U16
Luzula sylvatica-Vaccinium myrtillus tall-herb community

Synonymy
High cliff vegetation Petch 1933; *Luzula sylvatica* grassland McVean 1961, McVean & Ratcliffe 1962; Herb-rich birchwood, *Vaccinium-Luzula* treeless facies McVean & Ratcliffe 1962; *Luzula sylvatica-Vaccinium myrtillus* Association Birks 1973, Prentice & Prentice 1975; *Agrostis-Luzula sylvatica* nodum Prentice & Prentice 1975; *Luzula sylvatica* nodum Prentice & Prentice 1975; *Luzula sylvatica-Vaccinium* vegetation Jermy & Crabbe 1978; *Luzula sylvatica* grassland Association Jermy & Crabbe 1978; *Luzula sylvatica-Vaccinium myrtillus* nodum Huntley 1979; *Cicerbita alpina* tall-herb ledge Huntley 1979.

Constant species
Deschampsia flexuosa, *Galium saxatile*, *Luzula sylvatica*, *Vaccinium myrtillus*.

Rare species
Cicerbita alpina, *Salix lanata*, *S. lapponum*, *S. myrsinites*, *S. reticulata*.

Physiognomy
Luzula sylvatica is an occasional, and sometimes locally abundant, plant in a variety of upland grasslands and heaths but it is in this *Luzula-Vaccinium myrtillus* community that it makes its most consistently prominent contribution outside the confines of woodlands and scrub. It is generally the most abundant plant here, occasionally an overwhelming dominant in swards with but few sparse associates and, even where other species are more numerous and extensive in their cover, there is not usually that richness and variety in the flora that is characteristic of much of the *Luzula-Geum rivale* community, our other widespread tall-herb vegetation with the club-rush on mountain ledges and crags. One plant that is more important in the *Luzula-Vaccinium* community, however, is *V. myrtillus*, frequent among all but the most luxuriant growths of *L. sylvatica*, and often occurring as quite vigorous bushes, a few decimetres tall, sometimes forming an irregular second tier to the vegetation, usually intermixed as clumps among the club-rush tussocks, and quite commonly co-dominant. Other sub-shrubs figure only occasionally and usually with but moderate abundance: *V. vitis-idaea*, *Erica cinerea* and *Empetrum nigrum* all occur infrequently and in small quantities, and there may be a little *Calluna vulgaris*, particularly where stands occur among heath-covered slopes, where heather bushes become more common in the transitional zone (e.g. Jermy & Crabbe 1978). Then, there are sometimes bushes of *Salix aurita* and Arctic-Alpine willows, like *S. lapponum*, *S. lanata* or *S. myrsinites*, or small patches of *S. reticulata*, and these may thicken up locally in zonations to *Salix-Luzula* scrub, the understorey of which shows strong floristic continuity with the *Luzula-Vaccinium* community. Very occasionally, too, saplings of *Sorbus aucuparia*, *Betula pubescens* and *Fraxinum excelsior* may be found and, at lower altitudes, this kind of vegetation can occur in close association with woodland or scrub in which these species are dominant.

Apart from *L. sylvatica* and *V. myrtillus*, the only other constants of the community are *Deschampsia flexuosa* and *Galium saxatile*, but *Oxalis acetosella* and *Blechnum spicant* are fairly frequent throughout and, in some stands, these are joined by a variety of other ferns, with *Dryopteris dilatata* in particular becoming a common associate. *Deschampsia cespitosa* can be quite frequent, too, while in other stands fine-leaved grasses like *Anthoxanthum odoratum*, *Festuca ovina/vivipara*, *Agrostis canina*, *A. capillaris* and *Nardus stricta*, together with *Potentilla erecta*, provide strong continuity with Nardo-Galion pastures: around the more accessible fringes of ledges and over slopes with just light cropping from stock or deer, reduced covers of the palatable *L. sylvatica* and *V. myrtillus* in such grassier stands can represent a transition to surrounding swards. Apart from *Carex binervis*, which becomes quite common in such situations, and very occasional *C. bigelowii*, sedges are infrequent in the community, and

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the more basiphile species characteristic of the *Luzula-Geum* community, such as *C. pulicaris* and *C. flacca*, and the Arctic-Alpine rarities *C. vaginata* and *C. atrata*, are very rare or altogether absent.

Other plants occurring at low frequency throughout most *Luzula-Vaccinium* vegetation are *Alchemilla alpina* and *Rumex acetosa*, but herbs of moderate and tall stature are generally few in number. Certainly, species like *Angelica sylvestris*, *Geum rivale*, *Filipendula ulmaria*, *Alchemilla glabra*, *Crepis paludosa*, *Rhodiola rosea*, *Succisa pratensis* and *Geranium sylvaticum*, which are all to varying degrees characteristic of the *Luzula-Geum* community, are generally scarce here, although where two or three happen to occur together in this vegetation among more luxuriant club-rush with little bilberry, the *Luzula-Vaccinium* community comes close to its more species-rich relative. One very notable tall herb, however, which prefers this kind of vegetation, rather than the *Luzula-Geum* type, is *Cicerbita alpina*, an Arctic-Alpine perennial, highly palatable and much prized by collectors, now reduced to ten colonies around the Clova–Caenlochan area (Perring & Farrell 1977). It can be very abundant there on inaccessible ledges, even locally dominant in some of the most species-poor stands of the *Luzula-Vaccinium* community that there are, and lending a striking character to the vegetation in summer with its racemes of pale blue flowers (Raven & Walters 1956, McVean & Ratcliffe 1962, Huntley 1979).

Among the dense and shady herbage typical of the community, smaller dicotyledons fare badly and few of the preferentials of the different kinds of *Luzula-Vaccinium* vegetation are of this type. Except in the most luxuriant swards of club-rush, however, there are generally some bryophytes growing over the moist litter and soil or on the shoot bases of the vascular plants and, though few of the species are common throughout, quite a number are occasional to frequent. *Rhytidiadelphus loreus*, *R. squarrosus*, *Pleurozium schreberi*, *Dicranum scoparium*, *D. majus*, *Plagiothecium undulatum*, *Mnium hornum*, *Thuidium tamariscinum* and *Polytrichum commune* are the most characteristic of these, with *Hypnum cupressiforme s.l.*, *Diplophyllum albicans* and *Lophocolea bidentata s.l.* somewhat less common. The local occurrence of patches of Sphagna such as *S. capillifolium*, *S. subnitens* and *S. girgensohnii* emphasises the floristic relationship between this vegetation and the *Calluna-Vaccinium-Sphagnum* heath among which it can sometimes be found. Lichens typically make a very minor contribution to the community.

Sub-communities

***Dryopteris dilatata-Dicranum majus* sub-community:** Herb-rich birchwood, *Vaccinium-Luzula* treeless facies McVean & Ratcliffe 1962; *Luzula sylvatica-Vaccinium myrtillus* Association Birks 1973, Prentice & Prentice 1975; *Luzula sylvatica-Vaccinium* vegetation Jermy & Crabbe 1978; *Luzula sylvatica-Vaccinium myrtillus* nodum Huntley 1979 *p.p.*; *Cicerbita alpina* tall-herb ledge Huntley 1979. In this taller and more luxuriant kind of *Luzula-Vaccinium* vegetation, which is often confined to ledges and gullies and sometimes developed as festoons hanging down from them over rock faces, *L. sylvatica* and *V. myrtillus* are commonly both abundant, with scattered tufts of *Deschampsia flexuosa*. *D. cespitosa* is preferentially frequent here, too, sometimes with locally high cover, but more fine-leaved grasses are generally only occasional. *Oxalis acetosella* joins *Galium saxatile* as a constant associate, and in some stands there are scattered plants of *Anemone nemorosa*, *Viola riviniana* and *Huperzia selago*, with very occasional records for bigger herbs like *Alchemilla glabra*, *Crepis paludosa*, *Heracleum sphondylium*, *Succisa pratensis*, *Geranium sylvaticum*, *Filipendula ulmaria*, *Heracleum sphondylium* and *Angelica sylvestris*, particularly where bilberry is not so abundant. The most striking enrichment, though, comes from ferns, most especially from *Dryopteris dilatata*, which is often more common than *Blechnum*, and less frequently from *Gymnocarpium dryopteris*, *Thelypteris phegopteris*, *T. limbosperma*, *Athyrium filix-femina*, *A. alpestre* and *Dryopteris borreri*, each of which can occur with some modest local abundance. Some stands have bushes of the Arctic-Alpine willows, and it is in this kind of *Luzula-Vaccinium* vegetation that *Cicerbita* has been recorded.

Bryophytes are fairly numerous and can have quite high cover with *Rhytidiadelphus loreus*, *Plagiothecium undulatum*, *Dicranum majus*, *D. scoparium* and *Mnium hornum* the most common species, *Thuidium tamariscinum*, *Eurhynchium praelongum*, *Plagiothecium denticulatum*, *Rhizomnium punctatum* and *Atrichum undulatum* less frequent, though still preferential. And it is in this kind of *Luzula-Vaccinium* vegetation that there are occasional records for *Sphagnum subnitens*, *S. capillifolium*, *S. girgensohnii*, *S. russowii* and *S. palustre*. *Rhytidiadelphus squarrosus*, *Polytrichum commune* and *Pleurozium schreberi* can sometimes be found, but they are more characteristic of the next sub-community.

***Anthoxanthum odoratum-Festuca ovina* sub-community:** *Luzula sylvatica* grassland McVean 1961, McVean & Ratcliffe 1962; *Agrostis-Luzula sylvatica* nodum Prentice & Prentice 1975; *Luzula sylvatica* grassland Association Jermy & Crabbe 1978; *Luzula sylvatica-Vaccinium myrtillus* nodum Huntley 1979 *p.p.* The swards are often shorter here than in the *Dryopteris-Dicranum* sub-community and, though *V. myrtillus* remains a very frequent plant, it is not so commonly co-dominant with *L. sylvatica*. *Blechnum* is still frequently found, but other ferns are scarce, usually limited to just very occasional

crowns of *Dryopteris dilatata*, *Gymnocarpium dryopteris* and *Thelypteris limbosperma*. *Deschampsia cespitosa* sometimes occurs but it is fine-leaved grasses that provide the most distinctive preferential element here, *D. flexuosa* being often joined by *Anthoxanthum*, *Festuca ovina/vivipara*, *Agrostis canina*, *A. capillaris* and *Nardus stricta*. *Festuca rubra* occurs very occasionally and there can be a little *Carex binervis* and, in some stands, *Juncus squarrosus*. The high frequency, along with *Galium saxatile*, of *Potentilla erecta*, and the absence, apart from *Oxalis acetosella*, of most of the dicotyledons of the *Dryopteris-Dicranum* sub-community, confirm the similarities to Nardo-Galion swards and quite often this vegetation is found not on ledges but among the grasslands and heaths of more open slopes. Occasional bushes of *Calluna* and *Vaccinium vitis-idaea* sometimes accompany *V. myrtillus* in stands transitional to sub-shrub communities.

Apart from *Rhytidiadelphus loreus* and occasional *Hypnum cupressiforme s.l.*, *Plagiothecium undulatum* and *Mnium hornum*, the bryophytes are rather different from those of the *Dryopteris-Dicranum* sub-community, the commonest species being *R. squarrosus*, *Polytrichum commune*, *Pleurozium schreberi*, *Dicranum scoparium*, *Hylocomium splendens* and *Pseudoscleropodium purum*. Sparse thalli of *Cladonia impexa* and *C. uncialis* find a very occasional place in the shorter herbage.

Species-poor sub-community: *Luzula sylvatica* nodum Prentice & Prentice 1975. *L. sylvatica* is an overwhelming dominant here in vegetation that can be virtually pure. *Deschampsia flexuosa* remains common, but even *V. myrtillus* and *G. saxatile*, the other constants, are reduced in frequency, and although there can be occasional records for species like *Potentilla erecta*, *Rumex acetosa*, *Anthoxanthum* and *Agrostis capillaris*, all these associates typically occur as sparse, scattered individuals among the densely-crowded club-rush shoots. Bryophytes, too, are few in number and of low cover, with just very occasional shoots of *Rhytidiadelphus squarrosus*, *R. loreus* and *Polytrichum commune*.

Habitat

The *Luzula-Vaccinium* community is confined to inaccessible ground in the cold, wet uplands of north-west Britain, where there has been some protection from grazing and burning, but no opportunity for sustained succession to scrub or woodland. It occurs in a variety of rocky habitats and on more isolated open slopes, often shaded or with some modest flushing, over more base-poor substrates with humic soils. Stands are found mostly at moderate to high altitudes, frequently in situations well above the present forest limit, but they can also occur close to sea-level around the cool, oceanic coast of western Scotland.

Freedom from the predation of herbivores is an essential pre-requisite for the development of this kind of vegetation. *L. sylvatica* has a distinct preference for less impoverished circumneutral and base-poor soils that are moist though free-draining, and it occurs widely as an occasional in a variety of grasslands, heaths and woodland types throughout the wetter and cooler parts of the country. However, it is highly palatable and attains no more than sparse representation where grazing is sustained so, for the vigorous abundance characteristic of the *Luzula-Vaccinium* community, a measure of protection is required. Throughout the British uplands, where grazing by sheep or, more locally, by goats or deer, is virtually ubiquitous over the unenclosed slopes, it is usually broken topography which guarantees the necessary inaccessibility. In many localities, therefore, this vegetation is confined to such places as ledges, crags or the sides of ravines, to stretches of blocky talus and the tops of large boulders, or to smaller lake islands which escape pasturing or visits from all but very adventurous deer. Stands in these places are often small, sometimes fragmentary, and may show striking local peculiarities among the associated flora, as with the dominance of *Cicerbita*. In other cases, more extensive tracts of ground can be cut off, as on the huge sloping ledge of Coire na Poite on Beinn Bhan in Ross, where the *Luzula-Vaccinium* community contributes to an enormous varied stand of tall-herb and fern-dominated vegetation isolated by cliffs above and below (McVean & Ratcliffe 1962, Ratcliffe 1977). Then, the community can sometimes be found on more open cliff tops, hillsides and summits, forming small patches or areas up to several hectares in extent, where grazing happens to be not so intensive as on the surrounding slopes: in such more accessible situations, burning can be a further important factor limiting the occurrence of this vegetation, the dense litter that accumulates among the club-rush readily taking fire when it is dry.

Among the various communities that can capitalise on protection from such treatments, the *Luzula-Vaccinium* swards characterise the more base-poor extreme of a continuously variable range of edaphic conditions, being found mostly on siliceous sedimentaries or igneous rocks like granite, with strongly humic soils, often little more than thick rankers. There is often some flushing of the ground from seepage lines or from the trickling of run-off down the rock faces and this, together with the shaded and sheltered aspects that the community favours, accentuates the generally humid conditions maintained by high rainfall: most stands experience well over 1200 mm precipitation annually (*Climatological Atlas* 1952) with more than 180 wet days a year (Ratcliffe 1968), sometimes considerably more, although the drainage of the ground water is always free. The concentration of run-off may also bring some

modest enrichment with major nutrients, favourable to the luxuriant growth of the fairly mesophytic *L. sylvatica* (e.g. Pearsall 1950), and this effect may be enhanced by the accumulation of droppings from ledge-nesting birds. Bases, though, are typically in short supply: although *L. sylvatica* tends to favour the accumulation of moder humus, rather than harsh mor, the surface pH here is usually between 4 and 5, and McVean & Ratcliffe (1962) noted up to an 8-fold difference in calcium content between the soils beneath this kind of vegetation and those supporting the *Luzula-Geum* community which replaces it on more calcareous substrates. The two assemblages grade continuously one into the other, but the general poverty of bases here, and the probably much less brisk turnover of nutrients, are reflected in the floristic contrasts between them. In the *Luzula-Vaccinium* community, the flora is much less rich, with an average of only 24 as against 42 species per sample, with a marked scarcity in particular of more basiphile and mesophytic herbs and bryophytes. Plants such as *Geum rivale*, *Alchemilla glabra*, *Viola riviniana*, *Filipendula ulmaria*, *Carex pulicaris*, *Trollius europaeus*, *Saxifraga aizoides*, *Ctenidium molluscum* and *Bryum pseudotriquetrum* are very scarce and inconsistent in their occurrence, and even poor-fen plants like *Angelica sylvestris* and *Succisa pratensis* do not occur very often. By contrast, *V. myrtillus* and *G. saxatile*, and to a lesser extent such bryophytes as *Rhytidiadelphus loreus*, *Dicranum majus*, *Plagiothecium undulatum* and *Polytrichum commune*, are more important in the *Luzula-Vaccinium* community, though only the very rare *Cicerbita* gives any really striking expression to the more calcifuge character of the flora.

Although this kind of vegetation extends to moderately high altitudes, commonly attaining 500 m or more, and is frequently found where the mean annual maximum temperature is only 21 °C (Conolly & Dahl 1970), the representation of Arctic-Alpine herbs is very sparse. To a great extent, this is because many of these are of small stature, intolerant of competition and demanding of light, and thus very susceptible to being simply crowded out by the luxuriant *L. sylvatica*. Indeed, where this grows especially vigorously here, whether on rocky ground or over more open, ungrazed slopes, it is likely to overwhelm most other plants, giving rise to the vegetation included in the Species-poor sub-community. Often, the club-rush maintains a strong dominance in the *Anthoxanthum-Festuca* sub-community too, though this is shorter and grassier vegetation, and often found as a transition to those pastures and heaths in which *L. sylvatica* is reduced to insignificant occurrence by grazing and burning. Then dominance passes to mixtures of grasses like *Anthoxanthum*, *Festuca ovina*, *F. rubra*, *F. vivipara*, *Agrostis capillaris*, *A. canina* and *Nardus*, which are preferential to the *Anthoxanthum-Festuca* sub-community, or to sub-shrubs like *V. myrtillus*, *V. vitis-idaea* and *Calluna*, these last two becoming occasional in this kind of *Luzula-Vaccinium* vegetation. Apart from general observations such as those in Jermy & Crabbe (1978), indicating that the *Anthoxanthum-Festuca* sub-community can persist with light grazing, details of treatment are lacking, but it seems likely that it represents a spatial and seral intermediate between the *Dryopteris-Dicranum* sub-community and Nardetalia vegetation controlled by biotic factors.

Except where animals gain very occasional access, as by crossing conveniently-lodged drifts of snow or by landing safely on a ledge after a fall, when their sudden predations can become very evident (Huntley 1979), the *Dryopteris-Dicranum* sub-community is altogether free from grazing and hardly ever reached by fire. It is in this kind of *Luzula-Vaccinium* vegetation, then, that the opportunities for a richer development of more vulnerable associates are maximised, provided that the club-rush itself is not too vigorous. *V. myrtillus*, which is eagerly taken by stock and deer, can now become co-dominant and the characteristic ferns of the sub-community assume patchy abundance. It is possible, too, with the seepage and shelter found on many ledges, that conditions are more favourable in this kind of *Luzula-Vaccinium* vegetation for plants demanding of humidity and some nutrient enrichment. The vegetation tends to be taller in general than in more accessible habitats, although the varied topography of the ground allows for the occasional occurrence of some smaller herbs. However, the fine-leaved, grazing-resistant grasses of the *Anthoxanthum-Festuca* sub-community are largely crowded out.

The fully-developed flora of the *Dryopteris-Dicranum* sub-community is very similar to the field and ground layers of the more calcifuge of our sub-montane Quercion forest in north-west Britain: indeed, McVean & Ratcliffe (1962) included this kind of vegetation as a treeless facies of their *Betuletum Oxaleto-Vaccinetum*, part of what would be called in this scheme the *Quercus-Betula-Dicranum* woodland. And they noted the close floristic relationship, too, with the *Salix-Luzula* scrub, which represents a very local continuation of woody vegetation into the sub-alpine zone of the Scottish Highlands. It is also some of the common shrubs and trees of these communities that are found as occasional saplings and bushes in stands of this kind of *Luzula-Vaccinium* vegetation, strongly suggesting some successional relationship between them. Certainly, within the forest zone, through which the *Luzula-Vaccinium* community extends almost down to sea-level around the cool, oceanic western seaboard of Scotland, it is likely that the *Dryopteris-Dicranum* sub-community could in many places progress to rowan- or birch-dominated forms of the *Quercus-Betula-Dicranum* woodland,

provided seed of the trees was available and could get a hold. In fact, seed-parents are often few and far between, and the thick herbage and litter of the vegetation uncongenial for germination. At higher altitudes, the *Dryopteris-Dicranum* sub-community could be considered a seral precursor to the *Salix-Luzula* scrub: certainly, this kind of *Luzula-Vaccinium* vegetation often extends well over 200 m above the limit of submontane forests, and sometimes occupies ledges on crags where the Arctic-Alpine willows have a strong hold. Again, though, the availability of seed is probably a crucial hindrance to the colonisation of more isolated sites, while exposure to severe frosts may kill such bushes as get a hold but are left protruding from a shallow cover of winter snow. In such situations, then, the *Luzula-Vaccinium* community can be regarded as an effective climax.

Zonation and succession

The *Luzula-Vaccinium* community is sometimes found among grasslands and heaths where variations in grazing intensity or frequency of burning over open slopes and summits have determined the vegetation pattern. Very often, though, the protection necessary for the maintenance of the community depends on topographic discontinuities which set stands apart from the surrounding vegetation in stretches of broken, rocky ground. In such situations, the *Luzula-Vaccinium* community can sometimes occur with other tall-herb and fern-dominated assemblages, differences in soils determining the mixture of vegetation types, or with patches of scrub if there has been an opportunity for further succession.

Throughout the range of the community, and especially in the more oceanic west, the *Anthoxanthum-Festuca* sub-community can be found in zonations and mosaics over open slopes with a variety of grassland types. It is particularly distinctive over summits at moderate altitudes around the Atlantic seaboard of Scotland (McVean & Ratcliffe 1962) and on some cliff-top sites (e.g. Prentice & Prentice 1975), but it also occurs on hillsides and in smaller valleys and gullies. Often, such stands are little islands isolated within extensive tracts of other swards, but larger stretches of this kind of *Luzula-Vaccinium* vegetation are to be seen in some places, even quite far from the west of Scotland, as in the Moffat and Ettrick hills, and on Ben Loyal in Sutherland whole corries slopes are covered with the *Anthoxanthum-Festuca* sub-community (McVean & Ratcliffe 1962, Ratcliffe 1977). The great abundance of *L. sylvatica* is usually sufficient to provide a clear boundary between the vegetation types, despite the strong continuity among the associates, although a number of grasslands show patchy prominence of the club-rush, and then it may be hard to delimit the elements of transitional mosaics. These often involve *Nardus-Galium* or *Festuca-Agrostis-Galium* swards, particularly through the Southern Uplands, and in both of these the Nardo-Galion grasses, dicotyledons and bryophytes preferential to the *Anthoxanthum-Festuca* sub-community thicken up to form the bulk of the turf. On peatier soils in wetter areas, like the western Highlands, and particularly where slopes receive much run-off from precipitation or snow-melt, the *Anthoxanthum-Festuca* sub-community is found more often in close association with the *Deschampsia-Galium* grassland, with which there is again marked similarity among the associates, though which is typically dominated by *D. cespitosa*. Moderately snow-bound slopes where there is some drainage impedence can show a shift from the *Anthoxanthum-Festuca* sub-community to some kind of *Nardus-Carex* vegetation from which *L. sylvatica* is generally excluded by lack of free water movement, and with the shift to exposed summits at high altitudes, this kind of *Luzula-Vaccinium* vegetation can give way to *Carex-Racomitrium* heath. Throughout these zonations, variations in grazing intensity and the occurrence of burning can mediate transitions to a variety of sub-shrub communities. Towards lower altitudes, these are usually of the *Calluna-Vaccinium* or *Calluna-Erica* types, with *Calluna-Racomitrium* and *Vaccinium-Racomitrium* dwarfed heaths figuring on higher ground where exposure to wind and snow become important determining influences on the vegetation cover. In each case, increase in abundance of sub-shrubs other than *V. myrtillus*, and the eventual eclipse of *L. sylvatica*, are enough to mark the boundaries between the vegetation types. An altitudinal zonation from the *Anthoxanthum-Festuca* sub-community, through *Vaccinium-Racomitrium* heath to summit *Carex-Racomitrium* heath is a striking feature of the rather unusual vegetation cover of Ben Loyal (Ratcliffe 1977).

Species-poor *Luzula-Vaccinium* vegetation quite frequently replaces the *Anthoxanthum-Festuca* sub-community in patterns of the above types, but it can also be seen on ledges and among blocky talus, separated from surrounding communities by bare rock, or by stretches of open water where it occurs on islands. It is in such situations, too, that the *Dryopteris-Dicranum* sub-community is characteristically found, and there are places where a gradually more inaccessible topography is marked by a zonation from close-cropped Nardo-Galion swards, through a fringe of the *Anthoxanthum-Festuca* sub-community to the *Dryopteris-Dicranum* sub-community, with increasing luxuriance of the vegetation and the appearance of the more grazing-sensitive herbs. Occasionally, such a transition may run on into patchy scrub, with saplings of birch or rowan marking out fragmentary *Quercus-Betula-Dicranum* woodland or, at higher altitudes, Arctic-Alpine willows increasing

their cover to dominate in a stand of *Salix-Luzula* scrub. In each case, the *Luzula-Vaccinium* vegetation can run on virtually unchanged to form the field and ground layers of these communities. In other sites, particularly on north- or east-facing slopes, where shade, shelter and the persistence of snow maintain especially cool and humid conditions, the *Dryopteris-Dicranum* sub-community can mark out the most inaccessible areas of ground among mosaics of *Deschampsia-Galium* grassland and *Calluna-Vaccinium-Sphagnum* heath, with the latter of which the *Luzula-Vaccinium* community can show strong continuity in its associated herbs and bryophytes.

Quite often, however, the *Dryopteris-Dicranum* sub-community is completely isolated from the more accessible grasslands and heaths. Frequently, it occupies entire ledges or tracts of bouldery ground, though where there is some heterogeneity in the rocks making up the cliffs or screes, or variation in the quality of flushing waters seeping from them, there can be transitions to other kinds of grazing-sensitive vegetation. A shift to more base-rich and mesotrophic soils, for example, marking out exposures of calcareous sedimentaries or lime-rich intrusions or shatter zones, or some local base-rich seepage into largely impoverished soils, can see a shift to the *Luzula-Geum* community, with its richer and more basiphilous flora, or patches dominated by ferns. The close proximity of varied communities of this general kind was a feature of the ledges described from North Hoy by Prentice & Prentice (1975) and it is seen to spectacular effect on the giant ledge of Beinn Bhan, where streaks and patches of the different vegetation types mark out drier zones and seepage patches.

Distribution

The *Luzula-Vaccinium* community is widespread but rather local through the Scottish mountains, with outlying stands in the Lake District and the Cheviots.

Affinities

Although mountain-ledge plants have long attracted attention from flora recorders and collectors, it was not until the account of McVean & Ratcliffe (1962) that systematic attempts were made to describe the vegetation types in which they occur. In fact, the *Luzula-Vaccinium* community combines the less basiphilous and mesophytic vegetation sampled from ledges by these workers and others (Birks 1973, Prentice & Prentice 1975, Jermy & Crabbe 1978, Huntley 1979) with what are obviously closely-related *L. sylvatica*-dominated swards from more accessible habitats (McVean & Ratcliffe 1962, Prentice & Prentice 1975, Jermy & Crabbe 1978). The contrast between the two kinds of vegetation, preserved here in the recognition of the *Dryopteris-Dicranum* and *Anthoxanthum-Festuca* sub-communities, emphasises the affinities of the *Luzula-Vaccinium* community with, on the one hand, Quercion woodland and Salicion arbusculae sub-alpine scrub and, on the other, Nardetalia grasslands and heaths. Towards the sub-montane zone, the community can sometimes be regarded as an arrested developmental phase in succession to forest, but in more exposed situations and increasingly at higher altitudes, it can be seen as climax tall-herb vegetation with obvious floristic and ecological affinities with Betulo-Adenostyletea communities described from western Norway (Nordhagen 1922) and the Faroes (Ostenfeld 1908). McVean & Ratcliffe (1962) and Birks (1973) both favoured placing the more oligotrophic of their ledge vegetation in the Dryoptero-Calamagrostidion purpureae, together with the distinctly chionophilous *Cryptogramma-Athyrium* community, reserving the Cicerbition alpini for the more basiphilous and mesophytic vegetation of the *Luzula-Geum* assemblage. As noted above, these two grade continuously one into the other, though a distinction among what would otherwise be a very cumbersome syntaxon is well justified.

Floristic table U16

	a	b	c	16
Luzula sylvatica	V (1–10)	V (1–10)	V (8–10)	V (1–10)
Deschampsia flexuosa	V (1–6)	V (1–8)	V (1–4)	V (1–8)
Vaccinium myrtillus	V (1–9)	V (1–6)	III (1–3)	V (1–9)
Galium saxatile	IV (1–4)	IV (1–6)	II (1–3)	IV (1–6)
Oxalis acetosella	IV (1–4)	III (1–3)	I (1)	III (1–4)
Deschampsia cespitosa	IV (1–6)	II (1–4)		III (1–6)
Plagiothecium undulatum	IV (1–4)	II (1–6)		III (1–6)
Mnium hornum	IV (1–4)	II (1–3)		III (1–4)
Dryopteris dilatata	IV (1–4)	I (1–3)	I (1–3)	II (1–4)

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Floristic table U16 (*cont.*)

	a	b	c	16
Dicranum majus	IV (1–8)	I (1–4)		II (1–8)
Thuidium tamariscinum	III (1–4)	I (1–4)		II (1–4)
Eurhynchium praelongum	II (1–3)	I (1)	I (1)	I (1–3)
Plagiothecium denticulatum	II (1–3)	I (1)		I (1–3)
Rhizomnium punctatum	II (1–6)	I (1)		I (1–6)
Anemone nemorosa	II (1–3)	I (1–3)		I (1–3)
Polytrichum alpinum	II (1–3)	I (1–3)		I (1–3)
Gymnocarpium dryopteris	II (1–4)	I (1–4)		I (1–4)
Sphagnum subnitens	II (1–3)	I (1–6)		I (1–6)
Sphagnum capillifolium	II (1–3)	I (1)		I (1–3)
Huperzia selago	II (1–3)	I (1)		I (1–3)
Viola riviniana	II (1–3)	I (1–3)		I (1–3)
Salix lapponum	II (4–6)			I (4–6)
Atrichum undulatum	II (1–6)			I (1–6)
Sphagnum girgensohnii	II (1–5)			I (1–5)
Thelypteris phegopteris	II (1–4)			I (1–4)
Athyrium filix-femina	II (1–3)			I (1–3)
Conopodium majus	I (1–3)			I (1–3)
Fraxinus excelsior seedling	I (1–3)			I (1–3)
Arrhenatherum elatius	I (1–6)			I (1–6)
Crepis paludosa	I (1–3)			I (1–3)
Lonicera periclymenum	I (1–3)			I (1–3)
Athyrium distentifolium	I (1–7)			I (1–7)
Succisa pratensis	I (1–3)			I (1–3)
Hypnum callichroum	I (1–3)			I (1–3)
Cladonia bellidiflora	I (1–3)			I (1–3)
Alchemilla glabra	I (1–3)			I (1–3)
Chiloscyphus polyanthos	I (1–3)			I (1–3)
Salix lanata	I (4–5)			I (4–5)
Sphagnum palustre	I (1–3)			I (1–3)
Sphagnum russowii	I (1–3)			I (1–3)
Dryopteris borreri	I (1–3)			I (1–3)
Solidago virgaurea	I (1–4)			I (1–4)
Geranium sylvaticum	I (1–3)			I (1–3)
Tritomaria quinquedentata	I (1–3)			I (1–3)
Primula vulgaris	I (1–3)			I (1–3)
Plagiomnium undulatum	I (1–6)			I (1–6)
Rhytidiadelphus squarrosus	II (1–3)	IV (1–4)	II (1–5)	III (1–5)
Anthoxanthum odoratum	II (1–4)	IV (1–4)	II (1–3)	III (1–4)
Polytrichum commune	II (1–4)	IV (1–6)	I (1–3)	III (1–6)
Festuca ovina/vivipara	II (1–4)	IV (1–6)	I (1–3)	III (1–6)
Potentilla erecta	I (1–3)	IV (1–4)	II (1–4)	III (1–4)
Pleurozium schreberi	II (1–4)	IV (1–6)	I (1–3)	III (1–6)
Dicranum scoparium	III (1–3)	IV (1–4)		III (1–4)
Hylocomium splendens	II (1–6)	III (1–4)	I (1)	II (1–6)
Agrostis capillaris	I (1–4)	III (1–4)	II (1–4)	II (1–4)

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Nardus stricta	I (1)	III (1–5)	I (1–4)	II (1–5)
Carex binervis	I (1–3)	III (1–4)	I (1–3)	II (1–4)
Pseudoscleropodium purum	I (1–3)	II (1–3)	I (1)	I (1–3)
Vaccinium vitis-idaea	I (1–3)	II (1–3)		I (1–3)
Calluna vulgaris	I (1–4)	II (1–3)		I (1–4)
Juncus squarrosus		II (1–6)	I (1)	I (1–6)
Festuca rubra		I (1–4)		I (1–4)
Cladonia impexa		I (1–3)		I (1–3)
Cladonia uncialis		I (1–3)		I (1–3)
Rhytidiadelphus loreus	III (1–4)	III (1–4)	I (1–3)	III (1–4)
Blechnum spicant	III (1–4)	III (1–4)	I (1–3)	III (1–4)
Agrostis canina	III (1–4)	III (1–4)	I (1)	III (1–4)
Rumex acetosa	II (1–4)	II (1–4)	II (1–4)	II (1–4)
Lophocolea bidentata s.l.	II (1–3)	II (1–3)	I (1–3)	II (1–3)
Hypnum cupressiforme	II (1–4)	II (1–4)	I (1–4)	II (1–4)
Diplophyllum albicans	II (1–3)	II (1–3)		II (1–3)
Alchemilla alpina	II (1–4)	II (1–4)		II (1–4)
Erica cinerea	I (1–4)	I (1–3)	I (1–3)	I (1–4)
Carex bigelowii	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Dicranum fuscescens	I (5)	I (1–3)		I (1–5)
Thelypteris limbosperma	I (1–4)	I (1–4)		I (1–4)
Digitalis purpurea	I (1–3)	I (1–3)		I (1–3)
Campanula rotundifolia	I (1–3)	I (1–3)		I (1–3)
Racomitrium lanuginosum	I (1–5)	I (1–4)		I (1–5)
Empetrum nigrum	I (1–3)	I (1–4)		I (1–4)
Carex nigra		I (1–3)	I (1)	I (1–3)
Number of samples	28	25	12	55
Number of species/sample	29 (19–43)	24 (14–52)	9 (2–22)	24 (2–52)
Vegetation height (cm)	39 (18–60)	19 (10–25)	24 (15–40)	29 (10–60)
Vegetation cover (%)	90 (50–100)	98 (90–100)	100	94 (50–100)
Altitude (m)	493 (30–915)	483 (120–710)	379 (270–566)	469 (30–915)
Slope (°)	39 (0–85)	32 (1–60)	15 (2–35)	30 (0–85)

a *Dryopteris dilatata-Dicranum majus* sub-community
b *Anthoxanthum odoratum-Festuca ovina* sub-community
c Species-poor sub-community
16 *Luzula sylvatica-Vaccinium myrtillus* tall-herb community

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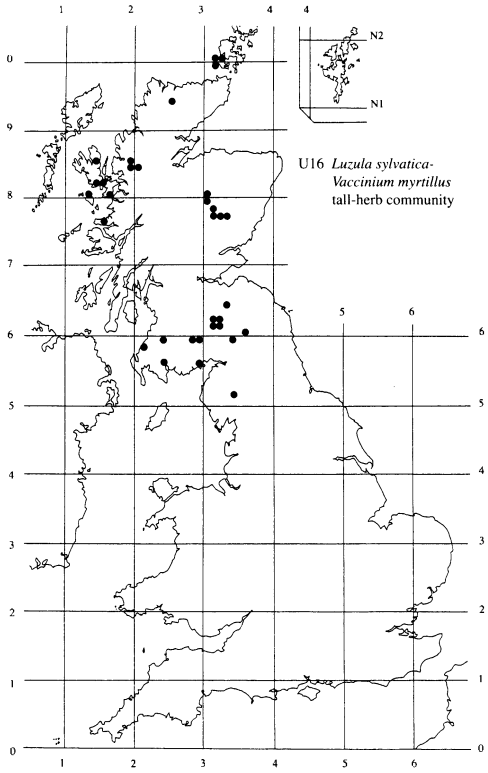

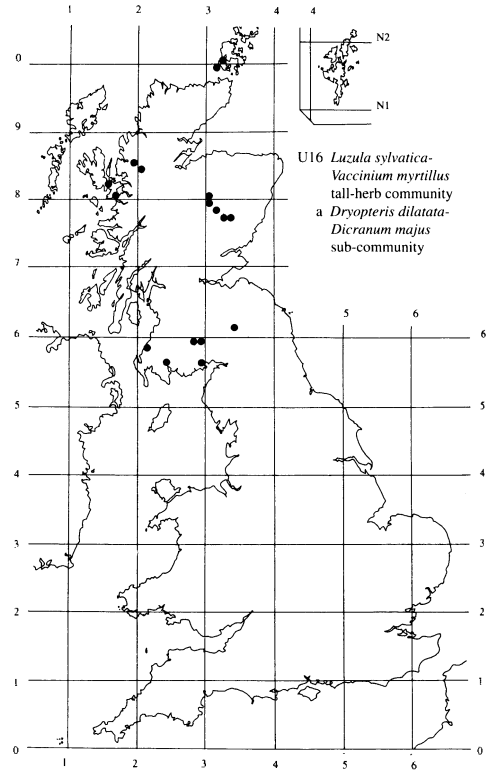

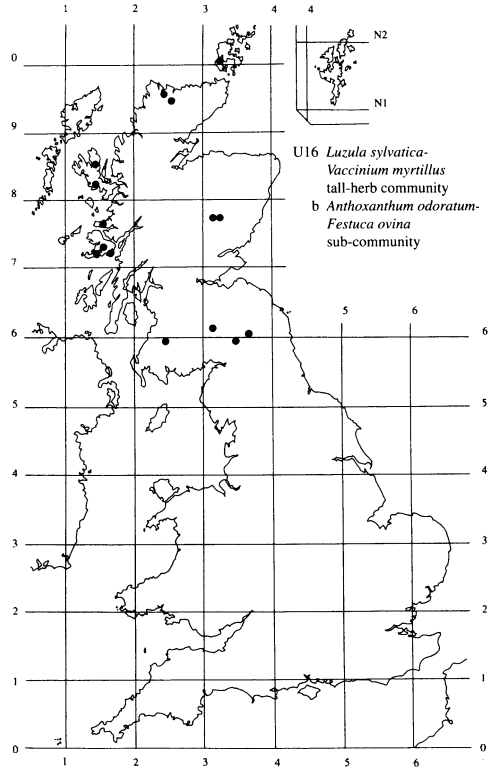

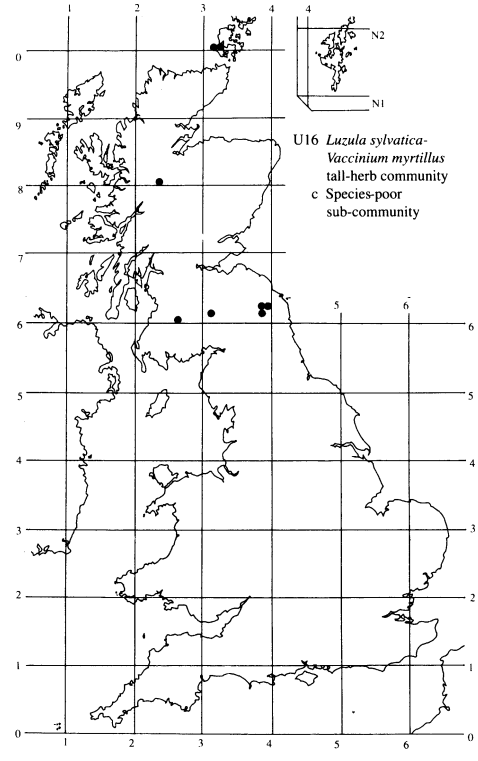

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