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Luzula sylvatica-Geum rivale tall-herb community

Synonymy
Ledge vegetation Smith 1911*a p.p.*, Ratcliffe 1960, Edgell 1969; *Luzula-Angelica-Rumex* Community Spence 1960; *Luzula-Dryopteris*, *Luzula-Deschampsia fluexuosa-Rhinanthus* and *Luzula-Blechnum-Solidago* Communities Spence 1960; Tall-herb nodum McVean & Ratcliffe 1962, Prentice & Prentice 1975; *Deschampsietum caespitosae alpinum* McVean & Ratcliffe 1962; *Sedum rosea-Alchemilla glabra* Association Birks 1973; *Luzula sylvatica-Silene dioica* Association Birks 1973; Cliff ledge communities Jermy & Crabbe 1978; *Saxifraga aizoides-Festuca-Deschampsia* nodum Huntley 1979; *Alchemilla glabra-Sedum rosea* nodum Huntley 1979.

Constant species
Angelica sylvestris, *Deschampsia cespitosa*, *Geum rivale*, *Luzula sylvatica*, *Rhodiola rosea*, *Hylocomium splendens*.

Rare species
Alchemilla filicaulis ssp. *filicaulis*, *Carex atrata*, *C. rupestris*, *C. vaginata*, *Cerastium alpinum*, *Draba incana*, *Epilobium alsinifolium*, *Meconopsis cambrica*, *Orthilia secunda*, *Poa alpina*, *P. glauca*, *Polystichum lonchitis*, *Potentilla crantzii*, *Salix lanata*, *S. lapponum*, *S. myrsinites*, *S. reticulata*, *Leptodontium recurvifolium*, *Mastigophora woodsii*, *Oxystegus hibernicus*, *Plagiochila carringtonii*, *Scapania ornithopodioides*.

Physiognomy
The *Luzula sylvatica-Geum rivale* community takes in varied and often species-rich assemblages of plants, among which taller and bulkier herbs predominate, frequently making luxuriant growth and giving the vegetation the appearance of 'hanging gardens' disposed over the ledges and crags that provide the typical habitat. Stands are commonly of irregular shape, often small and fragmentary, frequently with local peculiarities of floristics and structure and characteristically hard of access, all features which make it difficult to provide a comprehensive and succinct account of this vegetation, but which nevertheless themselves contribute to its highly distinctive appearance.

As in the *Luzula-Vaccinium* community, *Luzula sylvatica* is a constant plant here, often attaining big stature and flowering profusely, but it is not generally so abundant, showing consistently high cover in only one particular kind of *Luzula-Geum* vegetation. Indeed, there is no fixed pattern of dominance in this community, and any of the other constants, together with a number of the occasionals and sub-community preferentials, can show such local prominence as to give individual stands a peculiar stamp. Among the most frequent plants, *Angelica sylvestris*, *Geum rivale*, *Rhodiola rosea*, *Alchemilla glabra*, *Filipendula ulmaria* and *Succisa pratensis* together provide a reliable distinction from the *Luzula-Vaccinium* community and each can have high cover in dense patches, or they may dominate together in various mixtures, forming the bulk of lush, jumbled herbage, 3–4 dm tall. *Deschampsia cespitosa* can be fairly abundant, too: indeed as defined here, the *Luzula-Geum* community takes in some of the less closely grazed and more species-rich vegetation dominated by this grass, which McVean & Ratcliffe (1962) included in their *Deschampsietum caespitosae alpinum*. And it is in such stands, also, that other grasses, such as *Festuca ovina*, *F. vivipara*, *Anthoxanthum odoratum*, *Agrostis capillaris*, *A. canina*, *Deschampsia flexuosa* and *Nardus stricta* make their most obvious contribution though, in general, these more fine-leaved species are not structurally important here, occurring usually as sparsely-scattered individuals or as small tussocks in more open places around the taller herbs.

Other characteristic plants in this major physiognomic element of the flora include the Northern Montane *Trollius europaeus* and, south of the Great Glen, *Geranium sylvaticum* and *Heracleum sphondylium*, each able to show local dominance. Rather more occasional throughout and not usually so abundant are *Solidago virgaurea*, *Rumex acetosa*, the Continental Northern

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Crepis paludosa and *Cirsium helenioides*, and the Arctic-Alpine *Thalictrum alpinum*, *Polygonum viviparum*, *Saussurea alpina* and *Oxyria digyna*. In some stands, strikingly handsome montane Hieracia, notably of the sections Subalpina, Alpina and Cerinthoidea, are a conspicuous feature, often occurring in locally distinctive mixtures in different mountain ranges (e.g. Raven & Walters 1956, Perring 1968, Kenneth & Stirling 1970). The community also provides an important locus for the rare Arctic-Alpine fern *Polystichum lonchitis* though, on ledges here, this plant does not generally exhibit the gregarious habit found locally among boulders in block scree, and indeed it may be crowded out among dense herbage (Page 1982). Other ferns can be more abundant, particularly where the *Luzula-Geum* vegetation extends its range into the more equable western Highlands and to lower altitudes around the oceanic seaboard of Scotland where, along with scattered *Blechnum spicant*, there can be occasional local prominence of *Athyrium filix-femina*, *Dryopteris dilatata*, *D. borreri* and *Thelypteris limbosperma*. Some strongly fern-dominated vegetation of this general kind is probably best included here (e.g. Prentice & Prentice 1975, Jermy & Crabbe 1978), but further sampling is needed to provide a clear picture of these assemblages and, for example, the *Osmunda regalis* stands described from South Uist by Spence (1960). Ledge vegetation with abundant *Silene dioica* or *Epilobium angustifolium*, often found around the nesting sites of golden eagles or peregrines, can also be provisionally included in the *Luzula-Geum* community.

Mixed in among the tall herbs of many stands of this vegetation are some sub-shrubs. *Vaccinium myrtillus* is the commonest of these, though it only exceptionally has the abundance characteristic of much of the *Luzula-Vaccinium* community. *V. vitis-idaea* can also be found, though it is frequent only in one particular kind of *Luzula-Geum* vegetation and even there sparse, and very occasionally there can be some *Empetrum nigrum*. *Calluna vulgaris* is somewhat commoner, though it becomes abundant only where the community extends to lower altitudes, where transitions to heath vegetation are more frequent. It is in such situations, too, that occasional saplings of *Sorbus aucuparia* and *Populus tremula* tend to be found in this community. *Juniperus communis* can sometimes occur, as well, while on higher crags Arctic-Alpine willows like *Salix lapponum*, *S. lanata* and *S. myrsinites* are occasionally recorded, thickening up locally to form a low bushy cover in transitions to *Salix-Luzula* scrub.

Smaller herbs tend to be not so numerous or abundant among the tall and luxuriant herbage of the *Luzula-Geum* community as in the *Dryas-Silene* vegetation that replaces it on more exposed calcareous outcrops, but some species are quite common throughout and, around the less shaded margins of stands, where the cover becomes fragmented into crevice vegetation, or where it grades off into grazed swards, richer mixtures of associates can be seen. Among the most frequent plants of this element overall are *Alchemilla alpina*, *Viola riviniana*, *Ranunculus acris*, *Campanula rotundifolia*, *Potentilla erecta*, *Galium saxatile*, *Thymus praecox*, *Selaginella selagionoides* and *Anemone nemorosa*. More unevenly distributed among the different sub-communities but sometimes quite common there are *Saxifraga aizoides*, *S. oppositifolia* and *S. hypnoides*, the first in particular able to show local abundance, *Carex pulicaris*, *Rubus saxatilis* and *Oxalis acetosella*. Then, more occasional throughout are *Coeloglossum viride*, *Carex binervis*, *Taraxacum officinale* agg., *Parnassia palustris* and *Huperzia selago*, with small ferns such as *Cystopteris fragilis* and *Asplenium viride* often marking transitions to narrow shelves and crevices. Various kinds of *Luzula-Geum* vegetation also provide a locus for the rare Arctic-Alpines *Poa glauca*, *P. alpina* and *Potentilla crantzii*, with a number of other rarities strongly preferential to the richest sub-community.

Even among the denser herbage, bryophytes are often an important component of this vegetation, frequently forming lush patches over the stools and litter of the tall herbs and occasionally thickening up to become virtual dominants in more extensive carpets. *Hylocomium splendens*, *Thuidium tamariscinum* and *Ctenidium molluscum* are among the commonest and most abundant species, with *Rhytidiadelphus triquetrus* and *R. squarrosus* also very frequent, though not usually of high cover, *R. loreus* somewhat patchy in its occurrence but locally prominent. Quite common, too, though generally as scattered individuals, are *Mnium hornum*, *Rhizomnium punctatum*, *Calliergon cuspidatum* and *Pseudoscleropodium purum*, with occasional *Drepanocladus uncinatus*, *Fissidens adianthoides*, *Breutelia chrysocoma*, *Pellia epiphylla*, *P. endiviifolia*, *Cratoneuron commutatum*, *Racomitrium lanuginosum*, *Plagiothecium denticulatum*, *Plagiomnium rostratum*, *Rhizomnium pseudopunctatum* and *Ditrichum flexicaule*. In addition to these, particular sub-communities can show considerable further enrichment with species such as *Dicranum scoparium*, *D. majus*, *Polytrichum alpinum*, *Plagiomnium undulatum*, *Bryum pseudotriquetrum*, *Philonotis fontana*, *Lophocolea bidentata s.l.* and *Plagiochila asplenoides*, while especially towards the more oceanic north-west of Scotland, the *Luzula-Geum* community can provide a locus for such North Atlantic rarities as *Leptodontium recurvifolium*, *Mastigophora woodsii*, *Oxystegus hibernicus*, *Plagiochila carringtonii* and *Scapania ornithopodioides*. Lichens are scarce but sometimes occasional thalli of *Peltigera canina* are to be found.

Sub-communities

***Alchemilla glabra-Bryum pseudotriquetrum* sub-community:** Ledge vegetation Ratcliffe 1960; *Sedum rosea-*

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Alchemilla glabra Association Birks 1973 *p.p.*; Cliff ledge communities Jermy & Crabbe 1978 *p.p.*; *Saxifraga aizoides-Festuca-Deschampsia* nodum Huntley 1979. In this sub-community, mixtures of *Geum rivale*, *Deschampsia cespitosa*, *Angelica sylvestris*, *Rhodiola rosea* and, especially noticeable here, *Alchemilla glabra*, generally dominate, with *Luzula sylvatica* very common though not usually abundant. More occasional, and typically present as scattered plants, are *Filipendula ulmaria*, *Succisa pratensis*, *Crepis paludosa*, *Rumex acetosa*, *Solidago virgaurea*, *Trollius europaeus*, *Thalictrum alpinum*, *Saussurea alpina*, *Oxyria digyna* and *Valeriana officinalis*. *Vaccinium myrtillus* is unusually scarce and other sub-shrubs rare.

Smaller herbs are rather variable in their occurrence and, in contrast to much *Luzula-Geum* vegetation, *Alchemilla alpina* is infrequent, but *Saxifraga aizoides* is quite common and sometimes abundant, forming lush patches, with scattered plants of *Ranunculus acris*, *Viola riviniana*, *Campanula rotundifolia*, *Selaginella*, *Saxifraga hypnoides* and *Carex flacca* and, weakly preferential here, *C. demissa*, *Pinguicula vulgaris*, *Chrysosplenium oppositifolium*, *Thalictrum minus* and *Tussilago farfara*.

The community mosses *Hylocomium splendens*, *Thuidium tamariscinum* and *Rhytidiadelphus triquetrus* are all less frequent than usual, but *Ctenidium molluscum* is common and locally abundant and particularly striking is the frequency of *Bryum pseudotriquetrum* with, more occasional though still preferential, *Philonotis fontana*, *Campylium stellatum*, *Scapania undulata*, *Blindia acuta*, *Aneura pinguis* and *Drepanocladus revolvens*. Also quite common are *Fissidens adianthoides*, *Plagiochila asplenoides* and *Rhizomnium punctatum* with the rare *Leptodontium recurvifolium* and *Herbertus stramineus* recorded from this vegetation on Skye (Birks 1973).

***Geranium sylvaticum* sub-community:** Tall-herb nodum McVean & Ratcliffe 1962 *p.p.*; *Alchemilla glabra-Sedum rosea* nodum Huntley 1979. This is the most distinctive and species-rich kind of *Luzula-Geum* vegetation, though stands show considerable variation in dominance and in the range of less frequent associates, which are particularly numerous. Along with the typical tall herbs of the community, each of which can be abundant, *Geranium sylvaticum*, *Trollius* and *Heracleum sphondylium* are especially characteristic and these, too, can share dominance. *Alchemilla glabra* remains common and can have locally high cover and there is very frequently some *Filipendula ulmaria* and *Succisa pratensis*. Less abundant than these, though tending to be more frequent than elsewhere in the community, are *Solidago virgaurea*, *Thalictrum alpinum*, *Saussurea alpina* and *Oxyria digyna* with montane Hieracia and *Polystichum lonchitis* quite strongly diagnostic but usually occurring as scattered individuals. *Cirsium heleonioides* is occasional and sometimes quite abundant and *Silene dioica* can become prominent close to ledge eyries. Then, mixed in among these taller herbs, though typically not in any abundance, are *V. myrtillus*, *V. vitis-idaea* and *Calluna* with occasional *E. nigrum* ssp. *hermaphroditum*.

Among smaller plants, *Festuca ovina/vivipara* and *Anthoxanthum* are both very frequent, with *Agrostis capillaris* and *Deschampsia flexuosa* occasional, but none of these is generally of high cover and only exceptionally do stands have a grassy appearance. *Alchemilla alpina* is more common than in the first sub-community and there is frequently some *Viola riviniana* and *Potentilla erecta*, with *Campanula rotundifolia* and *Polygonum viviparum* weakly preferential. More distinctive in this element, though again not usually abundant, are *Carex pulicaris*, *C. flacca*, *Rubus saxatilis*, *Galium boreale* and *Linum catharticum*, with *Saxifraga oppositifolia* sometimes joining *S. aizoides* which remains quite common here. Then, some stands have scattered plants of *Anemone nemorosa* and *Mercurialis perennis* or occasionals like *Rhinanthus minor*, *Lotus corniculatus* and *Huperzia selago* or smaller ferns such as *Asplenium viride*. This kind of *Luzula-Geum* vegetation also provides a locus for the rare Arctic-Alpine sedges *C. atrata*, *C. vaginata* and *C. rupestris*, the last rather easily confused with *C. pulicaris*, but typically having flatter, wider and more curled leaves with reddish sheaths (Jermy *et al.* 1982). Other stands have records for *Draba incana*, *Cerastium alpinum*, *Alchemilla filicaulis* ssp. *filicaulis* or the rare Continental Northern wintergreens *Pyrola rotundifolia* and *Orthilia secunda*.

Bryophytes are quite numerous and they can be extensive, with *Hylocomium splendens*, *Thuidium tamariscinum*, *Rhytidiadelphus triquetrus* and *Ctenidium molluscum* all constant and locally abundant, *R. squarrosus* and *Mnium hornum* common but usually sparse. Particularly diagnostic is the high frequency of *Dicranum scoparium*, *Hypnum cupressiforme s.l.*, *Plagiochila asplenoides* and *Tortella tortuosa*, with *Barbilophozia floerkii* occasional. Also present at low frequency are *Rhizomnium punctatum*, *Calliergon cuspidatum*, *Pseudoscleropodium purum*, *Bryum pseudotriquetrum*, *Drepanocladus uncinatus* and *Fissidens adianthoides*. *Rhytidiadelphus loreus* and *Dicranum majus* occur occasionally but these are more characteristic of the next sub-community.

***Agrostis capillaris-Rhytidiadelphus loreus* sub-community:** *Luzula-Angelica-Rumex* Community Spence 1960; Tall-Herb nodum McVean & Ratcliffe 1962 *p.p.*; *Deschampsietum caespitosae alpinum* McVean & Ratcliffe 1962 *p.p.* The most abundant of the bigger common herbs here are usually *Deschampsia cespitosa*, *Angelica sylvestris* and *Rhodiola* with *Luzula sylvatica* patchily prominent and *Geum rivale* very common but generally of sparse cover. *Filipendula ulmaria* and

Succisa pratensis remain frequent but *Alchemilla glabra* is only occasional. *Trollius* and *Geranium sylvaticum* are still sometimes found and they can be locally prominent with *Solidago virgaurea*, *Thalictrum alpinum*, *Saussurea* and *Oxyria* also occurring at low frequency. In contrast to the *Geranium* sub-community, however, grasses tend to be more important. *Anthoxanthum*, *Agrostis capillaris* and *A. canina* all become constant along with *F. ovina/vivipara*, the first two often with moderately high cover, and there is quite frequently a little *D. flexuosa*, *F. rubra* and *Nardus*. *Rumex acetosa* is very common and small amounts of *V. myrtillus* are often found with *Calluna* occasional.

The herbage can be quite tall here, but it is not so densely shading as elsewhere and, along with *Alchemilla alpina* and *Viola riviniana*, a number of smaller herbs are common. *Ranunculus acris* tends to be more frequent than elsewhere and *Galium saxatile*, *Oxalis acetosella*, *Cerastium fontanum*, *Alchemilla filicaulis* ssp. *vestita* and *Euphrasia officinalis* agg. (including *E. scottica*) are also weakly preferential. There is also occasional *Selaginella*, *Thymus praecox*, *Saxifraga aizoides*, *S. hypnoides*, *S. oppositifolia*, *Carex binervis* and *C. bigelowii*.

Bryophyte cover can be high with *H. splendens* especially frequent and abundant, *T. tamariscinum* and *R. triquetrus* also very common and patchily prominent, *C. molluscum*, *M. hornum* and *Rhizomnium punctatum* often occurring but with low cover. Most distinctive, though, is the high frequency and occasional abundance of *Rhytidiadelphus loreus*, *R. squarrosus*, *Dicranum majus* and *Lophocolea bidentata s.l.* with *Plagiomnium undulatum*, *Plagiothecium undulatum*, *Diplophyllum albicans*, *Pleurozium schreberi*, *Chiloscyphus polyanthos* and *Polytrichum alpinum* less common, but still preferential. *Dicranum scoparium*, *Hypnum cupressiforme s.l.*, *Calliergon cuspidatum*, *Drepanocladus uncinatus*, *Pseudoscleropodium purum* and *Breutelia chrysocoma* are also sometimes found.

***Primula vulgaris-Hypericum pulchrum* sub-community:** *Luzula-Dryopteris*, *Luzula-Deschampsia flexuosa-Rhinanthus* and *Luzula-Blechnum-Solidago* Communities Spence 1960; Tall-Herb nodum McVean & Ratcliffe 1962 *p.p.*, Prentice & Prentice 1975; *Sedum rosea-Alchemilla glabra* Association Birks 1973 *p.p.*; *Luzula sylvatica-Silene dioica* Association Birks 1973; Cliff ledge communities Jermy & Crabbe 1978. *Luzula sylvatica* is more abundant than usual in this sub-community, often sharing dominance with *Rhodiola*, *Angelica* and *Geum*. *D. cespitosa* is a little less common, though still locally abundant, and there can be prominent *Filipendula*, with frequent scattered plants of *Rumex acetosa*, *Succisa*, *Cirsium helenioides* and *Solidago*. *Alchemilla glabra*, though, is uncommon.

V. myrtillus is only very occasional and typically sparse but *Calluna* attains its peak of frequency here and it can be abundant, giving a distinctly heathy aspect to some stands. In other cases, ferns can assume local dominance: *Blechnum spicant* is very frequent but more noticeable on occasion is the high cover of *Athyrium filix-femina*, *Thelypteris limbosperma*, *Dryopteris filix-mas*, *D. dilatata*, *D. borreri* or *Osmunda*. And sometimes there are saplings of *Sorbus aucuparia* or *Populus tremula* with *S. rupicola* recorded on Skye (Birks 1973). *Hypericum pulchrum* is strongly preferential and very frequently there are scattered plants of *Primula vulgaris* and *Valeriana officinalis* with occasional *Epilobium montanum*, *Cirsium palustre*, *Silene dioica*, *Plantago lanceolata* and *Hyacinthoides non-scripta*. *Carex panicea* and *C. binervis* sometimes accompany *C. pulicaris* and there is occasionally some *Holcus lanatus*, but, apart from *Festuca ovina/vivipara* and *Anthoxanthum*, fine-leaved grasses are not very common. Other smaller herbs commonly found here are *Potentilla erecta*, *Viola riviniana*, *Ranunculus acris*, with occasional *Selaginella*, *Thymus*, *Alchemilla alpina* and *Anemone nemorosa*.

As elsewhere, bryophytes can have high cover in this sub-community, but the abundant species are few, with *H. splendens* often the most extensive moss. Also frequent, though usually more sparse, are *T. tamariscinum*, *R. triquetrus*, *M. hornum* and *C. molluscum*, with *R. loreus*, *R. squarrosus*, *D. majus* and *Plagiomnium undulatum* occasional. Preferential species are few but *Eurhynchium praelongum*, *Frullania tamarisci* and *Hylocomium brevirostre* occur at low frequency.

Habitat

The *Luzula-Geum* community develops where there is protection from grazing and burning on more base-rich and mesotrophic soils in sheltered situations on damp, inaccessible ground through the cold, wet mountains of northern Britain. It is widespread, though characteristically local, on exposures of calcareous rocks at moderate to high altitudes in the Scottish Highlands, with fragmentary stands further south. Towards its upper limit in the sub-alpine zone, moderate snow cover enhances humidity and shelter but, with only sporadic invasion by montane willows, this vegetation can be considered a virtual climax there, with floristic variation dependent on the amount of irrigation and the extent of any sporadic grazing. Towards lower altitudes, which the *Luzula-Geum* community attains around the north-west seaboard of Scotland, the cool, equable climate maintains the required humidity and also lends the vegetation a more oceanic character, with partial progression to heath or scrub being more usual.

Like the *Luzula-Vaccinium* community, its counterpart on more base-poor and oligotrophic soils, this is a vegetation type of more inaccessible situations in the uplands and, as there, it is generally broken topography

which provides the protection from grazing and burning necessary for luxuriant growth of the palatable and fire-sensitive herbs. For the most part, then, the *Luzula-Geum* community is confined to ledges on cliffs and crags and in ravines, to ground among or on top of boulders and to islands in lakes where stock and deer, which have virtually unhindered access to the open slopes, penetrate only rarely, if at all. In such situations, the stands are often small and isolated, physical features which account for both the fragmentary nature of much of this vegetation and its frequent peculiarities of composition and structure. Sometimes, more extensive tracts are found, as where the community contributes to the tall-herb cover on the great Coire na Poite ledge on Beinn Bhan in Ross and other mountain slopes cut off by cliffs (McVean & Ratcliffe 1962). And there are places where big stands run off from ledges on to steep, but somewhat more accessible, hillsides where there is probably some light or occasional grazing, but this vegetation is not usually found on the more open cliff tops, slopes and summits where the *Luzula-Vaccinium* community can persist.

A further feature which contributes to the highly localised occurrence of the *Luzula-Geum* vegetation and which accounts for most of its floristic differences from the *Luzula-Vaccinium* community, is its dependence on base-enrichment from calcareous rocks or waters flushing from them. Among the range of tall-herb assemblages able to exploit freedom from grazing and burning in British mountains, this community includes all the more basiphilous and mesophytic. Typically, it marks out lime-rich rocks such as the limestones and calcareous metasediments and intrusions that support some of the most renowned stands in the Grampians between Breadalbane and Clova, and the more sporadic calcareous exposures among Moine rocks and Lewisian gneiss towards the north and west of Scotland. On Skye and Mull, Tertiary basalts can carry this kind of vegetation, with gabbro important too on the former island. Then, further south, limy partings in the Silurian rocks of the Moffat Hills, calcareous sections of the Borrowdale Volcanics in the Lake District and calcareous intrusions into the Ordovician rocks of Cader Idris support some far-flung stands.

Across this range, rainfall is everywhere high, always in excess of 1600 mm yr^{-1} (*Climatological Atlas* 1952), with at least 180 wet days annually (Ratcliffe 1968), with much wetter conditions where the community extends into the west of Scotland. Here, though, in contrast to conditions beneath the *Luzula-Vaccinium* vegetation, the strong tendency for surface leaching is offset by weathering of the lime-rich substrates, particularly where these are soft like the mica-schists, or by at least periodic irrigation with waters seeping through them. The soils vary considerably in depth, but they are usually loamy or silty in texture, with mull humus rather than moder, approaching brown earths where they show any degree of maturity. Surface pH is generally above 5, the upper limit for most soils beneath the *Luzula-Vaccinium* community, and sometimes as high as 7, with calcium up to eight times more plentiful in the profile (McVean & Ratcliffe 1962). Flushing with groundwater, snow-melt or precipitation run-off from the slopes above keeps the soils moist, and a shaded and sheltered aspect often reduces evapo-transpiration, such that the herbage can be kept dripping wet. Generally, though, there is a strong through-put of irrigating waters, so aeration in the profiles is typically good, incorporation of the substantial amounts of lush litter rapid and turnover of nutrients probably brisk.

All these edaphic features are reflected in the general composition of the *Luzula-Geum* community. Compared with the *Luzula-Vaccinium* vegetation, for example, the greater species-richness here and, in particular, the diversity of more basiphilous and mesophytic plants, are very marked. Calcifuge sub-shrubs, like *V. myrtillus*, *V. vitis-idaea* and even *Calluna*, can still play a part, sometimes with herbs and bryophytes of acid grasslands and heaths, but abundance of such species is the exception rather than the rule. Demanding calcicoles, in the sense of McVean & Ratcliffe (1962), are relatively few, though *Polystichum lonchitis* and *Saxifraga oppositifolia* are characteristic plants of this vegetation, with *Carex atrata*, *C. vaginata*, *C. rupestris*, *Draba incana* and *Potentilla crantzii*. More striking is the frequency throughout of *Geum rivale*, *Angelica sylvestris*, *Rhodiola rosea*, *Alchemilla glabra*, *Viola riviniana*, *Ranunculus acris*, *Filipendula ulmaria*, *Succisa pratensis*, *Crepis paludosa*, *Selaginella selaginoides* and *Thymus praecox* with *Carex pulicaris*, *C. flacca*, *Trollius europaeus*, *Geranium sylvaticum*, *Rubus saxatilis*, *Thalictrum alpinum*, *Heracleum sphondylium*, *Saussurea alpina*, *Oxyria digyna*, *Saxifraga aizoides*, *Primula vulgaris* and *Valeriana officinalis* common in one or other of the sub-communities. Among the bryophytes, the combination of *Thuidium tamariscinum*, *Rhytidiadelphus triquetrus*, *Ctenidium molluscum*, *Rhizominium punctatum*, *Calliergon cuspidatum* and *Pseudoscleropodium purum* reflects the same edaphic conditions. The only other context in which these plants occur together with any regularity is in the understorey of some stands of the *Salix-Luzula* scrub, which is fairly clearly a successional development from the *Luzula-Geum* vegetation where Arctic-Alpine willows have been able to get a hold on more mesotrophic soils in the absence of grazing. Occasional bushes do occur here, but the general scarcity of these plants is a good distinction between the two vegetation types.

The other obvious floristic affinity of this kind of assemblage is with the more basiphilous of the Arrhenatherion grasslands and tall-herb vegetation of lower,

warmer altitudes, of which the *Luzula-Geum* community can be seen as a montane counterpart. Transitional vegetation, with such Continental Northern and Northern Montane plants as *Cirsium helenioides*, *Geranium sylvaticum* and *Trollius europaeus*, is found in more inhospitable parts of the northern Pennines, persisting on moist, brown soils around the margins of woodlands, on ungrazed river banks and in traditionally treated hay-meadows. Here, there is a further shift towards a montane character, most stands occurring between 500 and 800 m where mean annual maximum temperatures are generally less than 21 °C, a little higher outside the Scottish Highlands (Conolly & Dahl 1970). Predominantly lowland plants like *Arrhenatherum elatius* thus become much scarcer, and the vegetation is enriched with Arctic-Alpines tolerant of partial shade or able to get an occasional hold in more open patches of herbage. *Rhodiola*, *Alchemilla alpina*, *Saussurea*, *Oxyria*, *Saxifraga aizoides* and *S. oppositifolia* all belong to this diagnostic group with, more rarely, *Draba incana*, *Carex atrata*, *C. vaginata*, *C. rupestris*, *Cerastium alpinum*, *Alchemilla filicaulis* ssp. *filicaulis*, *Poa glauca*, *P. alpina* and *Potentilla crantzii*. Most of these occur in other vegetation types characteristic of bleak localities in the British uplands but, together with the more widely distributed tall herbs of this community, they form a unique assemblage, and outlying stands of the *Luzula-Geum* vegetation provide an important locus for some of them towards the southern limit of their British ranges, as for example in the Moffat Hills (Ratcliffe 1959*b*), on Helvellyn and some other peaks in the Lake District (Ratcliffe 1960), and on Cader Idris (Edgell 1969, Ratcliffe 1977).

The scarcity of smaller Arctic-Alpine herbs and bryophytes is a consequence of the vigorous growth of the bulkier plants of the community, favoured not only by protection from grazing and the moist and more enriched character of the soils here, but also by shelter, not just from such drying sunlight as penetrates the frequent cloud cover, but also from wind and frost. For, though this is a vegetation type of less hospitable altitudes, it is usually found in locally sheltered situations. Many stands have a northerly or easterly aspect, clinging to cliffs which are protected from the prevailing south-west winds, these bitterly cold in winter. Shelter and shade also encourage the accumulation and persistence of snow: detailed observations are still lacking, but McVean & Ratcliffe (1962) considered that the vegetation included here in the *Geranium* and *Agrostis-Rhytidiadelphus* sub-communities probably carries a fairly thick accumulation in most winters, though melting out early in the spring. The difference which such protection makes is best seen by comparing the *Luzula-Geum* community with the *Dryas-Silene* vegetation, which replaces it on calcareous crags where herbage and soils are exposed to the full force of harsh winds and frost.

The most distinctive kind of *Luzula-Geum* vegetation, that of the *Geranium* sub-community, is characteristic of situations where all these environmental conditions are met. It is concentrated at higher altitudes and on the steepest, most inaccessible ledges, so has the best representation of grazing-sensitive plants and montane species. But it is consequently very local, occurring at scattered localities from Caenlochan in the east, through the Ben Lawers range to Ben Nevis and Beinn Laoigh in the west, with only fragmentary stands north of the Great Glen, where *Geranium sylvaticum* and *Heracleum* become very scarce. With all its floristic richness it has also suffered greatly from collectors unable to resist the seductive combination of very rare plants growing in hazardous places.

The *Agrostis-Rhytidiadelphus* sub-community, preserving much of the same general character as the *Geranium* type and having sporadic records for its numerous preferentials, includes more fragmentary and impoverished stands of *Luzula-Geum* vegetation on ledges through the central Highlands, together with the richest of the tall-herb vegetation north of the Great Glen on mountains like Beinn Dearg, Beinn Eighe and Foinaven. But it also extends on to somewhat more accessible slopes than the *Geranium* sub-community, where sporadic grazing is insufficient to eliminate the characteristic dicotyledons but reduces them to more occasional basal rosettes in a much grassier ground. The abundance of *Deschampsia cespitosa*, *Agrostis* spp., *Anthoxanthum*, *Galium saxatile* and bryophytes like *Rhytidiadelphus loreus*, *R. squarrosus* and *Dicranum majus* provides a strong link with the *Deschampsia-Galium* grassland, a community of cold, irrigated mountain slopes, where there has often been at least some grazing influence. And the *Agrostis-Rhytidiadelphus* sub-community is perhaps quite frequently an anthropogenic transition to such vegetation where irrigation brings a measure of base-enrichment to steep ground that provides an occasional bite.

Snow-lie and irrigation from melt-water may be of considerable importance in maintaining moist ground conditions in the above kinds of *Luzula-Geum* vegetation, though flushing is not necessarily constant. The *Alchemilla-Bryum* sub-community, on the other hand, seems to be characteristic of sites with more or less continuous seepage, the preferential frequency of plants such as *S. aizoides*, *Bryum pseudotriquetrum* and *Philonotis fontana* providing a floristic connection with assemblages of dripping, base-rich banks and spring surrounds. With its more sparse Arctic-Alpine element, the *Alchemilla-Bryum* sub-community takes in some of the *Luzula-Geum* stands outside the coldest parts of the Highlands and in southern Scotland, the Lakes and

Wales, though this is still largely a vegetation type of higher altitudes.

With a decisive shift to lower ground along the north-west seaboard of Scotland, the *Primula-Hypericum* sub-community becomes the characteristic kind of tall-herb vegetation on more base-rich, mesotrophic soils on ledges and in ravines and, particularly frequent here, on lake islands. Stands can be found on mountains in the north-west Highlands but are especially typical of sites below 300 m on Rhum, Skye, Uist, Orkney and Shetland. Throughout this zone, the climate is extremely humid, so the vegetation is less dependent on flushing with ground-water, though with frequent high winds, a sheltered aspect is preferred, which provides additional protection from drying sun. Also important is the equable temperature regime, with February minima here often above freezing at sea-level (*Climatological Atlas* 1952). This kind of *Luzula-Geum* vegetation sometimes provides a low-altitude locus for Arctic-Alpine herbs like *Saussurea* and *Oxyria*, but these do not make up a constant element in the flora and more obvious is the frequency and abundance of less montane and more oceanic plants, notably ferns. With less consistent flushing to offset leaching, the vegetation is also not nearly so basiphilous, *Calluna*, *Hypericum pulchrum* and *Lathyrus montanus* all indicative of surface pH that is often not much above 5. Freedom from grazing at these altitudes also allows more ready spread of sub-shrubs and saplings such that this kind of *Luzula-Geum* vegetation often has a heathy or scrubby aspect.

Zonation and succession

Usually, the inaccessibility necessary for the development of the *Luzula-Geum* community means that stands occur set apart from the grasslands and heaths of surrounding montane slopes among tracts of broken, rocky ground. Other herb and fern-dominated communities can share such ledge and cliff habitats, the vegetation types disposed according to variations in base-richness and wetness of the soils and the amount of exposure to wind and frost, with patchy occurrence of scrub representing the but sporadic succession to woody vegetation that is possible in isolated ungrazed situations in the sub-alpine zone. At lower altitudes towards the more oceanic west of Scotland, seral progression to sub-montane scrub is more probable, although burning is especially likely there to convert stands to heath.

The floristic and structural contrasts between the *Luzula-Geum* vegetation and its grazed counterparts on moist, base-rich and mesotrophic soils at similar altitudes are seen most clearly and instructively in the Breadalbane range and around Caenlochan in the Grampians, where corries and their adjacent slopes cut into calcareous rocks offer sites which are to varying degrees inaccessible to stock and deer. In these mountains, the *Geranium* sub-community occupies many of the most isolated ledges and crags where there is some shelter, with *Deschampsia cespitosa*-dominated swards on irrigated and often moderately snow-bound, though stable, hillsides around. The less basiphilous of this vegetation, developing where seepage is insufficient to offset leaching, can be included in the *Deschampsia-Galium* grassland, the *Anthoxanthum-Alchemilla* sub-community of which has occasional records for some of the characteristic *Luzula-Geum* herbs. Very often, though, the soils are sufficiently calcareous and mesotrophic to support richer vegetation than this over the open slopes, swards which experience at least some grazing, are grass-dominated with herbs nibbled down to rosettes, but often qualitatively indistinguishable from the *Agrostis-Rhytidiadelphus* sub-community of the *Luzula-Geum* vegetation. This is what McVean and Ratcliffe (1962) characterised as species-rich *Deschampsietum caespitosae alpinum*, and it forms a virtual continuum with tall-herb stands of the community where there is a gradual increase in slope or increasing fragmentation of the ground into systems of ledges running out on to cliffs.

In other places, the *Geranium* or the somewhat less rich *Agrostis-Rhytidiadelphus* sub-community, are found sharply separated by expanses of bare rock from *Deschampsia-Galium* swards or more high-altitude tracts of anthropogenic *Festuca-Agrostis-Thymus* or *Festuca-Agrostis-Alchemilla* grasslands where the surrounding grazed slopes are but modestly flushed. Sometimes, the *Luzula-Geum* vegetation occupies all available ledges in such cliff and ravine systems, but quite often there is some variety in the cover. Geological differences across outcrops, for example, or variations in the extent of flushing, can result in the juxtaposition of tall-herb stands of contrasting composition, more base-poor and oligotrophic soils often showing a shift to the *Luzula-Vaccinium* community. Such patterns are especially well seen through the western Highlands, where calcareous rocks tends to be of more localised occurrence. On Ben Hope, for example, calcareous hornblende schists provide some local enrichment in granulite outcrops, while in the Letterewe Forest there are Serpulite Grits and Fucoid Beds among Lewisian gneiss. Then, on the Bens Griam and North Hoy in Orkney, variations in Old Red Sandstone, and on Skye differences in Tertiary basalts can show this kind of variation (Birks 1973, Prentice & Prentice 1975, Ratcliffe 1977). Most celebrated of all, perhaps, is the variegation in the tall-herb cover on the great Coire na Poite ledge on Beinn Bhan, where base-rich seepage from the Torridonian Sandstone cliffs is marked by stripes of the *Luzula-Geum* community among stretches of *Luzula-Vaccinium* vegetation. The differences between the two assemblages can be very striking, with the much greater richness of

basiphile and mesophytic herbs in the *Luzula-Geum* community, but intergradations do occur, and increasingly towards the more oceanic west of Scotland, the great abundance of ferns in ungrazed vegetation often masks floristic variation among the smaller associates. The *Primula-Hypericum* sub-community in particular, the predominant form of the *Luzula-Geum* vegetation at lower altitudes through the Western Isles, Orkney and Shetland, can come very close in its composition to the *Luzula-Vaccinium* community (Spence 1960, Prentice & Prentice 1975).

On more calcareous mountains, as through Breadalbane, the *Luzula-Geum* vegetation is often the only tall-herb community, but differences in the amount of seepage and the degree of exposure can mediate transitions to other kinds of cliff and knoll vegetation. Where irrigation with base-rich water over rock faces is strong and constant, for example with soils and herbage kept in a dripping-wet condition, the *Luzula-Geum* community is typically replaced by the *Saxifraga-Alchemilla* vegetation. The *Alchemilla-Bryum* sub-community can be seen as transitional to this, and plants such as *Deschampsia cespitosa*, *Alchemilla alpina*, *A. glabra*, *Carex pulicaris*, *Thalictrum alpinum*, *Polygonum viviparum*, *Ranunculus acris*, *Ctenidium molluscum* and *Bryum pseudotriquetrum* continue to be very frequent, with other species like *Geum rivale*, *Rhodiola*, *Oxyria* and *Luzula sylvatica* also occurring occasionally. But in the *Saxifraga-Alchemilla* vegetation, dominance generally passes to *S. aizoides* and *S. oppositifolia*, which form sopping banks, hanging down over rock faces and earth slopes, with the other herbs scattered through. Some other plants, like *Pinguicula vulgaris*, *Parnassia palustris*, *Blindia acuta* and *Aneura pinguis*, also become very much more common.

A very different kind of transition, though equally characteristic of the calcareous crags of the Breadalbane mountains, is seen where ungrazed ledges become more exposed to the effects of fierce winds and, being blown clear of snow, to winter frosts. In such places, the *Dryas-Silene* community is the typical kind of vegetation, its varied patchworks of basiphile dwarf shrubs, tall herbs, cushion plants, grasses, sedges and bryophytes reflecting the skeletal, calcareous nature of the soils, subject to much freeze-thaw and solifluction. Some plants, like *Succisa*, *Angelica*, *Geranium sylvaticum*, *Alchemilla alpina*, *A. glabra*, montane Hieracia, *Geum rivale*, *Filipendula ulmaria*, *Rhodiola*, *Saussurea* and *Luzula sylvatica* can, by virtue of their locally luxuriant growth, give a measure of continuity between the *Dryas-Silene* community and the *Luzula-Geum* vegetation. Usually, however, where sheltered ledges pass above to windswept brows or, with a shift of aspect, are replaced by more exposed shelves of rock, the floristic and physiognomic changes are very striking. Many of the bulkier plants either disappear or become stunted in their growth and other species, crowded out among the tall-herb growth, are much more frequent: in particular, *Dryas octopetala*, *Thymus praecox*, *Silene acaulis*, *Ditrichum flexicaule* and *Tortella tortuosa* become a constant feature among the low carpets of these bleak crags. Transitions from such vegetation to grazed swards around are often marked by a switch to the *Festuca-Alchemilla-Silene* community, a parallel pattern to that involving the *Luzula-Geum* and *Deschampsia-Galium* communities, and mosaics of all four vegetation types are a memorable feature of parts of Ben Lawers, Meall Ghaordie, Beinn Laoigh and Caenlochan–Clova (Ratcliffe 1977).

Arctic-Alpine willows, particularly *Salix lapponum*, occasionally find a place in stands of both the *Luzula-Geum* and *Dryas-Silene* communities on high-altitude crags, and there seems little doubt that such colonisation can be a step towards the development of *Salix-Luzula* scrub, the climax woody vegetation of the low-alpine zone in the Scottish Highlands. In fact, invasion of this kind is often very problematic, because seed-parents are widely scattered, frequently growing in single-sex populations (Poore & McVean 1957), colonisation sites likewise very local and growth upon them perhaps so luxuriant as to prevent germination of fertile seed. Commonly, then, the *Luzula-Geum* community at these altitudes is an effective climax vegetation.

At lower levels, towards the western seaboard of Scotland, there is less climatic restriction on the succession of ungrazed tall-herb vegetation to scrub or woodland, although again seed-parents are often very local in their distribution. A likely development here, from the *Primula-Hypericum* sub-community, would be some kind of *Fraxinus-Sorbus-Mercurialis* woodland, probably dominated by *Sorbus aucuparia* and *Betula pubescens*: indeed, saplings of these are sometimes found in tall-herb vegetation in this region.

Distribution

Apart from a few far-flung outliers in the Southern Uplands, the Lake District and north Wales, the *Luzula-Geum* community is entirely confined to the Scottish Highlands and the Isles, and is even there a local vegetation type. The *Geranium* sub-community is the rarest form, largely restricted to the Grampians, with the *Agrostis-Rhytidiadelphus* sub-community somewhat more common and widespread. The *Alchemilla-Bryum* type occurs scattered throughout the range, taking in most of the more remote stands, while the *Primula-Hypericum* sub-community has a distinctly oceanic distribution, being limited to the western Highlands and Isles, Orkney and Shetland.

Affinities

Since McVean & Ratcliffe (1962) provided the first systematic account of the more species-rich tall-herb

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vegetation of the Scottish Highlands, further sampling has characterised a variety of related assemblages from there and elsewhere in Britain (Edgell 1969, Birks 1973, Prentice & Prentice 1975, Jermy & Crabbe 1978, Huntley 1979). The *Luzula-Geum* community provides a convincing integration of these data, and of earlier more general accounts of ungrazed montane vegetation (Smith 1911*b*, Ratcliffe 1959*b*, 1960, Spence 1960), and brings some order to the variation which McVean & Ratcliffe (1962) recognised but were unable to define clearly.

With systematic description of mesotrophic swards throughout Britain, it is also possible to see the *Luzula-Geum* community as a continuation into the sub-alpine zone of floristic trends already visible in the upland fringes. On cold, damp slopes on the Derbyshire and Craven Carboniferous Limestone, for example, and in a few places further north, the ungrazed vegetation of the *Filipendulo-Arrhenatheretum* begins to acquire something of a montane character. Similar developments can be seen in the *Anthoxanthum-Geranium* grassland, a community of traditionally treated hay-meadows on unimproved brown soils in the bleak north Pennines and rank transitions to scrub in field margins and stream sides there and on some Scottish river banks. With frequent records for Continental Northern and Northern Montane plants such as *Geranium sylvaticum*, *Cirsium helenioides* and *Trollius europaeus*, these vegetation types represent the nearest approach among the British Arrhenatherion to the Cicerbition alpini tall-herb assemblages of the sub- and low-alpine zones of northern Europe, and indeed they provide a southern locus for some Arctic-Alpine herbs like the rare lady's mantles of the *Alchemilla vulgaris* aggregate (Walters 1949).

But it is only in the *Luzula-Geum* community that this Arctic-Alpine element finds full expression and, though the vegetation is, as McVean & Ratcliffe (1962) put it, unorganised and fragmentary, it is the major British Cicerbition assemblage. In this scheme, the more oligotrophic tall-herb stands of this alliance remain separated off, as with McVean & Ratcliffe (1962), in a *Luzula-Vaccinium* community, although there is a fairly continuous gradation through the whole series, something that is very clear with the kind of oceanic perspective provided by Spence (1960), Birks (1973), Prentice & Prentice (1975) and Jermy & Crabbe (1978). The relationship of the *Luzula-Vaccinium* vegetation and the *Primula-Hypericum* sub-community, the kind of *Luzula-Geum* vegetation that comes closest to it, to the sub-montane fern communities that are so striking along the western Scottish seaboard, needs further investigation.

Clearly, though, the *Geranium* sub-community is well marked off from the more impoverished *Luzula-Vaccinium* vegetation and represents the nearest British equivalent to assemblages like the *Geranietum sylvatici alpicolum* described from very similar habitats in Norway by Nordhagen (1943) and Dahl (1956): the *Deschampsia flexuosa* variant of Nordhagen's community is particularly close to Scottish stands. Related tall-herb vegetation has also been characterised from Swedish Lappland (Rune 1965), Greenland (Böcher 1954) and Iceland (Steindorsson 1945). As in Scandinavia, there is a continuous transition from this rich kind of Cicerbition vegetation to sub-alpine birch and willow scrub of the Salicion arbusculae in Scotland, although seral progression to the *Salix-Luzula* scrub, the British climax in this habitat, is a haphazard affair.

As for the other affinities of the *Luzula-Geum* vegetation the *Agrostis-Rhytidiadelphus* sub-community provides a link mediated partly by grazing, partly by reduction in soil base-status, with the more impoverished *Deschampsia-Galium* swards of the Deschampsieto-Anthoxanthion. The *Alchemilla-Bryum* sub-community, by contrast, gives a connection through the dripping, basiphilous banks of the *Saxifraga-Alchemilla* vegetation, a Ranunculo-Anthoxanthion assemblage, with calcareous springs and mires.

Floristic table U17

	a	b	c	d	17
Luzula sylvatica	V (1–6)	V (1–4)	V (1–6)	V (1–8)	V (1–8)
Geum rivale	IV (1–3)	V (1–4)	V (1–6)	V (1–5)	V (1–6)
Deschampsia cespitosa	V (1–6)	V (1–4)	V (1–8)	III (1–4)	V (1–8)
Angelica sylvestris	IV (1–4)	V (1–4)	IV (1–6)	IV (1–6)	IV (1–6)
Rhodiola rosea	IV (1–6)	V (1–4)	IV (1–5)	IV (1–6)	IV (1–6)
Festuca ovina/vivipara	IV (1–4)	IV (1–4)	V (1–6)	IV (1–4)	IV (1–6)
Hylocomium splendens	I (4)	V (1–4)	V (1–8)	IV (1–6)	IV (1–8)
Alchemilla glabra	V (1–6)	V (1–4)	II (1–6)	II (1–4)	III (1–6)
Bryum pseudotriquetrum	IV (1–4)	II (1–3)	I (1–3)	I (1–3)	II (1–4)
Saxifraga aizoides	III (1–4)	III (1–6)	II (1–3)	I (1–4)	II (1–6)
Philonotis fontana	III (1–3)	I (1–3)	I (1–3)	I (4)	I (1–4)
Pinguicula vulgaris	II (1–3)	I (1)	I (2)	I (1–3)	I (1–3)
Campylium stellatum	II (1–4)	I (1)	I (1–3)	I (4)	I (1–4)
Tussilago farfara	II (1–4)	I (4)	I (1–4)		I (1–4)
Scapania undulata	II (1–3)	I (1–2)	I (1)		I (1–3)
Aneura pinguis	II (1–3)	I (1)	I (1–3)	I (1)	I (1–3)
Blindia acuta	II (1–4)	I (1)		I (1–4)	I (1–4)
Chrysosplenium oppositifolium	II (1–3)		I (1)		I (1–3)
Carex demissa	II (1–4)				I (1–4)
Thalictrum minus	II (1–4)				I (1–4)
Alchemilla alpina	II (1–3)	IV (1–4)	IV (1–4)	III (1–4)	III (1–4)
Vaccinium myrtillus	I (1)	IV (1–3)	IV (1–6)	II (1–6)	III (1–6)
Anthoxanthum odoratum	II (1–4)	IV (1–4)	IV (1–4)	III (1–4)	III (1–4)
Thuidium tamariscinum	I (1–3)	IV (1–8)	IV (1–6)	III (1–4)	III (1–8)
Rhytidiadelphus triquetrus	I (1–4)	IV (1–4)	IV (1–4)	III (1–4)	III (1–4)
Viola riviniana	III (1–3)	V (1–3)	III (1–3)	III (1–4)	III (1–4)
Ctenidium molluscum	III (1–4)	V (1–4)	III (1–3)	III (1–4)	III (1–4)
Carex pulicaris	I (1–4)	V (1–4)	II (1–4)	III (1–4)	III (1–4)
Solidago virgaurea	II (1–3)	IV (1–3)	II (1–3)	III (1–4)	III (1–4)
Rubus saxatilis	I (4)	IV (1–4)	II (1–4)	II (1–4)	II (1–4)
Trollius europaeus	III (1–4)	IV (1–4)	II (1–4)	II (1–4)	II (1–4)

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Geranium sylvaticum	I (1–4)	V (1–6)	II (1–5)		II (1–6)
Thalictrum alpinum	III (1–3)	IV (1–3)	II (1–3)	II (1–4)	II (1–4)
Plagiochila asplenoides	II (1–3)	IV (1–3)	II (1–3)	I (1)	II (1–3)
Dicranum scoparium	I (4)	IV (1–3)	II (1–3)	I (1)	II (1–4)
Campanula rotundifolia	II (1–3)	IV (1–3)	II (1–3)	I (1–2)	II (1–3)
Carex flacca	II (1–4)	IV (1–4)	I (1–4)	I (1)	II (1–4)
Vaccinium vitis-idaea	I (1–4)	IV (1–4)	II (1–3)	I (1)	II (1–4)
Hieracium spp.	I (1–3)	IV (1–3)	I (1)	II (1–3)	II (1–3)
Heracleum sphondylium	I (1–3)	IV (1–4)	I (1–4)	I (1)	II (1–4)
Polystichum lonchitis		IV (1–3)	I (1–3)	I (1–3)	II (1–3)
Saussurea alpina	II (1–6)	III (1–4)	II (1–4)	I (1–4)	II (1–6)
Oxyria digyna	II (1–4)	III (1–3)	II (1–4)	I (1–3)	II (1–4)
Polygonum viviparum	II (1–3)	III (1–3)	II (1–3)		II (1–3)
Saxifraga oppositifolia	I (1–3)	III (1–4)	II (1–3)	I (1)	II (1–4)
Hypnum cupressiforme	I (1)	III (1–4)	II (1–3)	I (1–3)	II (1–4)
Anemone nemorosa	I (1–4)	III (1–3)	I (1–4)	II (1–4)	II (1–4)
Tortella tortuosa	I (1–4)	III (1–4)	I (1)	I (1)	I (1–4)
Galium boreale	I (1)	III (1–4)	I (1)	I (1–4)	I (1–4)
Linum catharticum	I (1)	III (1–3)	I (1–2)	I (1–3)	I (1–3)
Rhinanthus minor	I (1–3)	III (1–3)	I (1–3)		I (1–3)
Silene acaulis		III (1–3)	I (1–2)	I (1)	I (1–3)
Draba incana	I (1)	II (1–2)	I (1)	I (1)	I (1–2)
Asplenium viride	I (1)	II (1–2)	I (1)	I (1)	I (1–2)
Lotus corniculatus	I (1)	II (1–4)	I (1)	I (1–3)	I (1–4)
Salix cinerea	I (1)	II (1–2)	I (1)	I (1)	I (1–2)
Carex atrata	I (1)	II (1–3)	I (1–2)		I (1–3)
Carex vaginata	I (4)	II (1–4)	I (1)		I (1–4)
Empetrum nigrum hermaphroditum	I (4)	II (1–3)	I (1–4)		I (1–4)
Huperzia selago	I (1–3)	II (1–3)	I (1–3)		I (1–3)
Pyrola rotundifolia	I (1)	II (1–4)	I (1)		I (1–4)
Orchis mascula		II (1–4)	I (1)	I (1–3)	I (1–4)
Alchemilla filicaulis filicaulis		II (1–4)	I (1–6)	I (1–3)	I (1–6)
Cerastium alpinum		II (1–3)	I (1)		I (1–3)
Barbilophozia floerkii		II (1–3)	I (1–2)		I (1–3)
Arabis hirsuta		II (1)	I (1)		I (1)
Mercurialis perennis		II (1–4)	I (1)		I (1–4)

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Floristic table U17 (*cont.*)

	a	b
Orthilia secunda		II (1–3)
Betula pubescens seedling		II (1–4)
Dryas octopetala		I (1)
Rumex acetosa	II (1–4)	I (1)
Ranunculus acris	III (1–4)	I (1)
Rhytidiadelphus squarrosus	I (1)	III (1–4)
Rhytidiadelphus loreus	I (1)	II (1–3)
Agrostis capillaris	I (1)	II (1–4)
Lophocolea bidentata s.l.	I (1)	II (1)
Agrostis canina	I (1)	I (1–2)
Deschampsia flexuosa	I (1)	II (1)
Dicranum majus	I (1)	II (1–3)
Plagiomnium undulatum		II (1–3)
Galium saxatile		II (1–3)
Oxalis acetosella	I (1)	
Polytrichum alpinum		
Cerastium fontanum	I (1)	I (1)
Euphrasia officinalis agg.	I (1)	I (1)
Chiloscyphus polyanthos		I (1)
Diplophyllum albicans		I (1–2)
Alchemilla filicaulis vestita		I (1)
Plagiothecium undulatum		
Pleurozium schreberi		
Carex bigelowii		
Sphagnum capillifolium		
Hylocomium umbratum		
Calluna vulgaris	I (1)	III (1–4)
Hypericum pulchrum	I (1)	I (1)
Valeriana officinalis	II (1–4)	I (1)
Blechnum spicant		I (1)
Primula vulgaris		

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

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Lathyrus montanus	I (1)	I (1)
Epilobium montanum	I (1)	I (1)
Silene dioica	I (1)	I (1–5)
Dryopteris filix-mas	I (1)	I (1)
Cirsium palustre	I (1)	
Thelypteris limbosperma		I (1)
Plantago lanceolata		I (1)
Athyrium filix-fermina		
Carex panicea		
Hylocomium brevirostre		
Eurhynchium praelongum		
Holcus lanatus		
Dryopteris borreri		
Sorbus aucuparia seedling		
Frullania tamarisci		
Hyacinthoides non-scripta		
Teucrium scorodonia		
Filipendula ulmaria	III (1–2)	IV (1–4)
Succisa pratensis	II (1–3)	V (1–6)
Mnium hornum	I (1–3)	III (1–3)
Potentilla erecta	I (1–3)	IV (1–4)
Rhizomnium punctatum	III (1–4)	II (1–3)
Festuca rubra	II (1–4)	I (1–5)
Crepis paludosa	II (1–3)	II (1)
Selaginella selaginoides	II (1–3)	II (1–3)
Calliergon cuspidatum	I (4)	II (1–3)
Thymus praecox	I (1–3)	II (1–3)
Pseudoscleropodium purum		II (1–3)
Nardus stricta	I (1–3)	II (2–4)
Saxifraga hypnoides	II (1–4)	I (1)
Drepanocladus uncinatus	I (1)	II (1–3)
Carex binervis	I (1)	I (1)
Fissidens adianthoides	II (1–3)	II (1–3)
Cirsium helenioides		II (1–4)
Breutelia chrysocoma		I (1)
Peltigera canina		I (1)

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I (1)	II (1–4)	I (1–4)
I (1)	II (1–3)	I (1–3)
I (1–4)	II (1–4)	I (1–5)
I (1)	II (1–4)	I (1–4)
I (1)	II (1–3)	I (1–3)
I (1–4)	II (1–4)	I (1–4)
	II (1–4)	I (1–4)
I (1)	II (1–6)	I (1–6)
I (1–4)	II (1–3)	I (1–4)
I (1)	II (1–4)	I (1–4)
I (1–4)	II (1–3)	I (1–4)
	II (1–4)	I (1–4)
	II (1–4)	I (1–4)
	II (1–3)	I (1–3)
	II (1–3)	I (1–3)
	II (1–4)	I (1–4)
	I (1–3)	I (1–3)
III (1–4)	IV (1–4)	III (1–4)
II (1–6)	IV (1–4)	III (1–4)
III (1–3)	III (1–3)	III (1–3)
I (1–3)	IV (1–4)	III (1–4)
III (1–4)	I (1–4)	II (1–4)
II (1–4)	II (1–4)	II (1–5)
II (1–3)	I (1–4)	II (1–4)
II (1–3)	I (1–3)	II (1–3)
II (1–3)	II (1–3)	II (1–4)
II (1–4)	II (1–4)	II (1–4)
II (1–3)	II (1–4)	II (1–4)
II (1–6)	I (1–4)	I (1–6)
II (1–3)	I (4)	I (1–4)
II (1–3)	I (1)	I (1–3)
II (1–4)	II (1–4)	I (1–4)
I (1)		I (1–3)
I (1–4)	II (1–4)	I (1–4)
II (1–4)	II (1–4)	I (1–4)
II (1–4)	II (1–3)	I (1–4)

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Floristic table U17 (*cont.*)

	a	b
Coeloglossum viride		II (1–3)
Pellia epiphylla	I (1–4)	I (1–3)
Cratoneuron commutatum	I (4)	I (1–3)
Taraxacum officinale agg.	I (1)	I (1–3)
Pellia endiviifolia	I (1)	I (1)
Thelypteris phegopteris	I (1)	I (1)
Racomitrium lanuginosum	I (1–4)	I (1)
Vaccinium uliginosum	I (4)	I (1–2)
Plagiothecium denticulatum	I (1)	I (1)
Plagiomnium rostratum	I (1)	I (1)
Parnassia palustris	I (1–3)	I (1–3)
Salix reticulata	I (1–4)	I (1–3)
Cystopteris fragilis	I (1–3)	I (1)
Drepanocladus revolvens	I (1–3)	I (1)
Ditrichum flexicaule	I (1)	I (1–3)
Rhizomnium pseudopunctatum	I (1)	I (1–3)
Poa glauca	I (1)	I (1–2)
Molinia caerulea	I (1)	I (4)
Nardia scalaris	I (1)	
Bazzania tricrenata	I (1)	
Cochlearia officinalis	I (1–4)	
Luzula multiflora	I (4)	
Polytrichum commune	I (1–2)	
Herbertus stramineus	I (1)	
Veronica officinalis		I (1)
Hookeria lucens		I (1)
Dryopteris dilatata		I (1)
Potentilla crantzii		I (1–3)
Campylium protensum		I (1–3)
Vicia sepium		
Armeria maritima		
Carex nigra		

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c	d	17
II (1–3)		I (1–3)
I (1)	I (1–3)	I (1–4)
I (1–3)	I (1)	I (1–4)
I (1–3)	I (1)	I (1–3)
I (1–3)	I (1)	I (1–3)
I (1–3)	I (1–3)	I (1–3)
I (1–3)	I (1–4)	I (1–4)
I (1–3)		I (1–4)
I (1–3)		I (1–3)
I (1–3)		I (1–3)
I (1–3)		I (1–3)
I (1–3)		I (1–4)
I (1–3)		I (1–3)
I (1–3)		I (1–3)
I (1–3)		I (1–3)
I (1–3)		I (1–3)
I (1)		I (1–2)
	I (1–3)	I (1–4)
I (1–3)	I (1)	I (1–3)
I (1–3)	I (1)	I (1–3)
I (1–3)	I (1)	I (1–4)
I (1–3)	I (1–3)	I (1–4)
I (1–3)	I (1–3)	I (1–3)
I (1)	I (1–3)	I (1–3)
I (1–3)	I (1)	I (1–3)
I (1–3)	I (1)	I (1–3)
I (1–3)	I (1–4)	I (1–4)
I (1)		I (1–3)
I (1–3)		I (1–3)
I (1–3)	I (1–3)	I (1–3)
I (1–3)	I (1–3)	I (1–3)
I (1–4)	I (1–4)	I (1–4)

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Sphagnum auriculatum
Mastigophora woodsii
Leontodon autumnalis
Plagiochila spinulosa

Number of samples	16	17
Number of species/sample	30 (13–48)	54 (32–76)
Vegetation height (cm)	37 (35–40)	31 (18–50)
Vegetation cover (%)	70 (10–100)	90 (60–100)
Altitude (m)	599 (400–810)	690 (560–860)
Slope (°)	44 (0–80)	55 (30–80)

a *Alchemilla glabra-Bryum pseudotriquetrum* sub-community
b *Geranium sylvaticum* sub-community
c *Agrostis capillaris-Rhytidiadelphus loreus* sub-community
d *Primula vulgaris-Hypericum pulchrum* sub-community
17 *Luzula sylvatica-Geum rivale* tall-herb community (total)

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I (1–3)	I (1–3)	I (1–3)
I (1–4)	I (1–3)	I (1–4)
I (1–3)	I (1–3)	I (1–3)
I (1)	I (1–3)	I (1–3)
18	22	75
48 (24–75)	42 (23–69)	42 (13–76)
40 (15–75)	34 (20–60)	34 (15–75)
99 (98–100)	93 (25–100)	86 (10–100)
669 (315–1038)	230 (15–570)	512 (15–1038)
38 (10–60)	28 (0–85)	39 (0–85)

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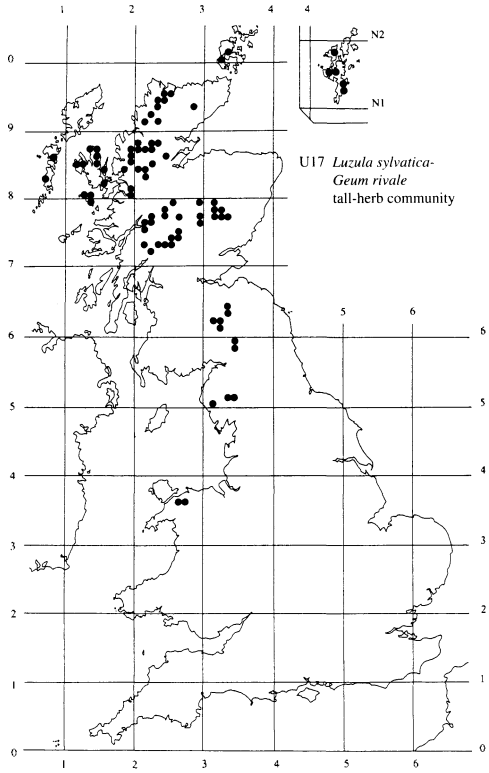

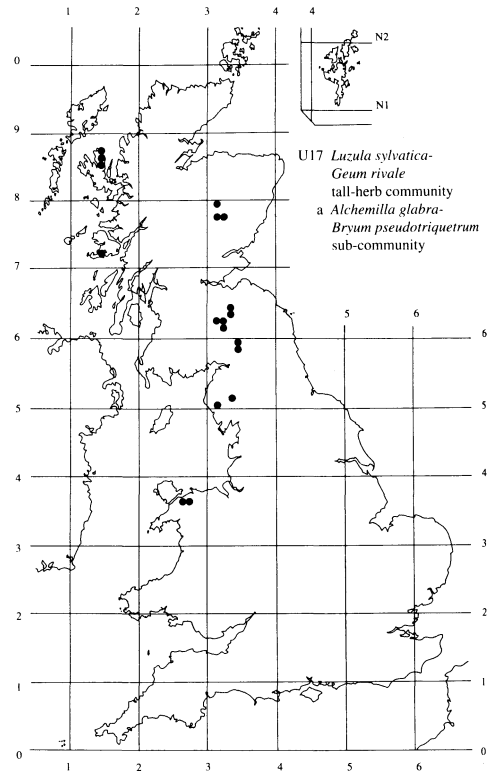

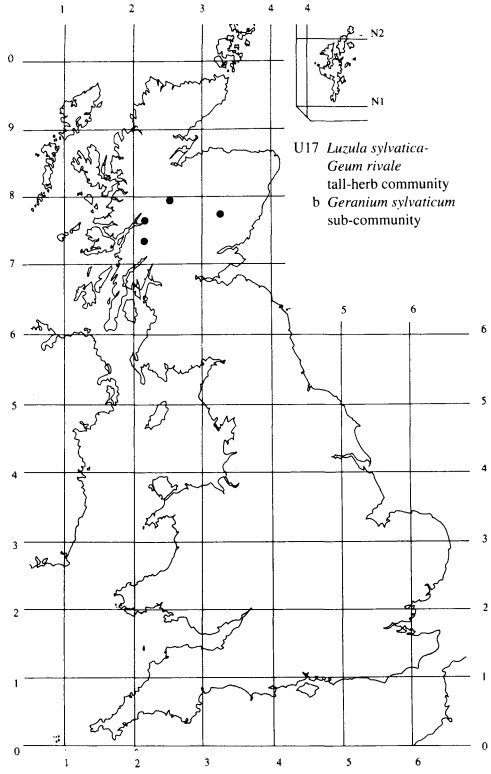

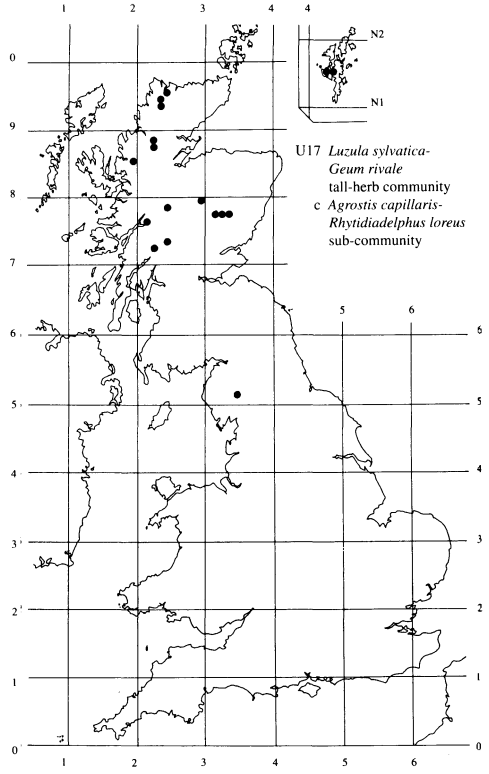

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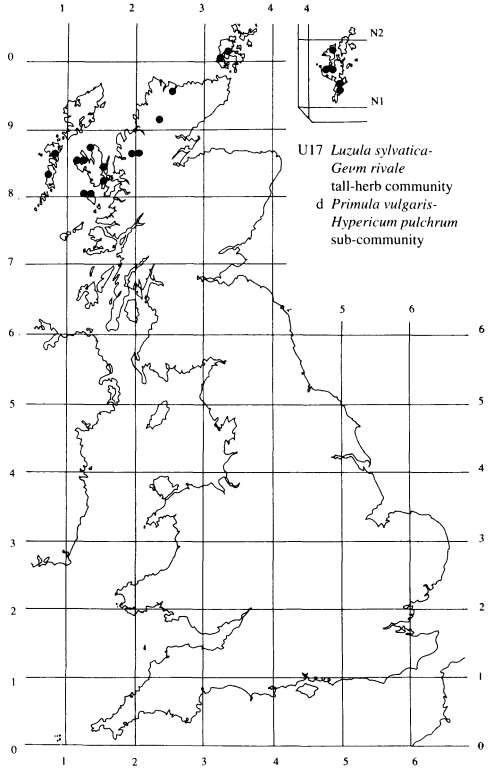

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