U13
Deschampsia cespitosa-Galium saxatile grassland

Synonymy
Rhytidiadelphus-Deschampsia caespitosa nodum Poore & McVean 1957; *Deschampsietum caespitosae alpinum* McVean & Ratcliffe 1962 *p.p.*; *Deschampsieto-Rhytidiadelphetum* McVean & Ratcliffe 1962 *p.p.*; *Deschampsia cespitosa-Rumex acetosa* nodum Huntley 1979; *Deschampsia cespitosa-Festuca rubra* nodum Huntley 1979; *Deschampsia cespitosa-Rhytidiadelphus loreus* nodum Huntley 1979.

Constant species
Agrostis capillaris, *Deschampsia cespitosa*, *Galium saxatile*, *Hylocomium splendens*, *Polytrichum alpinum*, *Rhytidiadelphus loreus*.

Rare species
Cerastium arcticum, *Minuartia sedoides*, *Sibbaldia procumbens*.

Physiognomy
The *Deschampsia cespitosa-Galium saxatile* grassland comprises short or rather rank tussocky swards in which grasses and bulky hypnaceous mosses are the most important structural elements. The commonest and most abundant grass throughout is *Deschampsia cespitosa* and its coarse, densely-tufted habit often gives this vegetation its distinctive stamp. Sometimes, the plants are recognisably of ssp. *alpina*, which always has at least some proliferous spikelets, more or less smooth panicle branches and lemmas with a short awn set high on the back (Tutin *et al.* 1980, Hubbard 1984), but in Scotland this taxon is morphologically less well defined from ssp. *cespitosa* than in Scandinavia (Hedberg 1958). In some of the vegetation included here, *D. cespitosa* is so overwhelmingly dominant that little else can compete with its vigorous growth, but in general the swards are richer than this and a variety of other grasses often make a modest contribution to the cover. Most frequent among these are *Agrostis capillaris*, *Festuca ovina/vivipara*, *Nardus stricta* and *Deschampsia flexuosa*, with *Anthoxanthum odoratum*, *Festuca rubra* and *Agrostis canina* rather more unevenly distributed. *Carex bigelowii* is also quite common, though it does not usually have the abundance that it shows in the drier sedge- and moss-heaths with which this vegetation is often found. *Luzula multiflora* occurs occasionally and some stands have a little *L. sylvatica*, a plant which can increase its contribution very substantially where the *Deschampsia-Galium* grassland grades to the vegetation of ungrazed ledges.

Other herbs have a rather variable representation and, among these, only *Galium saxatile* is constant throughout. But *Rumex acetosa*, *Alchemilla alpina* and *Viola palustris* are very common and characteristic and there are occasional records for *Potentilla erecta*, *Oxalis acetosella*, *Cerastium fontanum*, *Euphrasia frigida* and *Huperzia selago*, with *Sibbaldia procumbens*, *Ranunculus acris*, *Diphasium alpinum*, *Saxifraga stellaris* and *Thymus praecox* sometimes occurring in the more diverse of the grassy swards. In general, though, smaller plants such as *Salix herbacea*, *Silene acaulis* and *Armeria maritima*, typical of more open vegetation, are very infrequent here, and stands with *D. cespitosa* and tall herbs, some of which McVean & Ratcliffe (1962) included in a species-rich facies of their *Deschampsietum*, are in this scheme placed in the *Luzula-Geum* community. Finally, among the vascular associates, there is quite frequently a little *Vaccinium myrtillus*, very occasionally some *V. vitis-idaea*, but sub-shrubs are never a prominent component of this vegetation.

Often as abundant as the herbaceous companions, and sometimes exceeding even *D. cespitosa* in extent, are a number of mosses, among which *Rhytidiadelphus loreus* is the most common and abundant, with *Hylocomium splendens*, *Pleurozium schreberi* and *R. squarrosus* also very common and sometimes having quite high local cover. *R. triquetrus*, however, is only occasional here and McVean & Ratcliffe's (1962) *Deschampsieto-Rhytidiadelphetum triquetrosum* is mostly subsumed in the *Festuca-Alchemilla-Silene* community. *Polytrichum*

alpinum is constant and there is frequently some *Racomitrium lanuginosum* and occasionally a little *Pohlia nutans*. *Kiaeria starkei* has sometimes been found here in very small amounts, but neither this nor mosses like *Polytrichum sexangulare*, *R. heterostichum*, *Oligotrichum hercynicum* or *Conostomum tetragonum* are typical of even the most chionophilous vegetation included in the *Deschampsia-Galium* community.

Hepatics are much less numerous and extensive than mosses, but *Ptilidium ciliare* occurs quite commonly and there is very occasionally a little *Nardia scalaris*. Lichens, too, are few and sparse but *Cetraria islandica*, *Cladonia gracilis* and *Peltigera canina* are sometimes found.

Sub-communities

***Anthoxanthum odoratum-Alchemilla alpina* sub-community:** *Deschampsietum caespitosae alpinum*, species-poor facies McVean & Ratcliffe 1962; *Deschampsia cespitosa-Rumex acetosa* nodum Huntley 1979; *Deschampsia cespitosa-Festuca rubra* nodum Huntley 1979. Although there are stands included here in which hypnaceous mosses are quite prominent, *D. cespitosa* is the usual dominant in a grassy sward, and indeed this sub-community takes in the most impoverished kinds of *Deschampsia-Galium* vegetation where the grass is overwhelmingly abundant and strongly tussocky. Usually, though, the herbage is 1–3 dm tall with a more diverse mixture of grasses. *Agrostis capillaris*, *F. ovina/vivipara* and, preferential here, *Anthoxanthum odoratum* are all very common and together they can have moderately high cover. Less frequently, though sometimes with local abundance, there are records for *D. flexuosa*, *Nardus*, *F. rubra* and *Agrostis canina*, and it is in this sub-community too that *Luzula multiflora* and *L. sylvatica* occur occasionally. *C. bigelowii* is quite common, though usually present only as sparse tufts of shoots.

Alchemilla alpina and *Rumex acetosa* are somewhat more frequent here than in the *Rhytidiadelphus* sub-community, joining *G. saxatile* and *Viola palustris* as the most common dicotyledons. *V. myrtillus* occurs fairly often and among occasional preferentials are *Sibbaldia procumbens*, *Ranunculus acris*, *Diphasium alpinum*, *Saxifraga stellaris*, *S. hypnoides*, *Achillea millefolium*, *Thymus praecox*, *Alchemilla glabra*, *A. filicaulis*, *Campanula rotundifolia*, *Viola riviniana*, *Blechnum spicant* and *Dryopteris dilatata*. Along with *C. fontanum*, an occasional of the community, this kind of *Deschampsia-Galium* grassland also provides a locus for the two rare chickweeds, *Cerastium arcticum* and *C. alpinum*, and there is sometimes a little *Saussurea alpina*, though richer assemblages of tall herbs are lacking.

Among the bryophytes, which typically form a patchy carpet among the grass tussocks, *Hylocomium splendens*, *R. loreus* and, preferential here, *R. squarrosus*, are the most frequent and abundant species, with *Pleurozium schreberi* and *Polytrichum alpinum* also very common, though generally sparse. Occasionally, there can be some *Hypnum callichroum*, *Polytrichum commune*, *Plagiothecium undulatum*, *Rhytidiadelphus triquetrus*, *Drepanocladus uncinatus*, *Sphagnum capillifolium* and *Barbilophozia lycopodioides*.

***Rhytidiadelphus loreus* sub-community:** *Rhytidiadelphus-Deschampsia caespitosa* nodum Poore & McVean 1957; *Deschampsieto-Rhytidiadelphetum typicum* McVean & Ratcliffe 1962; *Deschampsia cespitosa-Rhytidiadelphus loreus* nodum Huntley 1979. *D. cespitosa* remains a constant in this vegetation but it is usually no more than a moderately abundant plant, dominance typically lying with *R. loreus* or mixtures of this with *H. splendens* and *P. schreberi*, often forming a thick carpet. *Polytrichum alpinum* is very common and sometimes attains local abundance in stands that are transitional to the *Carex-Polytrichum* moss-heath. *Racomitrium lanuginosum* is a little more frequent than in the *Anthoxanthum-Alchemilla* sub-community and, among hepatics, there is commonly some *Ptilidium ciliare* and occasionally *Barbilophozia floerkii* and *Anastrepta orcadensis*. *Cetraria islandica* and *Cladonia gracilis* occur fairly often, though not in any abundance.

Set in the moss mat along with *D. cespitosa* are frequent but generally scattered plants of *A. capillaris*, *F. ovina/vivipara*, *D. flexuosa*, *Nardus*, *G. saxatile* and *V. palustris*. *Vaccinium myrtillus* and *C. bigelowii* are also weakly preferential to this vegetation and the latter is sometimes quite abundant, even on occasions co-dominant with the hypnaceous mosses. Apart from these species, though, herbaceous associates are few and there is usually just very occasional *Cerastium fontanum*, *Oxalis acetosella*, *Potentilla erecta*, *Euphrasia frigida* and *Minuartia sedoides*.

Habitat

The *Deschampsia-Galium* grassland is characteristic of strongly-irrigated and often snow-bound slopes at moderate to high altitudes through the wettest and coldest of our mountains. It is almost entirely confined to the Scottish Highlands, where it is particularly common and extensive in the more oceanic western ranges and, even there, it often shows a strong preference for those aspects where the cool and humid character of the regional climate is accentuated. Although mostly a natural climax community, it is possible that at least some stands have been derived by the influence of grazing.

It is the maintenance of moist ground conditions throughout the year that seems to be of prime importance for the composition and distribution of this kind of

vegetation, although a number of factors are involved in meeting this requirement, and the ways in which these operate have quite an effect on floristic variation and habitat relations within the community. Of general significance, first, is high rainfall, because the *Deschampsia-Galium* grassland is strongly concentrated in the most consistently wet parts of Britain. Stands can be found throughout much of the Scottish Highlands wherever annual precipitation exceeds 1600 mm (*Climatological Atlas* 1952), and in a very few far-flung localities over high ground further south where the climate is as wet as this, but the community is much more prominent in the mountains of west Scotland, where there is often more than 2400 mm of rain annually and, more importantly, where there is a consistently high atmospheric humidity. For the most part, the range of the *Deschampsia-Galium* grassland falls within the 200 wet days yr^{-1} line (Ratcliffe 1968) where daytime cloudiness over the upper slopes is frequently more than 80% (Page 1982), and it is through this region that stands are particularly common, widespread and extensive, often covering many hectares (McVean & Ratcliffe 1962).

The second point of importance is that, even in these wetter areas, there is a strong tendency for the community to be concentrated on north- and east-facing slopes where, in the shaded and sheltered conditions, evaporation is minimised. It is in such situations, too, that the impact of snow-lie is at its greatest for, though the *Deschampsia-Galium* grassland may not always be absolutely dependent on this factor, it is in general a chionophilous community. It has a broad altitudinal range occurring widely between 500 and 1000 m, but at such levels, and especially towards the upper limits, much of the winter precipitation is received as snow, with often more than 100 days observed fall annually over the highest ground (Manley 1940). In western Scotland, the *Deschampsia-Galium* grassland is one of the most extensive kinds of vegetation over slopes in the low- and middle-alpine zones where the snow is caught and held for relatively long periods, on more sheltered hillsides, over the flanks of deep, sunless corries, in the fairly late snow-beds that develop in shallow depressions, and around the margins of really long-lasting fields. And it is shelter from frost and the redistribution of precipitation that come with the drifting and persistence of snow that help the community maintain a hold over suitable topographies in those Scottish mountains with a drier and more bitter climate, like the east-central Highlands, where it is a local feature on cold slopes and in gullies around Caenlochan and Lochnagar (Ratcliffe 1977, Huntley 1979).

The third factor concerns the way in which climate and topography interact through the soils. The *Deschampsia-Galium* grassland occurs over a wide variety of parent materials although on calcareous rocks, like the Dalradian mica-schists of Breadalbane and locally lime-rich Moine schists and gneiss through the north-west Highlands, it tends to be replaced by some kind of *Luzula-Geum* vegetation, what McVean & Ratcliffe (1962) called the species-rich facies of their *Deschampsietum*. And the great scarcity of the community on the granite of the Cairngorms, where there are eminently suitable topographies, suggests that this particular substrate may be too base-poor or sharply draining (McVean & Ratcliffe 1962). Between these extremes, the diversity of parent materials beneath the *Deschampsia-Galium* grassland generally weathers to fragmentary, though often quite humic, rankers or, with the heavy rainfall, to some kind of podzolised profile, frequently with poor horizonation and with bleaching masked by the incorporation of organic matter. Surface pH is usually between 4 and 5 (McVean & Ratcliffe 1962). The slopes over which the community develops are often quite steep, mostly from 10 to 30°, but the ground is generally stable and there is little of the solifluction associated with really long snow-lie or extreme exposure. Most important of all, perhaps, is the fact that a combination of rainfall, snow-melt, flushing from springs, seepage lines and dripping rock faces, together with the low evaporation, keep the soils moist through the whole of the year. Some profiles show signs of impedance with gleying below, particularly where the parent materials are clayey and the slope more gentle, but drainage is typically rapid. Furthermore, with the quite late snow-melt and mean annual maximum temperatures throughout the range of the community at 21 °C or less (Conolly & Dahl 1970), the plants experience a very short growing season while their roots are irrigated with what must be well-nigh frigid waters.

Much of the distinctive character of the *Deschampsia-Galium* grassland comes from the fact that *D. cespitosa* is so well able to capitalise on these conditions, perhaps especially ssp. *alpina*, although most of what we know about the behaviour of this grass in Britain relates to ssp. *cespitosa* (Davy 1980). The grass can thrive on a wide variety of soil types and though, across the lowlands of Britain, it occurs mainly on profiles with mull or moder humus, it is well able to tolerate oligotrophic situations. It is, in fact, possible that some of the soils on which the *Deschampsia-Galium* grassland is found are not so impoverished as might appear, at least when compared with the profiles that support sub-shrub or sedge-heaths on similarly snow-bound ground. But, in any case, the grass has an internal system of nutrient cycling from older to developing tillers which means that it can insulate itself somewhat against shortage of nutrients (Davy & Taylor 1974*b*, 1975). More important is its marked tolerance of very moist soils: it has well-developed root aerenchyma which, by lowering oxygen requirements in the tissues, can help maintain an oxidis-

ing environment around the roots, thus alleviating the impact of toxic reduced ions, like ferrous (Martin 1968, Davy & Taylor 1974*a*, Rahman 1976). This ability may be crucial for its vigorous growth here, where it can outcompete even plants like *Nardus*, an important grass in much moderately chionophilous vegetation, but one which prefers an oxidising environment in the upper soil layers in summer (Pearsall 1950).

The rise to prominence of *D. cespitosa* on moist and moderately acidic soils in the uplands can already be seen to some extent in the *Festuca-Agrostis-Galium* grassland, the major plagioclimax pasture of the submontane north and west of Britain: where this extends on to higher slopes in cooler, wetter regions, both *D. cespitosa* and *Rhytidiadelphus loreus* become preferentially frequent. And, in its general floristics, the *Deschampsia-Galium* grassland, though it extends to far greater altitudes than the *Festuca-Agrostis-Galium* swards, has as much in common with them as with most other high-montane vegetation found around it over upper slopes and plateaus. Most stands of the community fall within the 21 °C mean annual maximum isotherm, which forms a crude boundary for the range of many Arctic-Alpines in Britain (Conolly & Dahl 1970), but few of these plants find a place here. Indeed, only *D. cespitosa* ssp. *alpina*, *F. vivipara*, *C. bigelowii*, *Alchemilla alpina* and *Polytrichum alpinum* have more than occasional representation through the community as a whole and much of the character of the vegetation comes from plants like *F. ovina*, *A. capillaris*, *Galium saxatile*, *Potentilla erecta*, *Hylocomium splendens*, *Pleurozium schreberi* and *R. squarrosus* which maintain a strong continuity with the Nardo-Galion grasslands on lower slopes. In large measure, this is because many of the Arctic-Alpine plants of chionophilous communities need open ground, maintained by very long snow-lie or the downwash or solifluction processes that are infrequent here. And, of course, there is the very vigorous growth of *D. cespitosa* itself in many stands, highly effective in excluding more diminutive and competition-sensitive herbs. This may play some part, too, in the scarcity or low cover of snow-tolerant acrocarpous mosses, such as *Polytrichum alpinum* and *Dicranum fuscescens*, which become very important in the moderately late snow-beds of the drier mountains of the central and eastern Highlands.

Continuity with sub-montane swards is especially obvious in the *Anthoxanthum-Alchemilla* sub-community, which occurs throughout the range of the *Deschampsia-Galium* grassland, though with a preference for lower altitudes and steeper slopes. In the oceanic far-west of the Scottish Highlands, this kind of vegetation can be found below 400 m, though most stands occur between 600 and 900 m. Even at these altitudes, however, snow-lie does not seem to be so lengthy as over the *Rhytidiadelphus* sub-community, there is a somewhat longer and warmer growing season, and soil moisture perhaps depends as much on the high rainfall and seepage as on irrigation from melt-waters. Thus, though Arctic-Alpines such as *Sibbaldia procumbens*, *Diphasium alpinum* and *Saxifraga stellaris* find an occasional place here, the growth of *D. cespitosa* is very vigorous and the more striking preferentials are species like *Anthoxanthum*, *Rumex acetosa*, *Ranunculus acris*, *Festuca rubra* and *Achillea millefolium*, which give the swards the look of a more mesophytic Nardo-Galion grassland. The soils here tend to be not so strongly podzolised and, where there is a small measure of base-enrichment from the irrigating waters, the flora begins to show strong continuity with that of the *Luzula-Geum* or *Alchemilla-Sibbaldia* communities.

The *Rhytidiadelphus* sub-community is more strongly chionophilous than the *Anthoxanthum-Alchemilla* type, characteristic of higher altitudes, generally between 700 and 1000 m, on moderately steep slopes which catch and hold snow for long periods. With a shift to these conditions, the dominance of *D. cespitosa* becomes weakened, presumably by the longer snow-lie, and the representation of plants of sub-montane Nardo-Galion swards fades with the cooler climate. The increased prominence of *C. bigelowii*, *Polytrichum alpinum* and lichens suggests a similarity with the moderately late snow-beds of the eastern Highlands, but this kind of *Deschampsia-Galium* vegetation is only found in fragmentary form east of Creag Meagaidh and Ben Heasgarnich and provides a geographical replacement in the west for the *Carex-Polytrichum* sedge-heath. An abundance of *R. loreus* and other hypnaceous mosses is not unknown among chionophilous vegetation in regions with a drier and more bitter climate, but it tends to be seen at lower altitudes over moderately snow-bound slopes and in association with sub-shrubs which provide shelter and maintain high humidity. Increasingly, towards the west of Scotland, with its humid and more equable climate, the shade and shelter of north- and east-facing slopes, even up to very high altitudes and without a mantle of sub-shrubs, provide such conditions. Here, then, the *Rhytidiadelphus* sub-community may be among the most chionophilous vegetation types of the cloud-ridden upper slopes.

In most situations, and certainly in these more extreme habitats, it is possible to account for the distinctive features of the *Deschampsia-Galium* vegetation in terms of these climatic and edaphic factors, but in certain places it is possible that there has been some anthropogenic influence, particularly on the grassier swards of the *Anthoxanthum-Alchemilla* sub-community. Rather striking, for example, are those places where species-poor vegetation of this kind, strongly dominated by *D. cespitosa*, gives way to richer and more luxuriant

tall-herb assemblages of the *Luzula-Geum* or *Luzula-Vaccinium* communities, where the sole environmental difference seems to be that the latter are inaccessible to grazing stock, occurring on ledges and over cliff-bound slopes. Certainly, compared with many of the plants in such vegetation, *D. cespitosa* is unpalatable and favoured by grazing, although in the uplands its herbage is less rough and poorer in silica than at lower altitudes (von Horn 1935), and indeed in some countries it is regarded as providing quite good forage in mountain regions (Hitchcock & Chase 1950, Grümmer 1968, Dale 1973). However, it is possible that the snow-lie regime and pattern of irrigation are different on ledges than on the more open slopes and that the great abundance of *D. cespitosa* over the latter is largely natural (McVean & Ratcliffe 1962).

Zonation and succession

The *Deschampsia-Galium* grassland is usually found among patchworks of other chionophilous vegetation types where floristic variation depends on such factors as length of snow-lie, freedom of drainage for irrigating waters and the amount of solifluction. Regional and local climatic differences through the range of the community influence the different components of these sequences and there is some possibility of a mediation through grazing of transitions to tall-herb vegetation.

In some places, it is possible to see *Deschampsia-Galium* vegetation continuing upwards an altitudinal sequence of grassy swards from the sub-montane zone into the low-alpine. On Beinn Laoigh, for example, further north over parts of Creag Meagaidh and, to the north-west, in the Monar Forest and the Fannich and Letterewe Hills, mosaics of the *Nardus-Galium* and *Festuca-Agrostis-Galium* grasslands occur extensively over the lower slopes and, where these run up to the irrigated ground below snow-bound corries, transitions to the *Anthoxanthum-Alchemilla* sub-community are found. The strong dominance of *D. cespitosa* in many stands of the latter is usually sufficient to mark them out clearly, but more mixed grassy covers are quite widespread in this vegetation and then boundaries may be less well defined. Co-dominance of *Nardus* and *D. cespitosa* is sometimes seen, for example, and transitions to the *Luzula-Rhytidiadelphus* sub-community of the *Festuca-Agrostis-Galium* grassland can be especially gradual. In other places, where the ground below corries becomes more gently sloping and increasingly waterlogged, the *Anthoxanthum-Alchemilla* sub-community passes fairly sharply to *Juncus-Festuca* grassland, wet heath and blanket mire.

More commonly, though, the *Deschampsia-Galium* grassland occurs among zonations of sub-shrub vegetation, grass- and sedge-heaths and snow-bed communities that are related partly to altitude, partly to the degree of local shelter and partly to edaphic factors such as freedom of drainage and the base-richness of the irrigating waters. The characteristic pattern through the central section of the western Highlands is well seen over the Affric–Cannich and Fannich Hills and, to a lesser extent, in the Monar Forest and, further south, on Bidean nam Bian in Argyll. Here, both kinds of *Deschampsia-Galium* vegetation are widespread and the two can sometimes themselves be found in a gradation upslope, the *Anthoxanthum-Alchemilla* sub-community passing, often gently, to the *Rhytidiadelphus* heath with a switch in dominance from *D. cespitosa* to hypnaceous mosses. Often in this region, too, the community occurs with some type of *Vaccinium-Deschampsia* heath, replacing it with increased altitude and duration of snow-lie, or alternating with it over slopes that show some variation in the pattern of irrigation. The occurrence of porous block scree tumbling down hillsides, for example, can provide an environment buffered from the impacts of snow-melt and run-off and such areas often have stands of the *Hylocomium-Rhytidiadelphus* sub-community of the *Vaccinium-Deschampsia* heath, rich in hypnaceous mosses and with a vascular cover of grasses with *Vaccinium myrtillus* and *Empetrum nigrum*, the abundance of these last and the waning importance of *D. cespitosa* helping to define the boundaries. Much more locally through the north-west Highlands, the *Deschampsia-Galium* grassland can be found in similar situations with the hepatic-rich form of the *Vaccinium-Racomitrium* heath, this being especially characteristic of very sheltered and shady areas among boulders.

Differences in the amount of irrigation, particularly through the summer, probably play a part, too, in the disposition of the *Deschampsia-Galium* grassland in relation to the *Nardus-Carex* grass-heath, a community that is often found with it over moderately snow-bound slopes. The two have many species in common, notably *Nardus*, *F. ovina/vivipara*, *Alchemilla alpina* and hypnaceous mosses, and both grassier and more mossy *Deschampsia-Galium* swards can grade to different sub-communities of the *Nardus-Carex* grass-heath. The *Rhytidiadelphus* type comes especially close because there the dominance of *D. cespitosa*, which helps provide a general distinction, is much less pronounced.

Where the *Deschampsia-Galium* grassland, or mixtures of the two above communities, form a fringe around later snow-beds in this part of the western Highlands, they usually give way, where snow-lie is longer, to the *Polytrichum-Kiaeria* heath. Characteristically, this is a moss-dominated vegetation, with species such as *K. starkei* usually very abundant and *Polytrichum sexangulare* and *Oligotrichum hercynicum* a constant feature, and herbs such as *Saxifraga stellaris* and *Omalotheca supina* common. None of these occur more than very occasionally in the *Deschampsia-Galium*

community, but *D. cespitosa*, *C. bigelowii* and *Alchemilla alpina* can run on with some frequency into the late snow-bed and, where they remain patchily abundant, blur the boundary between the vegetation types. *D. cespitosa*, *A. alpina*, *G. saxatile*, *D. flexuosa*, *R. loreus* and *P. alpinum* also all remain very common in another strongly chionophilous community frequent in this part of the Scottish Highlands, the *Cryptogramma-Athyrium* vegetation, but mixtures of *C. crispa* and *A. distentifolium* typically dominate there and stands almost always mark out stretches of block scree, patches of tumbled boulders or rocky ledges.

More difficult to delineate precisely, or to interpret environmentally, are transitions to the *Alchemilla-Sibbaldia* community which are commonly seen in these mountains over the irrigated ground around late snow-beds. Mixtures of *A. alpina* and *S. procumbens* are the usual dominants, sometimes with *Minuartia sedoides*, *Thymus praecox* and *Omalotheca supina* in modest abundance, but grasses can be quite plentiful, among them *D. cespitosa*, *A. capillaris*, *Anthoxanthum* and *Nardus*, and there may be quite prominent patches of hypnaceous mosses. Such stretches of ground are often fed by the distinctive kinds of snow-bed springs, the *Pohlietum glacialis* or *Sphagno-Anthelietum*: scattered shoots of *D. cespitosa* are frequent in such vegetation but the striking dominance of the respective bryophytes is usually sufficient to mark them out clearly.

Finally, in this kind of pattern, the *Deschampsia-Galium* vegetation, in the form of the *Rhytidiadelphus* sub-community, frequently extends up to its highest altitudinal limits as small stands marking out sheltered hollows in *Carex-Racomitrium* heath, the characteristic moss-dominated sward of exposed summits in the more oceanic parts of the Highlands. Separation from stretches of the Typical sub-community of this vegetation, the most widely distributed form, is usually fairly easy, the change from abundance of *R. lanuginosum* to hypnaceous mosses being well defined. But increasingly towards the north-west, the *Carex-Racomitrium* heath is represented by the *Silene* sub-community where, under conditions of severe exposure, the carpet of *R. lanuginosum* often becomes fragmented, and where intermittent irrigation from snow-melt is marked by patches of *R. loreus*, *P. schreberi* and *H. splendens* and diminutive tussocks of *D. cespitosa*. The high frequency of mats and cushions of plants such as *Salix herbacea*, *Silene acaulis*, *Thymus praecox* and *Armeria maritima* generally helps define the *Carex-Racomitrium* heath but, over ablation fields, the cover is often broken and heterogenous and intimate mosaics of this vegetation with mossy *Deschampsia-Galium* snow-beds can be seen.

In shifting northwards, the balance among the elements in these sequences changes somewhat. The *Polytrichum-Kiaeria* snow-bed, for example, can be seen with the *Deschampsia-Galium* community as far north as Beinn Dearg and Ben Wyvis, but even on Beinn Eighe and the Letterewe Hills, and more obviously on Ben Hope, Foinaven and Ben More Assynt in Sutherland, the *Rhytidiadelphus* sub-community of the *Deschampsia-Galium* vegetation is often among the most chionophilous swards. It is in this part of the Highlands, too, that the similarities and contrasts between the community and the tall-herb *Luzula-Geum* vegetation, mediated perhaps by climatic and edaphic conditions, perhaps also by grazing, are to be seen in the swards disposed over slopes and ledges of the corries. *D. cespitosa*, *Alchemilla alpina*, *Agrostis capillaris*, *Anthoxanthum*, *D. flexuosa*, *G. saxatile*, *R. acetosa* and hypnaceous mosses all remain very frequent in Typical *Luzula-Geum* vegetation and there are transitional stands in which *D. cespitosa* occurs with particular abundance. But, generally, it is a subordinate plant in the tall-herb stands, and there is typically a good representation of species such as *Luzula sylvatica*, *Geum rivale*, *Rhodiola rosea*, *Angelica sylvestris*, *Filipendula ulmaria* and *Succisa pratensis*, and a ground carpet in which *Rhytidiadelphus triquetrus*, *Thuidium tamariscinum*, *Plagiomnium undulatum* and *Rhizomnium punctatum* are very common. Comparable transitions to this can also be seen where the substrates and seeping waters tend to be more base-poor, when the tall-herb vegetation is generally of the *Luzula-Vaccinium* type. Again, here, *D. cespitosa* may remain frequent and locally of modest abundance, but *V. myrtillus*, *Dryopteris dilatata*, *Blechnum spicant* and *Gymnocarpium dryopteris* are usually very frequent and, apart from the hypnaceous mosses, the floristic overlap is less than with the *Luzula-Geum* community.

East of Creag Meagaidh and Ben Heasgarnich in the central Highlands, the *Rhytidiadelphus* sub-community of the *Deschampsia-Galium* grassland becomes very fragmentary and is replaced geographically in moderately late snow-beds by the *Carex-Polytrichum* sedge-heath. Both kinds of vegetation are to be seen together on Creag Meagaidh and Ben Alder and in some localities, on Ben Lawers for example, there are quite extensive tracts of heath of a somewhat intermediate character (McVean & Ratcliffe 1962). Also in the central Highlands, on Ben Alder and Beinn Laoigh, are some snow-bound slopes where the *Deschampsia-Galium* community can be found with *Salix-Racomitrium* snow-beds as well as those of the *Polytrichum-Kiaeria* type, but there is usually little difficulty in distinguishing the patches of this strongly chionophilous vegetation with its cover of dwarf willow and diagnostic bryophytes. Further east, the *Anthoxanthum-Alchemilla* sub-community continues to find a place beyond the range of the *Rhytidiadelphus* sub-community among sequences of moderately chionophilous heaths and grasslands, as around Lochnagar and Caenlochan (Huntley 1979), but

it is a minor element in such patterns and sometimes looks very much like a replacement for tall-herb and fern vegetation that has been derived by grazing.

Distribution

The *Deschampsia-Galium* grassland, particularly the *Rhytidiadelphus* type, is strongly concentrated in the western Highlands. The *Anthoxanthum-Alchemilla* sub-community occurs somewhat more widely, extending into parts of the eastern Grampians, and in more fragmentary form into southern Scotland and north Wales.

Affinities

As understood here, the *Deschampsia-Galium* community includes the more species-poor kinds of *D. cespitosa* grassland and snow-bed first described in detail by McVean & Ratcliffe (1962). Even in their account, the very close relationship of their *Deschampsietum* and *Deschampsieto-Rhytidiadelphetum* was recognised and, in the light of further sampling (including Huntley 1979), it makes good sense to combine the less basiphilous stands among this vegetation, and to transfer the remainder to other communities where a more species-rich and calcicolous character is the norm.

The wider perspective that is now available also enables the *Deschampsia-Galium* community to be set in the context of other swards in which *D. cespitosa* plays an important part, and of the full range of dwarf- and tall-herb vegetation occurring over moderately snow-bound and irrigated ground at high altitudes. As far as the first perspective is concerned, the *Deschampsia-Galium* grassland can be seen as continuing a floristic trend that is already visible among sub-montane Nardo-Galion swards, where *D. cespitosa* attains local prominence when climate and soil combine to create congenial conditions. On this view, then, the community comprises an upland and calcifuge counterpart to the mesophytic *Holcus-Deschampsia* grassland, the major vegetation type with this grass on moist circumneutral soils through the British lowlands. This latter is clearly anthropogenic, usually replacing Alno-Padion or damp Carpinion forest, but it shows some edaphic continuity with the more montane swards and, if these too are sometimes biotically derived, the vegetation types are perhaps best seen as rather different products of the same ability of *D. cespitosa* to exploit situations which become suitable for it. It would be good to know how far the taxonomic difference between ssp. *cespitosa* and ssp. *alpina* corresponds to the definition of the various vegetation types between the climatic extremes across which they spread in this country.

In floristic terms, the affinities of the *Holcus-Deschampsia* grassland are with the lowland, mesophytic swards of the Arrhenatheretalia, among which this kind of vegetation has sometimes been thought worthy of separating off into a distinct Deschampsion alliance. The *Deschampsia-Galium* community, on the other hand, though its montane character is muted, clearly belongs among the kinds of vegetation which have been grouped in the Deschampsieto-Myrtilletalia, an order typical of moderately snow-bound or seasonally-irrigated ground with oligotrophic soils not liable to solifluction (Dahl 1956). A Deschampsieto-Anthoxanthion has been erected within this to contain swards floristically distinct from the chionophilous bilberry heaths of the Phyllodoco-Vaccinion and the moderately late snow-bed heaths with *Nardus* and *C. bigelowii* gathered into the Nardeto-Caricion. In Scandinavia, vegetation similar to the *Anthoxanthum-Alchemilla* sub-community has been included in the *Deschampsietum caespitosae alpicolum* of Nordhagen (1928, 1943) described from Sylene and Sikilsdalen, but counterparts of the *Rhytidiadelphus* sub-community are less obvious. Icelandic heaths sometimes have dominant *Hylococomium splendens* (McVean 1955) but *Rhytidiadelphus* spp. appear to be absent there and the nearest equivalent in Scandinavia looks to be the hydrophilous meadow vegetation of the *Ranunculetum acris acidophilum* of Gjaerevøll (1956).

An interesting unresolved question is how such swards in Britain relate to the dwarf-herb vegetation of irrigated ground such as is included in the *Alchemilla-Sibbaldia* and *Festuca-Alchemilla-Silene* communities on the one hand, and the tall-herb *Luzula-Geum* and *Luzula-Vaccinium* communities on the other. The former, which can take in the *triquetrosum* of McVean & Ratcliffe's (1962) *Deschampsieto-Rhytidiadelphetum*, show considerable floristic overlap with the *Deschampsia-Galium* grassland, but are probably distinguished environmentally by a preference for more base-rich ground subject to some solifluction, and belong among the Ranunculo-Anthoxanthion of the Salicetalia herbaceae (Gjaerevøll 1956). The latter, which accommodate the more species-rich of McVean & Ratcliffe's (1962) *Deschampsietum*, are also floristically close, but these are among our Cicerbition alpinae communities, typical of damp ledges inaccessible to grazing animals and transitional to sub-alpine willow scrub where there is a measure of continued protection and stability. How far the *Deschampsia-Galium* grasslands represent impoverished derivatives of such rich vegetation produced by grazing was an issue raised by McVean & Ratcliffe (1962) but still unanswered.

Floristic table U13

	a	b	13
Deschampsia cespitosa	V (4–10)	V (1–4)	V (1–10)
Galium saxatile	V (1–4)	V (1–6)	V (1–6)
Agrostis capillaris	V (1–4)	V (1–4)	V (1–4)
Rhytidiadelphus loreus	IV (1–8)	V (1–10)	V (1–10)
Polytrichum alpinum	IV (1–4)	IV (1–10)	IV (1–10)
Hylocomium splendens	IV (1–6)	IV (1–6)	IV (1–6)
Rumex acetosa	IV (1–4)	III (1–4)	III (1–4)
Alchemilla alpina	IV (1–6)	III (1–4)	III (1–6)
Rhytidiadelphus squarrosus	IV (1–9)	II (1–6)	III (1–9)
Anthoxanthum odoratum	IV (1–4)	II (1–6)	III (1–6)
Sibbaldia procumbens	III (1–4)	I (1–3)	II (1–4)
Ranunculus acris	III (1–4)		II (1–4)
Festuca rubra	II (1–4)	I (1–4)	II (1–4)
Luzula sylvatica	II (1–4)	I (1)	II (1–4)
Diphasium alpinum	II (1–6)	I (1)	II (1–6)
Hypnum callichroum	II (1–3)	I (1)	II (1–3)
Sphagnum capillifolium	II (1–3)	I (1)	I (1–3)
Peltigera canina	II (1–3)	I (1–3)	I (1–3)
Saxifraga stellaris	II (1–3)	I (1)	I (1–3)
Agrostis canina	II (1–4)	I (1–3)	I (1–4)
Luzula multiflora	II (1–3)	I (1)	I (1–3)
Achillea millefolium	II (1–3)	I (1)	I (1–3)
Thymus praecox	II (1–4)	I (1–4)	I (1–4)
Polytrichum commune	II (1–6)	I (1)	I (1–6)
Plagiothecium undulatum	II (1–3)	I (1)	I (1–3)
Blechnum spicant	II (1–3)		I (1–3)
Dryopteris dilatata	II (1–4)		I (1–4)
Alchemilla glabra	II (1–4)		I (1–4)
Barbilophozia lycopodiodes	II (1–3)		I (1–3)
Alchemilla filicaulis filicaulis	II (1–3)		I (1–3)
Campanula rotundifolia	II (1–3)		I (1–3)
Viola riviniana	II (1–4)		I (1–4)
Saxifraga hypnoides	II (1–3)		I (1–3)
Drepanocladus uncinatus	II (1–3)		I (1–3)
Rhytidiadelphus triquetrus	II (1–5)		I (1–5)
Cerastium alpinum	I (1–3)		I (1–3)
Saussurea alpina	I (1–3)		I (1–3)
Carex bigelowii	III (1–3)	IV (1–6)	III (1–6)
Vaccinium myrtillus	III (1–4)	IV (1–4)	III (1–4)
Ptilidium ciliare	II (1–3)	IV (1–3)	III (1–3)
Racomitrium lanuginosum	II (1–4)	III (1–4)	II (1–4)
Barbilophozia floerkii	I (1–4)	II (1–3)	I (1–4)
Anastrepta orcadensis	I (1–3)	II (1–3)	I (1–3)
Cladonia gracilis	I (1)	II (1–3)	I (1–3)
Cetraria islandica		II (1–3)	I (1–3)

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Floristic table U13 (*cont.*)

	a	b	13
Minuartia sedoides		I (1–6)	I (1–6)
Sphagnum russowii		I (1–3)	I (1–3)
Festuca ovina/vivipara	III (1–4)	III (1–5)	III (1–5)
Viola palustris	III (1–4)	III (1–3)	III (1–4)
Nardus stricta	III (1–4)	III (1–5)	III (1–5)
Deschampsia flexuosa	III (1–4)	III (1–4)	III (1–4)
Pleurozium schreberi	III (1–3)	III (1–3)	III (1–3)
Cerastium fontanum	II (1–3)	II (1–3)	II (1–3)
Potentilla erecta	II (1–4)	II (1–4)	II (1–4)
Oxalis acetosella	II (1–3)	II (1–3)	II (1–3)
Euphrasia frigida	II (1–3)	II (1–3)	II (1–3)
Pohlia nutans	II (1–6)	II (1–4)	II (1–6)
Huperzia selago	I (1–3)	I (1–3)	I (1–3)
Nardia scalaris	I (1–3)	I (1–3)	I (1–3)
Salix herbacea	I (1)	I (1–3)	I (1–3)
Carex pilulifera	I (1–3)	I (1–3)	I (1–3)
Hypnum cupressiforme	I (1–4)	I (1–4)	I (1–4)
Armeria maritima	I (1–3)	I (1–3)	I (1–3)
Vaccinium vitis-idaea	I (1–3)	I (1–4)	I (1–4)
Polygonum viviparum	I (1–3)	I (1–3)	I (1–3)
Silene acaulis	I (1–3)	I (1)	I (1–3)
Kiaeria starkei	I (1)	I (1)	I (1)
Selaginella selaginoides	I (1–3)	I (1)	I (1–3)
Omalotheca supina	I (1)	I (1)	I (1)
Number of samples	29	18	47
Number of species/sample	26 (8–53)	20 (12–30)	24 (8–53)
Vegetation height (cm)	20 (2–75)	6 (5–8)	15 (2–75)
Vegetation cover (%)	95 (30–100)	94 (80–100)	95 (30–100)
Altitude (m)	723 (294–1220)	871 (692–1100)	780 (294–1220)
Slope (°)	21 (0–50)	12 (0–30)	17 (0–50)

a *Anthoxanthum odoratum-Alchemilla alpina* sub-community
b *Rhytidiadelphus loreus* sub-community
13 *Deschampsia cespitosa-Galium saxatile* grassland (total)

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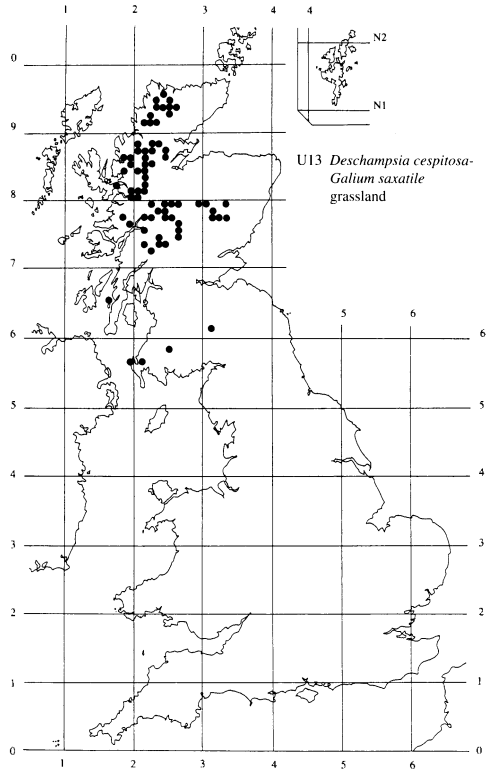

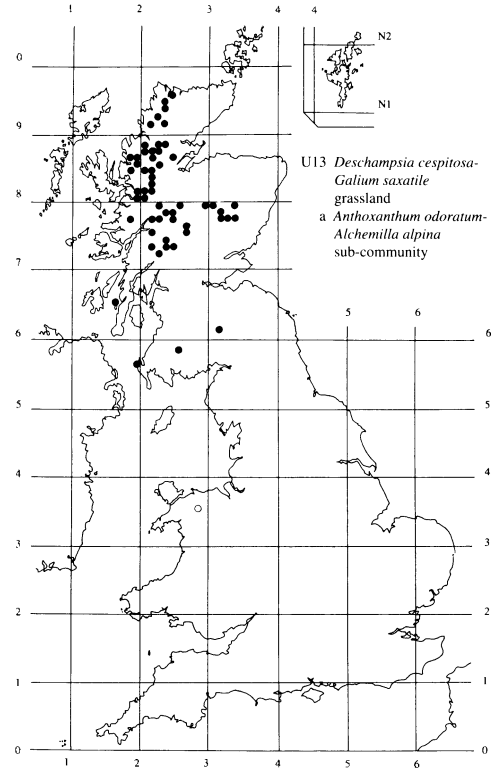

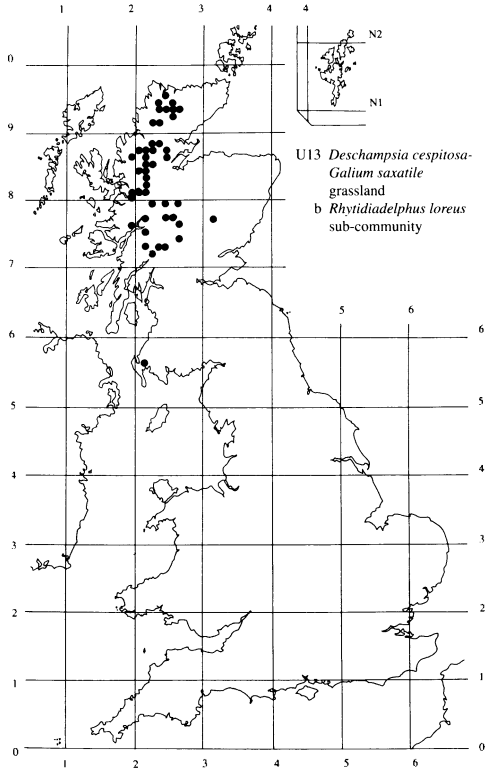

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