in stock densities with the formation of the great Highland runs. Red deer are also plentiful in many areas and, with the creation of deer forests to provide shooting in the middle of the last century, they were often encouraged locally. There are also small numbers of roe and, in some northern pinewoods, feral sika (Steven & Carlisle 1959). The effects of all these grazers and browsers is especially great in winter, when harsh weather at higher levels drives them into the shelter of the tree cover where some snow-free herbage is still available. At such times, too, drifting of snow over fences can give animals easy access to plantation stands.

By their browsing of *Vaccinium myrtillus* and *Calluna* (the latter also being eaten by grouse), stock and deer can prevent these sub-shrubs attaining dominance under more open canopies, thus favouring less palatable species (notably *V. vitis-idaea*) or completely counteracting the effect of increased light penetration, shifting the balance of dominance back towards bryophytes and *Deschampsia flexuosa*: the *Erica-Goodyera* sub-community can contain some heavily grazed stands of this kind where there are quite open covers of pine. The other impact of the herbivores is on the pine itself, because they can consume such seedlings as have managed to get a hold in more open situations and bite out the leaders of saplings that have breached the sub-shrub canopy (a process that may take 20 years) but which have not grown tall enough to be out of reach. In fact, *P. sylvestris* is fairly resistant to repeated topping and can readily replace damaged leaders: Carlisle & Brown (1968) reported good regrowth of native pine after it had been held in check by browsing for ten years. But the cumulative effect of sustained herbivore predation can severely hinder regeneration where conditions

are otherwise suitable (Steven & Carlisle 1959, McVean 1961, Carlisle 1977, Lowe 1977, Booth 1977, Millar 1977).

Ground fires can be similarly deleterious, destroying with speed the result of decades of natural regeneration (e.g. Booth 1977) and sometimes killing mature trees, especially those with thin plated bark (usually older specimens: Carlisle & Brown 1968). Fires may occur accidentally, through careless behaviour by visitors or, in the days of steam trains, by showering of hot coals, or by spread from adjacent muirburns; in the extension of sheep runs, some stands were deliberately destroyed by fire. That fires have been widespread in the history of the *Pinus-Hylocomium* woodland is abundantly clear in the frequent presence of carbon or recognisable fragments of charcoal in the A horizon of the soils (Manley 1961, McVean & Ratcliffe 1962, Carlisle & Brown 1968, Fitzpatrick 1977).

But fire is probably of considerable importance in creating suitable conditions for regeneration (e.g. Carlisle & Brown 1968, Carlisle 1977). *P. sylvestris* can produce large quantities of seed, though it is a sporadic fruiter and a fairly precise set of conditions must coincide with a good crop of seed for germination to approach an optimum (Carlisle & Brown 1968, Bunce & Jeffers 1977, where extensive bibliographies of the popular but controversial subject of pine regeneration are given). Generally speaking, natural regeneration seems to be more likely under more open covers of trees, where there is a patchy cover of mor or peat over freely-draining mineral horizons, where sub-shrubs are not luxuriant and where grazing is not too heavy. Pine seed is light and can be wind-blown a considerable way, but Carlisle & Brown (1968) gave 90 m as a crude limiting distance for seed-parents. Ground fires, which burn off the competing vegetation, partially destroy the felted mat of mor and also provide a valuable release of nutrients from the ash, may be the best single producer of such conditions, perhaps to such an extent that *P. sylvestris* is effectively a fire-dependent species (Carlisle & Brown 1968, Carlisle 1977). But other forms of disturbance, such as upheaving of the soil by wind-thrown big trees, or even the scuffing of the ground surface by herbivores, may also assist seedlings in getting a hold. Certainly, the impression gained from the study of individual sites (Steven & Carlisle 1959) is that some form of disturbance, often man-related, is advantageous for initiating natural regeneration, though many other factors may affect the survival of the seedlings and saplings. At the present time, regeneration is very patchy: some stands, particularly in the east, are regenerating well locally; elsewhere the characteristic prevalence of older trees is still very noticeable and often inexplicable.

Grazing and burning are just two elements in the long

history of human influence to which our native pine-woods have been subject. At the present time, the *Pinus-Hylocomium* woodland comprises fragments of semi-natural forest, much reduced in extent by man and widely affected by timber removal, and younger stands of planted origin, sometimes interposed within the more ancient framework, sometimes on ground that seems unlikely to have been occupied by pine for considerable periods of time, if ever. There is good palynological evidence (e.g. Birks 1970, O'Sullivan 1977, Carlisle 1977) to suggest that, in its more semi-natural stands, the *Pinus-Hylocomium* woodland represents a vegetation type of great antiquity, providing continuity over some 8000 years with the original post-Glacial forest cover that developed in many parts of the Scottish Highlands. Subsequent climatic change seems to have markedly affected its abundance towards the west, where it succumbed widely to blanket mire extension but, in the drier east, it appears to have remained a more extensive forest type until the period of human expansion. Present climatic differences in these two regions are still reflected in the floristics of the community (and perhaps, too, in the regenerative ability of *P. sylvestris*, though systematic data are very patchy) but it is not very easy to say which kinds of *Pinus-Hylocomium* woodland represent more closely the original or more natural pine forest (or forests). Certainly the *Sphagnum-Erica* and *Scapania* sub-communities are typically found beneath older and more open stands of pioneer trees, and plantations are much more common in the *Erica-Goodyera*, *Vaccinium* and *Luzula* types but this latter group, too, includes stands which are probably semi-natural. And, among all these kinds of *Pinus-Hylocomium* woodland, there seems to be a much greater purity in the canopy than was the case in the original forest cover. The cumulative effect of the various kinds of interference and treatment has been gradually to select for pine as the dominant here, so that it is now easier to characterise distinct communities on the basis of the pre-eminence of pine (this community), birch (the *Quercus-Betula-Dicranum* woodland) or juniper (the *Juniperus-Oxalis* woodland), a situation especially well seen in eastern Scotland, where plants like *Trientalis europaea* and *Rhytidiadelphus triquetrus* provide a Continental element in all three. What seems to have been originally the case is that all these trees contributed to a much more mixed kind of forest with spatial patchworks and probably temporal shifts in dominance.

Zonation and succession

The *Pinus-Hylocomium* woodland on Creag Fhiaclach in the Cairngorms is probably one of the very few stands of forest vegetation in Britain where trees can be seen growing at a natural, climatically-related altitudinal limit. Here, the community gives way, through a gradual

loss of its pine cover, to the more calcifugous kind of *Juniperus-Oxalis* woodland, the characteristic montane scrub vegetation in the east-central Highlands of Scotland.

Below this limit, and almost down to sea-level, the community survives as scattered stands in a number of geographical groupings, within some of which it constitutes a major element of the vegetation cover. In considering zonations, it is important to distinguish between such expanses of 'pine forest', defined on broad landscape criteria and containing a wide variety of vegetation types, including many non-wooded ones, and the stands of the different kinds of *Pinus-Hylocomium* woodland which form part of the mosaic.

Zonations within stands of the *Pinus-Hylocomium* woodland, between one sub-community and another, are generally related to edaphic variation and/or the density of the tree cover. In some places, notably the Speyside and Deeside forests, transitions from the *Vaccinium* sub-community to the *Sphagnum-Erica* sub-community can be seen as one moves from drier podzols to peaty podzols, a change that is often related on a broad scale to a shift to higher altitudes with their wetter climate. And, here and in the south-western forests around the Great Glen, there can be zonations from these sub-communities to the *Luzula* type where the soils become moderately enriched over less extreme substrates or because of gentle flushing.

Gradations from the *Vaccinium* or *Luzula* sub-communities to the *Sphagnum-Erica* sub-community are also typically associated with a decrease in the density of the pine canopy and the effect of this can be seen, too, over more uniformly dry soils, where the *Erica-Goodyera* sub-community passes to the *Vaccinium* sub-community as the canopy thins out. Indeed, such changes can be precipitated by thinning, and, in semi-natural stands, may represent a seral progression (see below).

Where a general uniformity in soil conditions is maintained, continued reduction in the pine cover usually marks a gradual zonation to some kind of heath, typically various sub-communities of the *Calluna-Vaccinium* heath (the floristic composition of which is essentially a *Pinus-Hylocomium* woodland without the pine) or the *Calluna-Arctostaphylos uva-ursi* heath, quite often a mosaic of both where burning patterns have been complex (McVean & Ratcliffe 1962). Where the ground conditions are moister, a frequent feature among stands of the *Sphagnum-Erica* sub-community towards the wetter west, these dry heaths are replaced in this kind of sequence by the *Scirpus-Erica* wet heath, a very widespread community of thin ombrogenous peats and the fringes of valley mires in western Britain. On such wetter ground, growth of *P. sylvestris* is much poorer (Carlisle & Brown 1968), so the zonation is essentially an

edaphic one rather than a seral one, though drainage and fertilising has often artificially extended the range of pine on to such soils in Scotland (and, of course, elsewhere outside the natural range of the tree). Where such wet heath becomes wooded, *Betula pubescens* is usually the leading coloniser (often the only one) and extension of its canopy can lead to the development of stands of the *Betula-Molinia* woodland among the *Pinus-Hylocomium* woodland, a situation marked by a strong continuity in the field layer with species such as *Molinia caerulea*, *Erica tetralix* and Sphagna remaining prominent in both communities.

Transitions to even wetter ground in valley and basin mires, which are quite a common feature among the complex undulating topography of fluvioglacial deposits, involve the occurrence of small stands of base-poor communities like the *Carex echinata-Sphagnum* or *Carex rostrata-Sphagnum* mires, or, where these have been colonised by trees, the *Betula-Molinia* or *Salix-Carex* woodlands. Where there is a local influence of more base-rich waters, the *Pinguiculo-Caricetum* and *Carici-Saxifragetum* mires can be found, or their wooded equivalent the *Alnus-Fraxinus-Lysimachia* woodland. Within the areas where the *Pinus-Hylocomium* woodland is represented, all these different kinds of soil-related zonations can often be found within a relatively small compass, a feature which adds greatly to the overall diversity of the vegetation and contributes to the unique assemblage of communities which we include within the broader landscape definition of pine forest.

Over the range of soil types represented within what seems to be the natural range of *P. sylvestris* in Britain, it is probably able to colonise and attain dominance on a fairly broad spectrum of more freely draining brown earths, brown podzolic soils and podzols and, in such situations, its natural precursors are probably the various dry and wet heaths with which it can be found associated today. Where invasion has been observed, an initial slow start within the sub-shrub canopy, followed by some period of check through herbivore damage, has been succeeded by fairly rapid growth to produce vegetation resembling the *Erica-Goodyera* or *Vaccinium* sub-communities or, where the initial density of seedlings was more sparse, the *Sphagnum-Erica* type (McVean & Ratcliffe 1962). In some places, it is possible that the latter sub-community can develop from the former in a seral progression (McVean & Ratcliffe 1962), though it seems likely that there is some edaphic and climatic check on which direction succession takes: there may be two types of climax pinewood, one in the drier low-altitude eastern region, the other at higher altitudes there and in the wetter west.

What does seem certain is that, in the past, progressions to pine woodland involved a greater contribution from other tree species, notably birch and juniper, which continued to be well represented in mosaics of forest, at least in the eastern Highlands of Scotland. Now, we see some greater separation in the roles which these species play. Birch-dominated calcifugous forest (often with some oak, derived in part from planted stock) of the *Quercus-Betula-Dicranum* woodland, survives as distinct stands within the areas of pine forest and finds fragmentary representation in gaps, but it also seems to have sprung up widely on ground that mixed pine forest previously occupied. And the *Juniperus-Oxalis* woodland, though also represented among stands of the *Pinus-Hylocomium* woodland, now survives largely in isolation at higher altitudes. The original patchworks of mixed dominance may have been of some considerable importance in tempering the tendency towards podzolisation, birch and juniper being less active encouragers of mor than pine, and the greater extent of the forest cover must certainly have restricted the spread of *Calluna*, the abundance of which among the heaths of eastern Scotland may be very deleterious for any future expansion of pine.

Distribution

The *Pinus-Hylocomium* woodland is confined to Scotland and best represented in the central and north-western Highlands. Stands are fragmented into some major geographical groupings which also have some vegetational significance because they experience rather different climatic conditions and show different edaphic trends, features represented in the distribution of the various sub-communities. The *Erica-Goodyera*, *Vaccinium* and *Luzula* sub-communities are essentially types of the drier east, being well represented in the Speyside and Deeside forests, more sporadically on drier ground in the south-western forests of the Great Glen and around Rannoch. The *Erica-Goodyera* sub-community is also very common in young plantations around the Moray Firth. The *Sphagnum-Erica* sub-community, by contrast, is largely a type of wetter areas, being widespread to the south-west and in the Wester Ross forests, but also occurring at higher altitudes in Speyside and Deeside. The *Scapania* sub-community seems to be confined to the very wet parts of Wester Ross.

Pine plantations outside the native range of *P. sylvestris* are, in this scheme, considered as replacements of other woodland types, notably in southern England, the *Quercus-Betula-Deschampsia* woodland. In areas of higher rainfall, as in parts of Surrey, the floristic similarity between such stands and the drier types of *Pinus-Hylocomium* woodland is considerable, though the distinctive low-frequency preferentials of the community are absent. *Goodyera repens* and *Ptilium crista-castrensis* occur in pine plantations in East Anglia but are thought to have been introduced with pine stock from Scotland (Petch & Swann 1968).

Affinities

The *Pinus-Hylocomium* woodland unites the two kinds of pine woodland described by McVean & Ratcliffe (1962) and, though adding further data from plantations (largely in the *Erica-Goodyera* sub-community) and from more enriched soils (the *Luzula* sub-community), mostly originating from the surveys of Birse (1980, 1982, 1984; see also Birse & Robertson 1976), the scheme preserves the major distinction which they recognised in the contrasts between the two groups of sub-communities. Although there are clear floristic differences between these two groups (and related environmental, and perhaps seral, variations), the preferential species are rather few in number and it seems best to retain them within a single community. Certainly, it is not possible to separate the sub-communities unequivo-cally into more and less natural types (cf. Birse 1980, 1984). Despite the great deal of recent interest in this kind of woodland (e.g. Bunce & Jeffers 1977), detailed understanding of their floristics has not progressed far beyond the surveys of McVean & Ratcliffe (1962) and Birse (1980 *et seq.*) and the account of the individual forests and their geographical groupings still remains largely as Steven & Carlisle (1959) left it.

The *Pinus-Hylocomium* woodland belongs, together with the *Juniperus-Oxalis* woodland, to the Vaccinio-Picetea and is best placed within the Dicrano-Pinion alliance. Its nearest equivalent in Europe is to be found in the pine forests of western Norway where, in Scandinavian terms, the climate is relatively oceanic (Aune 1977).

Floristic table W18

	a	b
Pinus sylvestris	V (6–8)	V (6–8)
Betula pendula	II (1–5)	
Picea sitchensis	I (4–7)	
Larix spp.	I (3)	
Picea abies	I (1)	
Juniperus communis communis	I (1)	
Sorbus aucuparia	I (1)	
Betula pubescens		
Hylocomium splendens	V (5–9)	V (7–9)
Pleurozium schreberi	V (1–7)	V (1–7)
Dicranum scoparium	V (1–6)	V (1–5)
Calluna vulgaris	IV (1–8)	V (2–7)
Deschampsia flexuosa	III (1–5)	V (1–5)
Plagiothecium undulatum	II (1–6)	IV (1–5)
Vaccinium myrtillus	I (1–3)	V (5–8)
Rhytidiadelphus loreus	I (1)	V (1–5)
Vaccinium vitis-idaea		V (5–9)
Rhytidiadelphus triquetrus	IV (1–9)	V (1–7)
Pseudoscleropodium purum	III (3–5)	III (1–4)
Dicranum fuscescens		III (1–5)
Erica cinerea	IV (1–8)	I (2–4)
Goodyera repens	V (1–4)	II (1–3)
Pinus sylvestris seedling	II (1)	I (1)
Lepidozia reptans	II (1–2)	
Nardus stricta	I (1–3)	
Luzula pilosa	I (1)	
Galium saxatile	I (1)	I (1)
Oxalis acetosella	I (1)	

c	d	e	18
V (5–8)	V (5–7)	V (6–7)	V (5–8)
I (1)			I (1–5)
			I (4–7)
			I (3)
	I (1)		I (1)
I (2–6)			I (1–6)
	I (1–2)	I (5)	I (1–5)
	I (1)	II (1–5)	I (1–5)
V (2–9)	V (1–9)	V (5–8)	V (1–9)
V (1–6)	V (1–5)	V (3–5)	V (1–7)
V (1–4)	IV (1–3)	V (1–3)	V (1–6)
V (1–8)	V (1–8)	V (2–8)	V (1–8)
V (3–7)	IV (1–3)	V (2–5)	V (1–7)
IV (1–5)	IV (1–3)	IV (1–3)	IV (1–6)
V (3–9)	V (4–8)	V (6–8)	IV (1–9)
IV (1–8)	IV (1–5)	V (4–7)	IV (1–8)
V (2–9)	IV (3–8)	IV (3–5)	IV (2–9)
V (1–7)	I (4)		III (1–9)
III (1–4)	I (2–4)	I (2–4)	III (1–5)
III (1–3)		I (1)	II (1–5)
I (4)	II (1–4)	II (1–2)	II (1–8)
II (1–2)			II (1–4)
I (1)	I (1–5)		I (1–5)
I (1)			I (1–2)
			I (1–3)
V (1–4)			II (1–4)
III (1–6)		I (1–2)	I (1–6)
III (1–4)		II (2–4)	I (1–4)

Floristic table W18 *(cont.)*

	a	b
Sphagnum capillifolium/quinquefarium		II (1–4)
Dicranum majus	I (3)	II (1–3)
Pteridium aquilinum	I (1–3)	
Erica tetralix	I (1)	I (3)
Molinia caerulea		I (3–7)
Sphagnum girgensohnii		
Leucobryum glaucum		
Calypogeia trichomanis		
Bazzania trilobata		
Barbilophozia floerkei		
Calypogeia muellerana		
Sphagnum russowii		
Scapania gracilis		
Thuidium tamariscinum		
Diplophyllum albicans		
Anastrepta orcadensis		
Ptilium crista-castrensis	I (1)	IV (1–7)
Lophocolea bidentata s.l.	V (1–6)	III (1–3)
Hypnum jutlandicum	V (1–4)	II (1–3)
Melampyrum pratense		III (1–4)
Empetrum nigrum nigrum		IV (1–4)
Blechnum spicant		I (1)
Listera cordata	I (2)	I (1)
Polytrichum commune	I (1–4)	I (1–4)
Betula pubescens seedling	I (1)	I (1–4)
Festuca ovina	I (2)	
Aulacomnium palustre	I (2)	I (1)
Cladonia cornuta	I (1)	I (1)
Agrostis canina montana	I (1)	I (1–5)
Potentilla erecta		I (1–3)
Cladonia macilenta	I (1)	I (1)

c	d	e	18
I (1)	V (1–8)	V (4–8)	III (1–8)
I (3–4)	III (1–4)	V (1–5)	III (1–5)
I (1–2)	II (1–3)	II (1–4)	I (1–4)
II (1–2)	III (1–6)		II (1–6)
	II (1–8)		I (1–8)
	I (1–5)		I (1–5)
	I (1–4)		I (1–4)
	I (2–3)		I (2–3)
	I (1–3)		I (1–3)
	I (2–3)		I (2–3)
	I (1–3)		I (1–3)
	I (8)		I (8)
	II (1–3)	IV (1–2)	II (1–3)
I (1)	I (1–2)	III (1–3)	I (1–3)
		III (1–2)	I (1–2)
	I (3)	II (1–3)	I (1–3)
III (1–5)	III (1–9)	III (2–7)	III (1–9)
III (1–4)	III (1–3)	I (1)	III (1–6)
II (1–4)	II (1–4)	IV (2–3)	III (1–4)
IV (1–5)	II (1–2)	III (1–3)	III (1–5)
II (1–2)	IV (1–9)	II (1–3)	III (1–9)
III (1–4)	I (1–2)	III (1–3)	II (1–4)
I (1)	I (1–2)	I (1)	I (1–2)
I (1–4)	I (1–4)		I (1–4)
I (1)	I (1–2)		I (1–4)
I (4)	I (1–3)		I (1–4)
	I (1–4)		I (1–4)
	I (2)		I (1–2)
I (4)			I (1–5)
I (1–5)		I (2)	I (1–5)
			I (1)

Woodlands and scrub

Polytrichum juniperinum	I (1)	I (1)
Cladonia digitata	I (1)	
Trientalis europaea	I (1)	
Agrostis capillaris	I (1–3)	
Cladonia arbuscula	I (2)	
Hypnum cupressiforme		I (1)
Cladonia pyxidata		I (1)
Cladonia impexa		I (1)
Luzula multiflora		
Polytrichum formosum		
Campylopus paradoxus		

Number of samples	12	25
Number of species/sample	16 (12–21)	18 (14–20)
Tree height (m)	15 (9–21)	14 (9–20)
Tree cover (%)	50 (40–60)	48 (30–70)
Herb height (cm)	18 (3–46)	37 (12–70)
Herb cover (%)	25 (1–85)	75 (60–90)
Ground height (mm)	no data	no data
Ground cover (%)	94 (80–100)	80 (60–90)
Altitude (m)	93 (38–160)	342 (274–411)
Slope (°)	5 (0–16)	10 (0–35)

a   *Erica cinerea-Goodyera repens* sub-community
b   *Vaccinium myrtillus-Vaccinium vitis-idaea* sub-community
c   *Luzula pilosa* sub-community
d   *Sphagnum capillifolium/quinquefarium-Erica tetralix* sub-community
e   *Scapania gracilis* sub-community
18 *Pinus sylvestris-Hylocomium splendens* woodland (total)

			I (1)
I (1)			I (1)
I (1)			I (1)
I (1–4)			I (1–4)
	I (1–2)		I (1–2)
	I (1–2)		I (1–2)
	I (1)		I (1)
	I (1)		I (1)
I (1)	I (1–2)		I (1–2)
I (5)	I (2–5)		I (2–5)
I (2)	I (1–3)		I (1–3)
12	18	10	77
20 (16–29)	18 (12–29)	21 (18–24)	18 (12–29)
13 (6–18)	no data	15 (12–18)	14 (6–21)
49 (25–60)	no data	37 (30–45)	47 (25–70)
25 (10–60)	55 (30–65)	49 (10–100)	38 (3–100)
73 (40–95)	no data	67 (45–75)	63 (1–95)
no data	no data	no data	no data
73 (10–90)	no data	79 (60–90)	81 (10–100)
376 (229–465)	180 (16–390)	159 (30–250)	260 (16–465)
12 (2–25)	5 (0–20)	21 (8–33)	10 (0–35)

W18 *Pinus sylvestris-Hylocomium splendens* woodland

W18 *Pinus sylvestris-Hylocomium splendens* woodland

a *Erica cinerea-Goodyera repens* sub-community

W18 *Pinus sylvestris-Hylocomium splendens* woodland

b *Vaccinium myrtillus-Vaccinium vitis-idaea* sub-community

W18 *Pinus sylvestris-Hylocomium splendens* woodland

c *Luzula pilosa* sub-community

W18   *Pinus sylvestris-
Hylocomium splendens*
woodland

d   *Sphagnum capillifolium/
quinquefarium*
sub-community

W18   *Pinus sylvestris-
Hylocomium splendens*
woodland

e   *Scapania gracilis*
sub-community