W19
Juniperus communis ssp. *communis-Oxalis acetosella* woodland

Synonymy
Birch-juniper wood Tansley 1939; Juniper heath Pigott 1956*a*; Juniper scrub Poore & McVean 1957; *Juniperus-Thelypteris* nodum McVean & Ratcliffe 1962; Fern-rich juniper scrub McVean 1964*a*; *Thelypterido-Juniperetum* Graham 1971; *Juniperus-Vaccinium* nodum Huntley & Birks 1979*a*; *Juniperus-Campanula* nodum Huntley & Birks 1979*a*; *Trientali-Juniperetum* Birse 1980; *Trientali-Betuletum pendulae* Birse 1982 *p.p.*

Constant species
Juniperus communis ssp. *communis*, *Agrostis canina* ssp. *montana*, *A. capillaris*, *Galium saxatile*, *Luzula pilosa*, *Oxalis acetosella*, *Vaccinium myrtillus*, *Hylocomium splendens*, *Thuidium tamariscinum*.

Rare species
Linnaea borealis, *Orthilia secunda*, *Potentilla crantzii*, *Pyrola media*.

Physiognomy
Juniperus communis ssp. *communis* is always the most abundant woody species in this community, though some stands have an open over-canopy of birch, almost invariably *Betula pubescens* and usually ssp. *carpatica*, with multi-stemmed trees typically less than 10 m high and showing bushy, contorted growth (Forbes & Kenworthy 1973, Huntley & Birks 1979*a*; Birse 1980, 1982). Increased amounts of birch, over juniper and the associated flora here, generally mark transitions to the *Quercus-Betula-Dicranum* woodland or, on somewhat less acidic and more fertile soils, the *Quercus-Betula-Oxalis* woodland. Such transitions often take the form of ill-defined mosaics (a feature especially well seen in the east-central Highlands of Scotland: Ratcliffe 1977, Huntley & Birks 1979*a, b*) and then separation of the different communities may be a question of the proportions of the two woody species. Similar problems can arise with *Pinus sylvestris*, which can occur here as isolated trees up to about 15 m tall, but which thickens up considerably in zonations to the *Pinus-Hylocomium* woodland.

The cover and physiognomy of the *Juniperus* itself here are rather variable. Very widely scattered bushes within a heathy or grassy context would not qualify for inclusion in this woodland type, but many stands have less than 60% cover of juniper and extensive stretches of a closed canopy are rather exceptional: the usual picture is of a patchy cover with some more open areas and others where the bushes form a virtually impenetrable thicket. The individual bushes themselves are also of very diverse form: in some stands, low plants with decumbent branches reaching little more than a metre predominate; in others, pyramidal, conical or narrow, cylindrical forms are in the majority, occasionally attaining 5 m in height. Some of this variation has a genetic basis, the distinctive characters persisting in cultivation, but bushes also change shape with age, innermost branches often being killed by self-thinning and older bushes tending to fall open. Exposure also has some effect on growth-form and this can sometimes be seen in relation to altitude: in both Scottish sites and in Teesdale, bushes at lower levels are taller, those in the highest situations sometimes as low as 50 cm (Ratcliffe 1977, Gilbert 1980). And grazing and browsing by stock and deer can also affect the canopy physiognomy, restricting the height of the bushes and opening up denser covers, in extreme cases leaving the juniper looking very straggly and moribund (Huntley & Birks 1979*a*, Gilbert 1980). Fungal attack has also been noted on sickly or dying bushes in Teesdale, with needle cast (*Lophodermium juniperinum*) and purple-shoot fungus (*Phomopsis* sp.) especially prevalent (Gilbert 1980). Where juniper populations in this community have been aged (a difficult procedure because of the often numerous, eccentric boles, which can rot with age), both even- and uneven-aged stands have been detected and old individuals, exceeding 100 years, encountered (Malins-Smith 1935, Kerr 1968, Gilbert 1980). In some stands,

young junipers are decidedly scarce (Pigott 1956*a*, Gilbert 1980).

The other major elements in this kind of woodland are ericoids, ferns, herbs and bryophytes. *Vaccinium myrtillus* is the commonest sub-shrub with *V. vitis-idaea* and *Calluna vulgaris* somewhat less frequent, but the prominence of all three is very much affected by the evergreen shade of the juniper and by soil differences and grazing. *Calluna* especially is strongly limited by shade, *V. vitis-idaea* somewhat less so, *V. myrtillus* least of all, but the fairly dense growth of even isolated, younger juniper bushes generally confines all of them to the areas between, where they occur in various mixtures in a sub-shrub canopy that can attain half a metre or more in height. All of these species are more common and abundant on the more acidic soils of the *Vaccinium-Deschampsia* sub-community but, throughout, the prominence of *V. myrtillus* and *Calluna* can be greatly reduced by herbivores, shifting the balance of dominance in this layer of the vegetation.

Very often, the other physiognomically prominent element in this kind of woodland comprises ferns. None of these is itself constant but usually two or more are well represented and together they give the vegetation a very striking character. Commonest among them is *Blechnum spicant* but more distinctive, and often more abundant, is *Gymnocarpium dryopteris* and, somewhat less frequent, *Thelypteris phegopteris*. *T. limbosperma* can also be found and there are occasional records for *Pteridium aquilinum*, *Dryopteris dilatata* and *D. filix-mas*. Some of these species are demanding of a certain amount of shelter and shade and all of them seem to thrive best here among fairly close set, but not too densely crowded, juniper where there is probably also some protection from herbivores.

Between these bulkier components of the vegetation, there is distributed a fairly rich assemblage of herbs, forming a discontinuous but, in less heavily grazed stands, quite luxuriant sward. Among the grasses, *Agrostis capillaris* and *A. canina* ssp. *montana* are constant and *Anthoxanthum odoratum* is occasional to frequent, and each or all of these can be abundant in particular stands. Also common, but preferential for different kinds of *Juniperus-Oxalis* woodland, are *Deschampsia flexuosa* (more frequent on the more acidic soils of the *Vaccinium-Deschampsia* sub-community) and *Festuca ovina*, *F. rubra* and *Holcus mollis* (all encountered more often on the more fertile soils of the *Viola-Anemone* sub-community). In moister situations, there can be a little *Deschampsia cespitosa*. Another very common monocotyledon in the community, though generally not very abundant, is *Luzula pilosa*, and *L. multiflora* can also sometimes be found. *Carex pilulifera* and *C. binervis* occur occasionally and, where there is some base-enrichment, *C. flacca*.

The most frequent dicotyledons of this kind of woodland are *Oxalis acetosella*, *Galium saxatile*, *Potentilla erecta* and the Northern Montane *Trientalis europaea*, especially common in the centre of the range of the community in eastern Scotland but some of whose more far-flung localities are in stands of *Juniperus-Oxalis* woodland. *Veronica officinalis* occurs occasionally and *Melampyrum pratense* is sometimes found and, then, on the more fertile soils of the *Viola-Anemone* sub-community, there is a consistent enrichment of this element with an increased frequency of *Viola riviniana*, *Anemone nemorosa*, *Campanula rotundifolia*, *Cardamine flexuosa* and numerous less common preferentials and differentials. Other species of more restricted distribution in Britain which have been recorded in the community include the Northern Montane *Listera cordata*, *Rubus saxatilis* and *Linnaea borealis* and the Continental Northern *Pyrola minor*, *P. media* and *Orthilia secunda*.

Bryophytes almost always make a prominent contribution to the vegetation, often forming a patchy carpet among the herbs and extending into the centres of the more open ericoids and junipers. The most frequent species are *Hylocomium splendens* and *Thuidium tamariscinum* with *Pseudoscleropodium purum*, *Rhytidiadelphus squarrosus*, *Lophocolea bidentata s.l.*, *Dicranum scoparium* and *Plagiochila asplenoides* (including var. *major*) also very common, *Plagiomnium rostratum*, *Mnium hornum*, *Polytrichum formosum*, *P. commune*, *Plagiothecium denticulatum*, *Hypnum jutlandicum* and *Ptilium crista-castrensis* occasional. Then, there are distinctive suites of preferential species in each of the sub-communities, with more marked calcifuges like *Plagiothecium undulatum*, *Rhytidiadelphus loreus*, *Dicranum majus* and *Pleurozium schreberi* becoming more frequent in the *Vaccinium-Deschampsia* sub-community, *Rhytidiadelphus triquetrus*, *Plagiomnium undulatum* and *P. affine* occurring more commonly in the *Viola-Anemone* sub-community.

Sub-communities

***Vaccinium vitis-idaea-Deschampsia flexuosa* sub-community:** Juniper heath Pigott 1956*a*; Juniper scrub Poore & McVean 1957; *Juniperus-Thelypteris* nodum McVean & Ratcliffe 1962; Fern-rich juniper scrub McVean 1964*a*; *Thelypterido-Juniperetum*, Sub-association of *Lophozia* and *Campylopus* Graham 1971; *Juniperus-Vaccinium* nodum Huntley & Birks 1979*a*; *Trientali-Juniperetum*, Typical sub-community Birse 1980; *Trientali-Betuletum*, *Vaccinium vitis-idaea* Subassociation Birse 1984 *p.p.* This sub-community includes the more heathy and calcifugous stands of the *Juniperus-Oxalis* woodland in which there is often a rather open cover of juniper bushes, an abundance of

ericoid sub-shrubs and an enriched suite of bryophytes growing luxuriantly over the accumulations of mor. *Vaccinium myrtillus*, though a constant throughout the community, is more frequent here than in the *Viola-Anemone* sub-community and often markedly more abundant, but better preferentials at most sites are *V. vitis-idaea* (not in Teesdale) and *Calluna vulgaris*, the former especially often rivalling or exceeding *V. myrtillus* in cover. Ferns can be prominent here among the woody species and the constant and frequent herbs of the community are all well represented. Indeed, among the vascular plants, only *Deschampsia flexuosa* is preferential to this sub-community: it becomes constant here and is often an abundant element in the grassy sward. A distinctive feature of this kind of *Juniperus-Oxalis* woodland in Morrone Birkwoods is a spatial patterning built around a hummock-hollow topography, with the ericoids largely confined to the tops of the hummocks which have a highly organic soil, the herbs growing on the less humic profiles of the hollows (Huntley & Birks 1979*a*). The cause of this physiography is unknown: it has been suggested that it might have developed from the wind-throw of trees which have now disappeared, though Huntley & Birks (1979*a*) noted that at least some of the hummocks were former nests of the wood-ant, *Formica lugubris*. Perhaps a more likely explanation in view of the harshness of the climate is that the hummocks are the product of frost-heaving (Cotton 1968).

Apart from the prominence of ericoids, it is bryophytes which give this sub-community its distinctive character. *Dicranum scoparium* increases in frequency here but much stronger preferentials are *Plagiothecium undulatum*, *Rhytidiadelphus loreus*, *Pleurozium schreberi*, *Hypnum cupressiforme* (including *H. jutlandicum*) and *Dicranum majus*. *Lophozia ventricosa* and *Scapania gracilis* occur occasionally and, growing epiphytically over decumbent, litter-clothed trunks, Graham (1971) reported an abundance of *Campylopus paradoxus* and *Barbilophozia floerkii*.

***Viola riviniana-Anemone nemorosa* sub-community:** *Thelypterido-Juniperetum*, Typical sub-association Graham 1971; *Juniperus-Campanula* nodum Huntley & Birks 1979*a*; *Trientali-Juniperetum*, *Anemone* sub-community Birse 1980. The juniper canopy in this sub-community tends to be consistently denser than above, though a sparser cover of ericoid sub-shrubs between the bushes means that the vegetation can look more open. In fact, of the ericoids, *V. myrtillus* remains very frequent here, though its cover is usually very low, with just a few sparse shoots or widely-scattered bushes; *V. vitis-idaea* and *Calluna* are reduced in both frequency and abundance, occurring only occasionally and then typically in small amounts.

Grasses figure prominently in the sward between the juniper bushes and, along with the community species, *Agrostis capillaris*, *A. canina* ssp. *montana* and *Anthoxanthum odoratum*, three good preferentials become frequent: *Festuca ovina*, *F. rubra* and, a little less common, *Holcus mollis*. *Deschampsia flexuosa*, by contrast, is scarce and only rarely abundant. The shift towards a flora of less markedly acidic, dry and impoverished soils can be seen, too, among the dicotyledons. Here *Viola riviniana* and *Anemone nemorosa* are especially good markers: these species are, at most, occasional in the *Vaccinium-Deschampsia* sub-community while here they are a constant, and in the case of *Anemone* sometimes abundant, element in the field layer. Less frequent, though also strongly preferential, are *Campanula rotundifolia*, *Cardamine flexuosa*, *Cerastium fontanum*, *Urtica dioica*, *Stellaria holostea*, *Fragaria vesca*, *Galium boreale* and *Adoxa moschatellina*. Other species recorded more occasionally include *Prunella vulgaris*, *Galium verum*, *Potentilla sterilis*, *Epilobium montanum* and *Lathyrus montanus* and, very exceptionally, where there is more marked base-enrichment, there can even be some *Mercurialis perennis* or *Carex flacca*. In more heavily grazed stands, many of these plants only attain any degree of luxuriance where there is some local protection against herbivores: with the ferns of the community, they tend therefore to be most marked within rings of juniper bushes or in the centre of older individuals that have begun to open out. In such situations on moister soils at Morrone, Huntley & Birks (1979*a*) also noted tall herbs such as *Cirsium helenioides*, *Geranium sylvaticum*, *Filipendula ulmaria* and *Trollius europaeus*.

Bryophyte cover remains high here, though there are some marked changes in the species represented. The mosses and hepatics typical of the community all remain frequent but more calcifugous species characteristic of the *Vaccinium-Deschampsia* sub-community become, at most, occasional. On the positive side, there is a marked increase in the occurrence of *Rhytidiadelphus triquetrus* and *Plagiomnium undulatum* and occasional records for *P. affine*, *Cirriphyllum piliferum*, *Drepanocladus uncinatus*, *Barbilophozia barbata* and *Isothecium myurum*.

Habitat

The *Juniperus-Oxalis* woodland is a community of high altitudes, mostly within the colder and relatively dry parts of north-west Britain. It occurs on quite a wide variety of soils and edaphic differences, together with grazing and browsing, have important influences on the floristics of the vegetation. Although the community has some claim to represent climax montane scrub, its present prominence at some sites may be due to the destruction of a tree canopy in which pine and birch probably figured abundantly.

The centre of distribution of the *Juniperus-Oxalis* woodland lies within the east-central Highlands of Scot-

land where the climate has a distinctly continental character (Ratcliffe 1968, Green 1974). Rainfall is low for these latitudes with only 800–1200 mm yr^{-1} (*Climatological Atlas* 1952) or about 160 wet days yr^{-1} (Ratcliffe 1968) and annual accumulated temperatures are within the range 280–550 °C (Page 1984) with the lowest February minima of any part of the country. Snowfall totals are moderate but morning snow-lie occurs on more than 60 days yr^{-1}, late frosts are very frequent and the mean annual maximum temperature is below 23 °C (Conolly & Dahl 1970, Huntley & Birks 1979*a*). None of these variables seems to be of direct importance in the actual favouring of the prominence of juniper itself, but the cold, dry nature of the climate has a clear influence on the associated flora: this is seen in the presence of Northern Montane plants, especially *Trientalis europaea* but also the less frequently recorded *Rubus saxatilis*, *Trollius europaeus* and the very rare *Linnaea borealis*, the Continental Northern wintergreens, *Galium boreale* and *Cirsium helenioides* and the Arctic-Alpine *Polygonum viviparum* and *Potentilla crantzii*. None of these species is confined to this community: *Trientalis* in particular is characteristic of eastern Scottish stands of a number of woodland types and the less basiphilous of the very rare plants among them are more frequent in the *Pinus-Hylocomium* woodland. But, taken together, they give our northern stands of juniper a very different look from the vegetation in which this tree dominates in the south-eastern lowlands; moreover, some of the more southerly stations of certain of these species, in Northumberland and the Pennines, occur in association with juniper in stands of this community (e.g. Pigott 1956*a*).

The *Juniperus-Oxalis* woodland has been recorded in the available samples at altitudes between 300 and 650 m. Towards the upper part of this range, harsh climatic conditions may also play a part in excluding some of the other woody dominants which, at lower levels, are commonly found over the associated flora characteristic here. This would certainly be true of oak (which is, in any case, rather uncommon in semi-natural woods in eastern Scotland: McVean & Ratcliffe 1962) and probably of *Betula pendula* and perhaps also *B. pubescens* ssp. *pubescens* (Forbes & Kenworthy 1973); and, at the very highest altitudes, as on Creag Fhiaclach in the Cairngorms, it may be true also of *Pinus sylvestris* (McVean & Ratcliffe 1962, Carlisle & Brown 1968). In extreme situations, then, the *Juniperus-Oxalis* woodland may be a climatic climax community; at lower levels, it is probably a seral scrub which, for the most part, does not progress to mature forest for quite other reasons.

Throughout this altitudinal range, the *Juniperus-Oxalis* woodland can be found on a wide variety of soils. What the profiles have in common is that they are free-draining, being derived in most cases from pervious bedrocks or coarser-textured superficials. However, though the community typically avoids gleyed soils, the profiles are never drought-prone with the moderately high rainfall they receive and are often kept quite moist by a moderate amount of flushing or by virtue of a northerly aspect (McVean & Ratcliffe 1962, Huntley & Birks 1979*a*): a striking contrast to the frequently parched conditions which juniper favours in its southern lowland localities. Freedom from dryness plus good aeration, combined with the effect of the only moderately acid litter of juniper, all help maintain a humus regime which is not of the extreme mor type and in which there is probably quite an active and speedy incorporation and nutrient turnover. This is reflected in the floristics of the community as a whole in features like the constancy of *Oxalis acetosella* (Packham 1978), the prominence of ferns like *Gymnocarpium dryopteris* and *Thelypteris phegopteris* (Page 1982) and the frequency throughout of less demanding calcifuge herbs such as *Agrostis capillaris* and *Luzula pilosa* and bryophytes like *Hylocomium splendens*, *Thuidium tamariscinum*, *Rhytidiadelphus squarrosus*, *Pseudoscleropodium purum*, *Plagiomnium rostratum* and *Plagiochila asplenoides*.

Nonetheless, there is always a tendency to surface eluviation of the soils here and more demanding species such as *Vaccinium myrtillus*, *Galium saxatile* and *Agrostis canina* ssp. *montana* retain a frequent representation throughout. And, where the parent materials are more siliceous, as over quartzites, gneisses or rhyolites or on sandy superficials, or where there is no influence of flushing with more base-rich waters, this potential is fully realised in the development of strongly podzolised profiles. On such soils, the *Vaccinium-Deschampsia* subcommunity is characteristic with its much more obvious calcifuge elements: an abundance of ericoid sub-shrubs, frequent records for *Deschampsia flexuosa* and a prominent contribution from more exacting bryophytes. In such stands, the flora of the *Juniperus-Oxalis* woodland takes on much of the character of the *Pinus-Hylocomium* or *Quercus-Betula-Dicranum* woodlands and, as there, more open covers of trees may favour podzolisation by permitting the spread of *Calluna* and the accumulation of substantial amounts of mor.

In other situations, various factors can offset the tendency towards surface leaching, most notably the local occurrence of more calcareous bedrocks or superficials, or seepage from them of base-rich waters. The effects of such variation are well seen in the east central Highlands where schists and limestones occur within the Dalradian and Moine meta-sediments (Ratcliffe 1977, Huntley & Birks 1979*a*), in the Lake District where andesites are found among the Borrowdale Volcanics (Pearsall & Pennington 1973), in Teesdale where there is seepage from Carboniferous Limestone into soils derived from Whin Sill dolerite and its drift (Pigott 1978*b*) and in scattered localities on Silurian and Carboniferous

shales where limy partings are interbedded. Where the effects of such variation prevail, the profiles tend towards the brown earth type with much better incorporation of mull-like humus and a rise in surface pH (from about pH4 to pH6, limited data from Morrone suggest: Huntley & Birks 1979*b*). On such soils, the *Viola-Anemone* sub-community is the characteristic type of *Juniperus-Oxalis* woodland, with a fading contribution from strongly calcifuge sub-shrubs, *D. flexuosa* and bryophytes, and a preferential rise in frequency of species indicative of less acidic and more fertile soils: *Viola riviniana* and *Anemone nemorosa* themselves, grasses like *Festuca rubra* and *Holcus mollis*, dicotyledons such as *Campanula rotundifolia*, *Cerastium fontanum*, *Cardamine flexuosa* and even *Urtica dioica*, and bryophytes like *Plagiomnium undulatum*, *P. affine* and *Cirriphyllum piliferum*. Then the vegetation comes to resemble closely the flora found occasionally on less extreme soils in the *Pinus-Hylocomium* and *Quercus-Betula-Dicranum* woodlands but much more consistently associated with the *Quercus-Betula-Oxalis* woodland, the major oak- and birch-dominated forest of brown earths in the north-western parts of Britain. And when plants such as *Adoxa moschatellina*, *Mercurialis perennis*, *Cirsium helenioides* and *Geranium sylvaticum* appear in sites where there is a more pronounced rise in the base-richness and calcareous character of the soils within the *Viola-Anemone* sub-community the field layer comes close to that found under mixtures of *Fraxinus excelsior*, *Betula pubescens* and *Corylus avellana* in the *Fraxinus-Sorbus-Mercurialis* woodland.

Edaphic variation on a combined axis of base-richness and fertility can account for most of the floristic differences between the sub-communities but its effects are overlain and confused by the influence of grazing and browsing. Most of the stands of the *Juniperus-Oxalis* woodland appear to be open to large herbivores, occurring as part of unenclosed upland, within areas used as sheep ranges and with unhindered access for deer; at lower altitudes, cattle are sometimes pastured and, locally, horses (Ratcliffe 1977, Huntley & Birks 1979*a, b*; Gilbert 1980). And, as in the south-eastern lowlands (e.g. Ward 1973, Fitter & Jennings 1975), rabbits could be important in some sites.

As in other kinds of north-western woodlands, the general effects of grazing and browsing of the field layer are to reduce the cover of the palatable ericoids, *Vaccinium myrtillus* and *Calluna*, and of many of the ferns and dicotyledons and to favour the spread of tillering grasses and of the bryophytes which benefit indirectly by the reduction of competition. The impact of such developments can be seen in both sub-communities in a transformation of lush and varied scrub into what is, in effect, a grassland with juniper bushes; and, because grazing and browsing tend to have their most obvious effects on the preferentials of the two sub-communities, herbivore predation tends to favour a floristic convergence of the two kinds of *Juniperus-Oxalis* woodland. In the *Vaccinium-Deschampsia* sub-community, the less palatable *V. vitis-idaea* may persist in some abundance to give an obvious clue as to the affinities of the vegetation but, in some cases, careful scrutiny of the closely-cropped sward and its bryophyte mat is required to distinguish which species remain.

Compared with, say, *V. myrtillus*, juniper itself is not a very palatable plant and, indeed, can confer some measure of protection on more favoured species growing within rings of bushes or in the centre of older individuals that have begun to open out. But browsing by deer and, when they are sufficiently abundant, by sheep or cattle, has a clear effect on the physiognomy of bushes that are within reach: in more open stands, especially where the juniper is of lower stature, all the bushes may be accessible; in denser stands or where the juniper is taller, only the marginal individuals or lower branches can be browsed (e.g. Huntley & Birks 1979*a*, Gilbert 1980). In extreme cases, it seems likely that deer and stock can actually open up thicker stands and perhaps even eliminate the juniper; and, where horses browse, a rare occurrence but recorded in Teesdale (Gilbert 1980), bushes can be killed by gnawing of the bark.

Furthermore, by grazing out seedlings and young plants of juniper, herbivores can probably play a large part in controlling regeneration and help determine the eventual number and density of the bushes. The scarcity of established young junipers in stands of this community was commented on by Pigott (1956*a*) and Gilbert (1980) and, though the latter noted some losses from erosion, burning, fungal attack and the exceptional drought of 1976, monitoring of individual plants and enclosure showed conclusively that herbivores were a very important cause of destruction. These observations were confined to Teesdale and, as Huntley & Birks (1979*b*) stated, we are in urgent need of data on the exact impact of grazing and browsing on this vegetation in the centre of its distribution in Scotland. For the moment, the work of Gilbert (1980) and studies on southern juniper scrub (Ward 1973, Fitter & Jennings 1975) suggest that simple reduction or withdrawal of grazing may not itself be sufficient to ensure regeneration. Juniper seed is quite widely dispersed by birds, though Gilbert (1980) noted that excreted seeds were often eaten, probably by the woodmouse *Apodemus sylvaticus*. And germination seems to be achieved only with some difficulty (Miles & Kinnaird 1979).

Also of great importance is that establishment requires either bare ground or a short sward, where there is freedom from shade, conditions which are maintained by the disturbance and cropping that herbivores them-

selves provide (Ward 1973, Fitter & Jennings 1975). As with birch then (Pigott 1983), regeneration may thus depend more on the sudden relaxation of grazing than on the maintenance of continuously low herbivore numbers. This may account for the occurrence of markedly even-aged stands of juniper in this community and the persistence of many of the Teesdale stands around farms and on the boundaries between the in-by and out-by land where fluctuations in grazing intensities would be most strongly felt. Indeed, Gilbert (1980) went further than this observation with the interesting suggestion that the survival of the *Juniperus-Oxalis* woodland in Teesdale and parts of Northumberland, and perhaps also in the Lake District, was related to the dual economy of farming and mining over the past few centuries, with its erratic variation in the rigour with which the land was pastured. Miles & Kinnaird (1979) also pointed out that, like the *Pinus-Hylocomium* woodland, this community may be partly dependent on the occurrence of burning for the regeneration of its juniper cover: at Tynron in Dumfries, an accidental fire stimulated the first regeneration seen for many years, but subsequent attempts to encourage regeneration using various other techniques failed (Kerr 1968). Patchy burning of juniper was used by farmers as a means of limiting its encroachment on upland grazing land and, in the past, this may actually have ensured its perpetuation.

In Teesdale, juniper was cut until the early part of this century to provide firewood and large boughs were used as a base for making haystacks (Gilbert 1980). Such use may have been widespread and account for some of the present restriction of this community to more scattered sites towards the south of its range. But perhaps of more obvious importance to the present appearance of this vegetation is that, at lower altitudes at least, it may have lost a cover of other tree species by a combination of timber removal, burning and grazing. Part of the evidence for this is circumstantial: it is that the *Juniperus-Oxalis* woodland survives over a wide range of soil types which one would expect, in the more hospitable situations, to carry mixtures of pine and birch with rowan and, in more fertile sites at the lowest altitudes, perhaps a little ash and oak. But such a view receives strong support from palynological evidence, at least in the east-central Highlands, where just such a mixed pine-birch-juniper forest seems to have persisted from Boreal times until a few centuries ago (e.g. Birks 1970, O'Sullivan 1977). Juniper still figures in this region as an understorey component in other woodland types but, for the most part, the original mixed forest cover has been segregated out into remnants of *Pinus-Hylocomium* woodland and birch-dominated *Quercus-Betula-Dicranum* and *Quercus-Betula-Oxalis* woodlands, many stands of which seem to be fairly young sub-spontaneous developments on neglected land. In other places, juniper remains as the woody dominant in *Juniperus-Oxalis* woodland, in effect a relic understorey, stabilised by grazing and into which there has been no sustained re-invasion of trees.

Zonation and succession

Zonations between the two sub-communities of the *Juniperus-Oxalis* woodland are most frequently a reflection of edaphic variation. Soil differences are involved, too, in transitions from the community to other vegetation types but, throughout, grazing, burning and timber removal have confused these patterns. Complex treatment histories also make it difficult to see how the community relates to other vegetation types in seral sequences and in natural altitudinal zonations of climax communities.

Soil variations within stands of the *Juniperus-Oxalis* woodland are generally related to differences in parent materials or the degree of flushing, with the *Vaccinium-Deschampsia* sub-community typically giving way to the *Viola-Anemone* sub-community wherever there is an increase in base-richness and fertility. Sometimes, as where there is an abrupt and marked shift in bedrock type, the edaphic and vegetational contrasts are sharp; often, especially where the community occurs over heterogenous superficials or experiences diffuse flushing, the change is a much more gradual one, manifest in ill-defined mosaics rather than clear zonations, a feature very well seen over the complex geology of the Morrone Birkwoods (Huntley & Birks 1979*a*, *b*).

Often, now, the landscape context of stands of the *Juniperus-Oxalis* woodland is one dominated by various types of heath or grassland and, at lower altitudes, it is clear that the vegetation pattern is strongly related to biotic factors, partly deer-grazing but also various kinds of human interference. Nonetheless, zonations often preserve a measure of edaphic control. For example, transitions to *Vaccinium-Deschampsia* heath sometimes reflect an obvious move to drier and more strongly podzolised profiles, a switch which is sometimes related to the occurrence of highly siliceous parent materials or a complete waning of any impact of flushing with base-rich waters (e.g. Huntley & Birks 1979*a*). In other cases, this type of soil and vegetation zonation is a reflection of slope and aspect: in the east-central Highlands, the *Juniperus-Oxalis* woodland sometimes marks out damp hollows and north-facing slopes in tracts of heather moorland (McVean & Ratcliffe 1962). In the opposite direction, on free-draining soils which are increasingly base-rich and calcareous, the community typically passes to some kind of calcicolous sward, often preferentially grazed by deer and stock because of its nutritious bite. On limestone or schist outcrops in the Dalradian and Moine rocks of eastern Scotland, such zonations

usually involve the *Festuca-Agrostis-Thymus* grassland (e.g. Huntley & Birks 1979*a*); in Teesdale, with the switch from intruded Whin Sill dolerite to Carboniferous Limestone, the *Sesleria-Galium* grassland is represented (e.g. Pigott 1956*a*, Graham 1971, Gilbert 1980).

In situations such as these, the *Juniperus-Oxalis* woodland occupies the moister sites, where aspect or seepage prevent the development of excessively-draining soils. In other cases, as where heavy-textured superficials dominate among the parent materials, it may mark out better-drained areas, passing to various kinds of mires in hollows where there is ground-water gleying or a strong influence of soligenous waters. At Morrone, for example, a complex of flush communities occurs among the *Juniperus-Oxalis* woodlands with *Pinguiculo-Caricetum* mire figuring prominently in more base-rich situations, the *Scirpus-Erica* wet heath in the more base-poor (Huntley & Birks 1979*a*).

In the absence of enclosure experiments or any sustained observations on the effects of burning within such sequences as these, it is difficult to know how far the limits of the *Juniperus-Oxalis* woodland are natural. However, waterlogging is strongly inimical to juniper, so the absence of the community from more hydromorphic soils probably represents a real edaphic boundary though, if there were no grazing, one might expect the *Juniperus-Oxalis* woodland to give way to mire scrub or forest in such situations, perhaps the *Alnus-Fraxinus-Lysimachia* woodland in more base-rich places or the *Salix-Carex* woodland in the less. On drier soils, grazing and burning have almost certainly reduced the extent of the community, the former favouring an extension of grasslands, the latter, especially on more base-poor profiles, encouraging a spread of heaths, and especially the dominance of *Calluna*. In many sites, the composition of the *Vaccinium-Deschampsia* heath adjacent to the community is very similar (essentially it is often *Juniperus-Oxalis* woodland without the juniper) and the balance between ericoids and juniper in the invasion process after burning may be quite a fine one.

Information on the precise effects of burning and herbivore predation is urgently needed for the sensitive conservation of this community. It would also enable us to see something of the seral processes in which juniper is involved and to assess the successional status of the community. To the north of its British range, juniper obviously colonises and maintains itself on a much broader spectrum of soil types than is the case in the southern lowlands and, in more natural circumstances, the community may develop along a number of seral pathways. Early invasion of very open habitats with fragmentary soils could be the normal mode of establishment for this light-demanding tree, in which case its colonisation of existing ungrazed herbaceous vegetation might depend on erosion on steeper slopes or clearance of the ground by spontaneous fires (e.g. Fitter & Jennings 1975, Miles & Kinnaird 1979). Over rocky ground and on ledges, juniper can also invade coincidentally with ferns, ericoids and tall herbs, occasionally finding a place in vegetation types like the *Luzula-Vaccinium* and *Luzula-Geum* communities (McVean & Ratcliffe 1962, Huntley & Birks 1979*a*). These ungrazed communities show a considerable floristic overlap with the *Juniperus-Oxalis* woodland, the former, characteristic of more base-poor rocks, resembling the *Vaccinium-Deschampsia* sub-community, the latter, typical of more base-rich situations, sharing many species with the *Viola-Anemone* sub-community. Where juniper is able to overtop the associates, it essentially converts the vegetation to the *Juniperus-Oxalis* woodland, though stands on ledges are very fragmentary.

Subsequent developments probably depend on a number of factors. In theory, one would expect stands at lower altitudes to progress to forest dominated by pine and/or birch, with the *Vaccinium-Deschampsia* sub-community on more acidic, impoverished soils moving to the *Quercus-Betula-Dicranum* or *Pinus-Hylocomium* woodlands, the *Viola-Anemone* sub-community on more base-rich and fertile soils to the *Quercus-Betula-Oxalis* woodland or the *Luzula* sub-community of the *Pinus-Hylocomium* woodland. In some places, the different kinds of *Juniperus-Oxalis* woodland can be seen in gaps within these other woodland types, the field layers showing considerable continuity. In fact, re-invasion of junipers and ericoid-dominated covers is very difficult for both pine and birch, because they are light-demanding, and with pine there is the additional problem of rather erratic fruiting and a less efficient wind-dispersal of seed than is the case with birch (Carlisle & Brown 1968, Carlisle 1977). Grazing can open up the ground but destroys seedlings; burning without grazing may be more effective but tends to allow *Calluna* to invade first; and widespread removal of timber, especially common and more critical with pine, has reduced the number of seed-parents. Just such a combination of factors seems to have converted the original patchwork of pine, birch and juniper forests in the east-central Highlands to the pattern of woodland fragments among extensive tracts of heath and grassland that we see today (e.g. McVean & Ratcliffe 1962, O'Sullivan 1977).

Widespread forest destruction has also left very few places where the *Juniperus-Oxalis* woodland can be seen as a convincing altitudinal replacement for sub-montane forest: the best site is probably Creag Fhiaclach where the community forms a scrubby fringe between the *Pinus-Hylocomium* woodland and montane heath (McVean & Ratcliffe 1962). Elsewhere, though, the *Juniperus-Oxalis* woodland does persist as a fragmentary belt above a wide zone now largely converted to heath and grassland (Watt & Jones 1948, Poore & McVean 1957, McVean & Ratcliffe 1962). In such

situations as these, the community occupies an analogous position to the juniper scrub of the 'lower-alpine' zone in Scandinavia (Du Rietz & Du Rietz 1925, Nordhagen 1943). As there, though in much more fragmentary fashion, it shares this zone with scrub dominated by Arctic-Alpine willows like *Salix lapponum*, *S. myrsinites* and *S. reticulata* which replaces the *Juniperus-Oxalis* woodland on wetter soils but has quite a strong floristic overlap with the *Viola-Anemone* sub-community. On the highly acidic rocks of the north-western parts of Scotland, this altitudinal zone is characterised by a scrubby heath in which *J. communis* ssp. *nana* plays a major role.

Distribution

The *Juniperus-Oxalis* woodland is largely confined to the east-central Highlands of Scotland, particularly the hills of the Cairngorm and Monadhliath ranges. More isolated stands have been recorded from southern Scotland, Northumberland, the Pennines and the Lake District.

Affinities

This community unites a variety of previously-described kinds of scrub or woodland dominated by *J. communis* ssp. *communis*, with or without small amounts of birch (Pigott 1956*a*, McVean & Ratcliffe 1962, Graham 1971, Huntley & Birks 1979*a*, Birse 1980, 1982), and preserves the major floristic distinction between more and less calcifugous types recognised in Teesdale (Graham 1971), at Morrone (Huntley & Birks 1979*a, b*) and more widely in the east-central Highlands (Birse 1980, 1982). The close floristic affinities with the *Pinus-Hylocomium* woodland and, over much of the altitudinal range, the seral relationship to that community, argue for placing the *Juniperus-Oxalis* woodland in the Vaccinio-Picetea, perhaps in the alliance Vaccinio-Juniperion Passarge 1968 or within the Dicrano-Pinion (Libbert 1933) Matuszkiewicz 1962. If the climatic climax character of high-altitude stands is stressed, the most obvious floristic affinities are with Scandinavian sub-alpine juniper scrubs like the *Junipereto-Betuletum nanae myrtilletosum* (Nordhagen 1928, 1943) which Dahl (1956) placed with the montane *Nardus stricta* and *Carex bigelowii* communities. In these scrubs, however, the juniper is *J. communis* ssp. *nana* and there is a good representation of *Betula nana*: in Scotland, there is no evidence of an association between juniper and *B. nana* (Poore & McVean 1957).

Floristic table W19

	a	b	19
Betula pubescens	II (5–7)	I (6)	I (5–7)
Sorbus aucuparia		I (1)	I (1)
Juniperus communis communis	V (5–10)	V (7–10)	V (5–10)
Oxalis acetosella	V (1–7)	V (3–7)	V (1–7)
Hylocomium splendens	V (1–8)	IV (1–8)	V (1–8)
Vaccinium myrtillus	V (1–8)	IV (1–7)	V (1–8)
Galium saxatile	V (1–5)	IV (1–6)	V (1–6)
Luzula pilosa	IV (1–5)	IV (1–5)	IV (1–5)
Agrostis capillaris	IV (1–6)	IV (1–7)	IV (1–7)
Agrostis canina montana	IV (1–5)	IV (1–5)	IV (1–5)
Thuidium tamariscinum	IV (1–5)	IV (1–9)	IV (1–9)
Dicranum scoparium	V (1–4)	III (1–4)	III (1–4)
Plagiothecium undulatum	V (1–5)	II (1–4)	III (1–5)
Deschampsia flexuosa	V (2–6)	II (1–7)	III (1–7)
Vaccinium vitis-idaea	IV (1–8)	II (1–5)	III (1–8)
Rhytidiadelphus loreus	IV (1–4)	II (1–3)	III (1–4)
Pleurozium schreberi	IV (1–4)	II (1–4)	III (1–4)
Calluna vulgaris	IV (1–4)	II (1–4)	III (1–4)
Hypnum cupressiforme	IV (1–5)	II (1–5)	III (1–5)
Dicranum majus	III (1–5)	I (1–3)	II (1–5)
Lophozia ventricosa	I (1–3)		I (1–3)
Scapania gracilis	I (1)		I (1)

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Floristic table W19 *(cont.)*

	a	b	19
Isothecium myosuroides	I (1–2)		I (1–2)
Barbilophozia hatcheri	I (1–6)		I (1–6)
Listera cordata	I (1)		I (1)
Pyrola minor	I (1)		I (1)
Cladonia pyxidata	I (1–2)		I (1–2)
Viola riviniana	II (1–3)	V (1–5)	III (1–5)
Anemone nemorosa	II (2–3)	IV (1–6)	III (1–6)
Rhytidiadelphus triquetrus	II (1–7)	IV (1–8)	III (1–8)
Festuca ovina	II (2–5)	III (1–5)	III (1–5)
Plagiomnium undulatum	I (1–2)	III (1–6)	II (1–6)
Festuca rubra	I (1–2)	III (1–5)	II (1–5)
Campanula rotundifolia	I (1–3)	III (1–4)	II (1–4)
Cardamine flexuosa	I (1–3)	III (1–4)	II (1–4)
Urtica dioica	I (2)	II (1–5)	I (1–5)
Holcus mollis	I (3–5)	II (1–8)	I (1–8)
Cerastium fontanum	I (1–2)	II (1–3)	I (1–3)
Barbilophozia barbata	I (1)	II (1–6)	I (1–6)
Drepanocladus uncinatus	I (1)	II (1–5)	I (1–5)
Rubus idaeus	I (1)	II (1–6)	I (1–6)
Cirriphyllum piliferum	I (1)	II (1–4)	I (1–4)
Stellaria holostea		II (1–4)	I (1–4)
Fragaria vesca		II (1–4)	I (1–4)
Plagiomnium affine		II (2–4)	I (2–4)
Adoxa moschatellina		II (1–4)	I (1–4)
Galium boreale		II (2–4)	I (2–4)
Mercurialis perennis		I (2–7)	I (2–7)
Galium verum		I (1–2)	I (1–2)
Prunella vulgaris		I (2)	I (2)
Carex flacca		I (2–3)	I (2–3)
Geum rivale		I (3)	I (3)
Potentilla sterilis		I (2–3)	I (2–3)
Epilobium montanum		I (1–5)	I (1–5)
Isothecium myurum		I (1–4)	I (1–4)
Lathyrus montanus		I (1–2)	I (1–2)
Polygonum viviparum		I (1–2)	I (1–2)
Pyrola media		I (1)	I (1)
Ranunculus acris		I (2–3)	I (2–3)
Poa trivialis		I (1–3)	I (1–3)
Rumex acetosa		I (1–2)	I (1–2)
Blechnum spicant	III (1–4)	III (1–5)	III (1–5)
Lophocolea bidentata s.l.	III (1–4)	III (1–5)	III (1–5)
Pseudoscleropodium purum	III (1–6)	III (1–4)	III (1–6)
Potentilla erecta	III (1–4)	III (1–4)	III (1–4)
Trientalis europaea	III (1–5)	III (1–3)	III (1–5)
Rhytidiadelphus squarrosus	III (1–5)	III (1–5)	III (1–5)
Plagiochila asplenoides	III (1–4)	III (1–5)	III (1–5)

Anthoxanthum odoratum	II (1–5)	III (1–6)	III (1–6)
Veronica officinalis	II (1–2)	II (1–5)	II (1–5)
Plagiomnium rostratum	II (1–5)	II (1–4)	II (1–5)
Gymnocarpium dryopteris	II (1–8)	II (3–7)	II (1–8)
Mnium hornum	II (1–4)	II (1–5)	II (1–5)
Polytrichum formosum	II (1–2)	II (1–2)	II (1–2)
Pteridium aquilinum	II (1–5)	II (1–5)	II (1–5)
Plagiothecium denticulatum	II (1–4)	II (1–4)	II (1–4)
Dryopteris dilatata	II (1–4)	I (2–4)	I (1–4)
Hypnum jutlandicum	II (2–5)	I (1–4)	I (1–5)
Ptilium crista-castrensis	II (1–6)	I (2–4)	I (1–6)
Carex pilulifera	I (1)	I (1–3)	I (1–3)
Deschampsia cespitosa	I (4)	I (1–4)	I (1–4)
Dryopteris filix-mas	I (1)	I (1)	I (1)
Thelypteris phegopteris	I (1–3)	I (1–2)	I (1–3)
Atrichum undulatum	I (2)	I (1–2)	I (1–2)
Eurhynchium praelongum	I (1–2)	I (2–7)	I (1–7)
Plagiothecium succulentum	I (1)	I (1–4)	I (1–4)
Polytrichum commune	I (1–5)	I (1–5)	I (1–5)
Thelypteris limbosperma	I (4–6)	I (1–3)	I (1–6)
Melampyrum pratense	I (2)	I (2)	I (2)
Luzula multiflora	I (1–3)	I (1–3)	I (1–3)
Carex binervis	I (1)	I (1)	I (1)
Rubus saxatilis	I (2)	I (1–2)	I (1–2)
Geranium sylvaticum	I (1)	I (2)	I (1–2)
Hylocomium umbratum	I (1)	I (1)	I (1)
Number of samples	31	38	69
Number of species/sample	28 (24–34)	32 (22–46)	30 (22–46)
Tree height (m)	7 (7–8)	9 (7–10)	8 (7–10)
Tree cover (%)	5 (0–50)	2 (0–30)	3 (0–50)
Shrub height (m)	1 (0.8–2.1)	1 (0.4–2.0)	1 (0.4–2.1)
Shrub cover (%)	62 (45–90)	78 (40–90)	73 (40–90)
Herb height (cm)	18 (5–30)	18 (5–35)	18 (5–35)
Herb cover (%)	65 (50–75)	59 (30–80)	61 (30–80)
Ground height (mm)	no data	no data	no data
Ground cover (%)	67 (50–80)	65 (25–85)	66 (25–85)
Altitude (m)	445 (365–556)	448 (366–663)	447 (365–663)
Slope (°)	10 (4–22)	14 (4–30)	12 (4–30)

a *Vaccinium vitis-idaea-Deschampsia flexuosa* sub-community

b *Viola riviniana-Anemone nemorasa* sub-community

19 *Juniperus communis communis-Oxalis acetosella* woodland (total)

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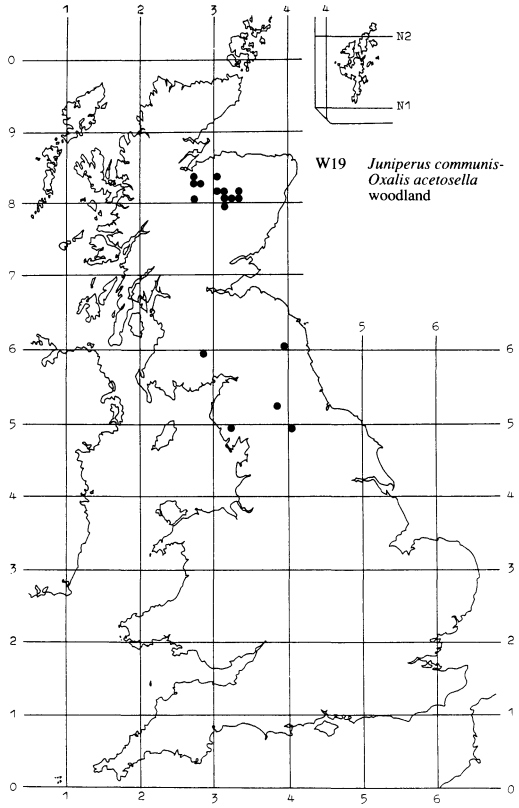

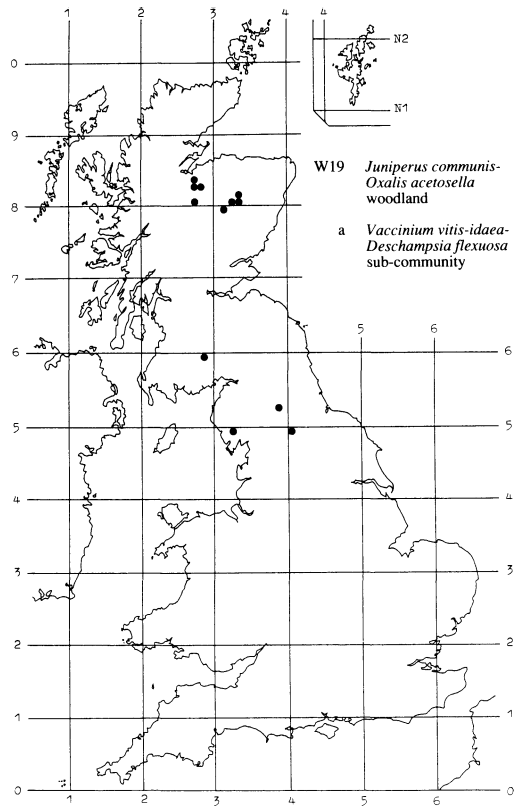

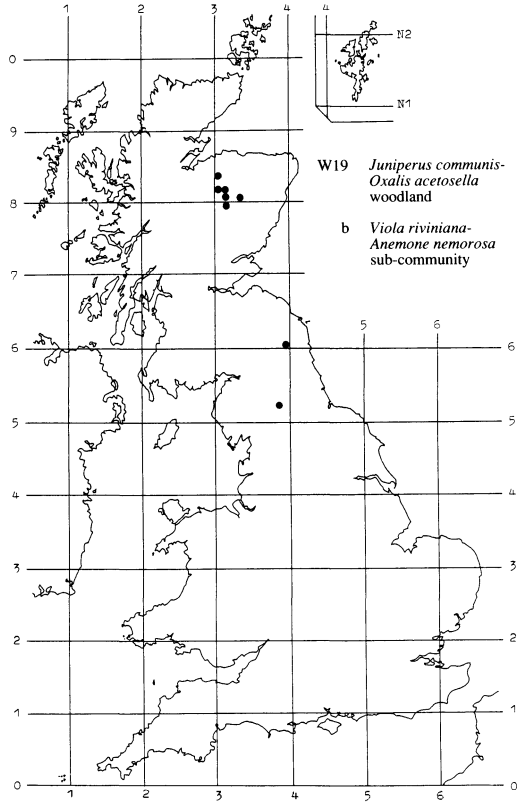

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