U7

Nardus stricta-Carex bigelowii grass-heath

Synonymy

Arctic-Alpine Grassland Smith 1911b p.p.; Rhacomitreto-Vaccinietum Smith 1911b p.p.; Nardus stricta-Carex bigelowii-Deschampsia flexuosa vegetation Watt & Jones 1948; Nardetum Metcalfe 1950, Burges 1951 p.p.; High altitude Nardus stricta sociation Poore 1955c; Nardus snow-beds Poore & McVean 1957; Low-alpine Nardus noda McVean & Ratcliffe 1962; Nardetum medio-alpinum McVean & Ratcliffe 1962; Nardus stricta-Vaccinium myrtillus Association Birks 1973; Nardus stricta-Carex bigelowii nodum Huntley 1979; Lycopodium alpinum-Nardus stricta community Birse 1980.

Constant species

Carex bigelowii, Galium saxatile, Nardus stricta, Vaccinium myrtillus, Racomitrium lanuginosum, Cladonia uncialis.

Rare species

Loiseleuria procumbens, Kiaeria starkei, Anastrophyllum donianum, Cetraria delisei.

Physiognomy

The Nardus stricta-Carex bigelowii grass-heath brings together some fairly diverse kinds of vegetation in which Nardus stricta is generally the dominant plant, with varying amounts of Carex bigelowii and Racomitrium lanuginosum, but where the local frequency and abundance of a range of associates can create some striking floristic and structural effects. The herbage is characteristically short, usually just a decimetre or so high, and the cover is generally closed or almost so, but in appearance the community varies from quite lush grassy swards, through heathy vegetation, to stands in which a ground layer of mosses or lichens plays a prominent part in the structure.

The overall abundance of *Nardus* often helps to pick out tracts of this community at a distance, the straw colour of its dead foliage contrasting sharply with the

dull greys and greens that usually prevail over the surrounding slopes. Generally, it is the most extensive plant, sometimes overwhelmingly abundant, and with its dense tussocky growth it can exert a controlling influence on the distribution and vigour of many of the smaller associates. But C. bigelowii is equally characteristic of this vegetation: its high frequency is one of the best features distinguishing the community from subalpine Nardus-Galium grassland and it, too, can be quite abundant, growing especially robust in damper swards and frequently forming clonal patches that occur in mosaics with the Nardus clumps. Much less common throughout, but of local importance where the community extends on to wetter peaty soils, and then sometimes abundant over many hectares in this vegetation, is Scirpus cespitosus.

Vaccinium myrtillus is the only sub-shrub to be found with any frequency in all types of Nardus-Carex grassheath, and, though it is often present as scattered sprigs, it can show modest abundance. Empetrum nigrum ssp. hermaphroditum and V. uliginosum are much more restricted in their occurrence but, with preferential frequency, they can give one of the sub-communities the character of an Arctic-Alpine heath and, when all three of these species are found together with quite high cover, they make for a strong element of continuity with adjacent chionophilous sub-shrub vegetation. V. vitisidaea also occurs occasionally, but Calluna vulgaris, which can penetrate to these altitudes only in more exposed situations, is noticeably scarce. The community can provide a locus for the rare Loiseleuria procumbens, but this too is characteristically a plant of wind-blasted heaths at these levels.

Among other vascular plants, grasses apart from *Nardus* do not usually play an important role here. *Deschampsia flexuosa* occurs fairly often throughout and it can get a locally abundant hold on the surface humus. Then, in some stands, there is occasional *Agrostis capillaris* and *Festuca ovina*, with *F. vivipara* sometimes recorded separately too, but it is only in transitions

to sub-alpine swards that such plants become really prominent. *Galium saxatile* is the most frequent dicotyledonous herb, but *Potentilla erecta* also occurs commonly. Then, rather typically here, there are often scattered plants of *Diphasium alpinum* and *Huperzia selago*.

There are almost always some bryophytes and lichens present and, in many stands, some species or other contribute to an extensive ground cover. R. lanuginosum is the most characteristic moss overall, but it is not always abundant and, indeed, in some kinds of Nardus-Carex vegetation, it becomes rather patchy and can be altogether absent. Other species occurring frequently are Dicranum scoparium, D. fuscescens, Polytrichum alpinum, P. commune and bulky pleurocarps such as Rhytidiadelphus loreus, Pleurozium schreberi, Hypnum cupressiforme and Hylocomium splendens, and most of these can show a measure of abundance, though they are not so structurally important as in the moss-dominated snow-beds. Hepatics tend to be less common but Ptilidium ciliare occurs frequently and Barbilophozia floerkii more occasionally, and the Nardus-Carex vegetation can provide important outposts in sheltered situations away from the western seaboard for some oceanic hepatics.

Lichens are generally less numerous, but *Cladonia uncialis*, *C. arbuscula* and *Cetraria islandica* occur with fair regularity throughout and in one particular subcommunity become especially frequent and often accompanied by a variety of other species.

Sub-communities

Empetrum nigrum ssp. hermaphroditum-Cetraria islandica sub-community: Nardetum Metcalfe 1950, Burges 1951 p.p.; Nardus snow-beds Poore & McVean 1957; Nardus-Trichophorum nodum, Nardus-Rhacomitrium provisional nodum & Nardetum medio-alpinum Mc-Vean & Ratcliffe 1962. This sub-community includes most of the more heathy and lichen-rich Nardus-Carex vegetation, though even then there is considerable variation in the detailed composition and structure. Nardus is often a clear dominant but E. nigrum ssp. hermaphroditum and V. uliginosum frequently join V. myrtillus here and in various combinations these plants can be subdominant in a low, patchy cover. C. bigelowii remains very common, though it is unusually sparse and the most prominent monocotyledonous associate is often Scirpus cespitosus, growing among the sub-shrubs or sometimes replacing them as the main subordinate plant in the swards. Juncus squarrosus, not a common species through many stands of the *Nardus-Carex* grass-heath, also occurs quite frequently here. Other herbs are few: Diphasium alpinum is fairly common, but even Galium saxatile and Deschampsia flexuosa become a little patchy here and, apart from these, there is usually just occasional *Potentilla erecta* and *Huperzia selago*.

The ground layer, by contrast, is characteristically rich in species, diverse and often extensive, too, with R. lanuginosum in particular having high cover. Some other mosses, notably D. scoparium and R. loreus, are also frequent, though usually much less abundant and, among the hepatics, Ptilidium ciliare is occasionally accompanied by such oceanic species as Diplophyllum albicans, Bazzania tricrenata, Pleurozia purpurea, Anastrepta orcadensis and the rare Anastrophyllum donianum. Lichens are often even more numerous and noticeable with Cladonia uncialis, C. arbuscula and Cetraria islandica all especially common here, and frequently joined by Cladonia bellidiflora, C. gracilis and, more occasionally, by C. pyxidata, C. leucophaea, C. impexa, C. tenuis and the rare Cetraria delisei.

Typical sub-community: Nardus stricta-Carex bigelowii-Deschampsia flexuosa vegetation Watt & Jones 1948; Nardetum Metcalfe 1950, Burges 1951, p.p.; High altitude Nardus stricta sociation Poore 1955c; Nardus-Pleurozium nodum McVean & Ratcliffe 1962; Nardus stricta-Vaccinium myrtillus Association Birks 1973; Nardus stricta-Carex bigelowii nodum Huntley 1979; Lycopodium alpinum-Nardus stricta community Birse 1980. In this kind of Nardus-Carex vegetation, Nardus is often a strong dominant, with various mixtures of C. bigelowii, V. myrtillus, D. flexuosa and G. saxatile making up most of the remaining vascular cover, and with occasional records for Festuca ovina/vivipara, Agrostis capillaris, A. canina and Carex pilulifera, many stands have a grassy heath structure.

In contrast to the previous sub-community, *R. lanugi-nosum* is rather uneven in its occurrence here and rarely very abundant, but some of the pleurocarps can have locally high cover, particularly *P. schreberi* and *R. loreus* and, in other stands, the rare *Kiaeria starkei* is a distinctive associate. Lichens are rarely very numerous or extensive and many stands have just scattered *Cladonia uncialis*, *C. arbuscula* or *Cetraria islandica*.

Alchemilla alpina-Festuca ovina sub-community: Arctic-Alpine Grassland Smith 1911b p.p.; Rhacomitreto-Vaccinietum Smith 1911b p.p.; Carex bigelowii-Festuca vivipara Association (Birse & Robertson 1976) Birse 1980. Nardus is not so overwhelmingly abundant in this sub-community and it often shares dominance with C. bigelowii, V. myrtillus, D. flexuosa and, preferentially frequent here, Festuca ovina/vivipara. Agrostis canina and A. capillaris are also common, with Carex pilulifera and Luzula multiflora occasional and, in contrast to grassier stands of Typical Nardus-Carex vegetation, there is often a little Alchemilla alpina in the sward. V. vitis-idaea also tends to be rather more

common than usual, but it is not abundant. Lichens are few and generally sparse in their cover, but along with moderate amounts of *R. lanuginosum* there is usually some *Rhytidiadelphus loreus*, *P. schreberi* and *D. scoparium*, with occasional *Polytrichum piliferum* and *P. juniperinum*.

Habitat

The Nardus-Carex grass-heath is a community of snowbound slopes at higher altitudes through the cold and wet uplands of northern Britain, occurring over gentler ground where irrigation by rain and melt-water enhance drainage impedence in peaty mineral soils. It is found in and around moderately late snow-fields and, though the vegetation may experience some grazing during the summer months, it is essentially the edaphic and climatic conditions which maintain the community as a climax.

Apart from a few far-flung stands in locally suitable situations on high ground in the Southern Uplands and the Lake District, the Nardus-Carex grass-heath is confined to the mountains of the Scottish Highlands, becoming common there only above about 600 m, where mean annual maximum temperatures are usually less than 22 °C (Conolly & Dahl 1970). Arctic-Alpine plants, well adapted to the short growing season and inhospitable winters at these altitudes, are thus an important diagnostic feature of the community, helping to distinguish it from the mat-grass vegetation of the subalpine zone, the Nardus-Galium grassland. Carex bigelowii, Diphasium alpinum, Polytrichum alpinum and Cetraria islandica are especially striking in this respect, with Empetrum nigrum ssp. hermaphroditum and Vaccinium uliginosum less uniformly characteristic of the community as a whole, but likewise having geographical distributions roughly coincident with it (Perring & Walters 1962, Conolly & Dahl 1970). Conversely, the contribution from sub-montane herbs, very obvious in the *Nardus-Galium* grassland, is that much weaker here.

For the most part, then, this is a vegetation type of the low-alpine zone and above, often extending to 900 m, and exceptionally up to 1200 m and beyond, at which levels Nardus can retain great vigour among its more strictly montane associates (Chadwick 1960), but where its abundance is often related to the influence of snowlie, rather than the anthropogenic factors which encourage its dominance at lower altitudes. However, although the general character of this community is closer to snow-bed than to pasture, Nardus still shows its characteristic preferences for moist, humic soils over these higher slopes (Pearsall 1950), occurring typically here over peaty podzols, sometimes gravelly below, and often with signs of gleying. The impact of snow cover may thus be felt not so much through protection from frosts and biting winds, as through various influences on soil moisture, the redistribution of precipitation, the provision of melt-water in the summer and the consequent tendency for increased drainage impedence with the irrigation of gentler ground (McVean & Ratcliffe 1962). One important floristic effect of this is seen in the balance in the community between *Nardus* and *V*. myrtillus: among our moderately chionophilous vegetation types, the former assumes dominance over the latter as is typically the case here, not just where the growing season in the snow-free summer months becomes critically short for the bilberry, but also where periodic flooding with melt-water renders drainage insufficiently free. The converse tendency is seen in the Vaccinium-Deschampsia heath, which shows extensive floristic continuity with the Nardus-Carex vegetation beneath a bilberry canopy, but which is generally found on slopes that have shorter snow-lie and/or sharper drainage, often therefore on steeper ground at somewhat lower altitudes. Here, the slope is generally less than 10°, the community being best developed in shallow hollows, over the gently-sloping sides and bottoms of corries and on flat or rounded brows and watersheds where there is some measure of shelter.

Such situations already receive substantial irrigation with run-off in these rainy regions: everywhere through the range of the community, precipitation is at least 1600 mm yr⁻¹ (Climatological Atlas 1952) with more than 180 wet days annually (Ratcliffe 1968). But, with such cold winters, much of this falls as snow, the impact of which is especially severe and extensive through the eastcentral Highlands, where minimum temperatures are particularly low, and locally concentrated wherever shelter encourages accumulation and persistence. There are usually 50-100 days with observed snow-fall at these altitudes (Manley 1940) and more substantial depressions can have deep beds, which last long where a northerly or easterly aspect gives protection from warming spring sunshine. Some stands here experience five months of snow-cover, with the melt not complete until late May or early June (Poore & McVean 1957, McVean & Ratcliffe 1962).

Much of the floristic and structural variation within the Nardus-Carex grass-heath seems to reflect the varying influence of precipitation, particularly snow-fall, with differences in regional climate and local topography across the considerable geographical range of this vegetation. The Empetrum-Cetraria sub-community is the most strongly chionophilous type, characteristic in general of the gentlest and most sheltered slopes at the higher altitudes reached by the Nardus-Carex grassheath. It is especially striking in the northern Grampians, where it is always found within the area with over 100 days of snow-lie, and most often in places with locally prolonged accumulations in moderately late snow-fields and around the longest-lasting beds, as on the northern slopes of the Cairngorms, Monadhliath

and Lochnagar. Here, it can extend up to over 1200 m and exhibit its most obviously Arctic-Alpine character, with E. nigrum ssp. hermaphroditum, V. uliginosum and Cetraria islandica having their most frequent representation, and the rare C. delisei occurring quite often. But essentially similar vegetation also extends through the north-west Highlands, again frequently marking out distinct snow-beds, as over the Monar and Affric hills and on Beinn Dearg, though not usually attaining such high altitudes in this part of Scotland. Quite commonly, too, it occurs over more open, though still somewhat sheltered, slopes where snow-lie is perhaps not so long, but where there is substantial irrigation from melt-water and also from rain. Outside the snowiest parts of Scotland, this kind of vegetation is almost always found within the 220 wet days yr⁻¹ line (Ratcliffe 1968) where soils on gentler slopes can be kept in a permanently moist state. It is in such situations, and more locally in the east-central Highlands where snow-beds provide the necessary humidity, that the Nardus-Carex grass-heath has occasional records for such oceanic hepatics as Pleurozia purpurea, Bazzania tricrenata and Anastrophyllum donianum.

The Typical sub-community is less demanding in its habitat requirements and less strikingly Arctic-Alpine in its floristics. Overall, this vegetation occurs on somewhat steeper slopes and lower altitudes through areas that are not so consistently snow-bound as with the Empetrum-Cetraria sub-community. It is widespread through the central and eastern Highlands, within the area which has at least 60 days morning snow-lie (Climatological Atlas 1952), and is the characteristic vegetation of moderately late snow-beds through the Breadalbane-Clova mountains, occurring also on Creag Meagaidh and Ben Alder. But, again, it is found widely through the western Highlands and on some of the Isles, like Skye (Birks 1973) and Arran, over slopes with fairly long snow-lie or irrigation from melt-water and rain, though where run-off is a little sharper than with the Empetrum-Cetraria sub-community. In this case, stands to the west occur within the 200 wet days yr⁻¹ line (Ratcliffe 1968), and locally cold slopes, of northerly or easterly aspect, in the wettest parts of south-west Scotland, can support outlying stands of this vegetation.

The trend away from the distinctly Arctic-Alpine kind of Nardus-Carex grass-heath continues further in the Alchemilla-Festuca sub-community. This can still be found at high altitudes, but it is characteristic of uncommonly steep slopes for the community, so that, even where there is some opportunity for snow to accumulate and persist, the melt and any irrigating rain water draining from the slopes above run sharply away. This vegetation occurs throughout the range of the community, though the stands of the Nardus-Carex grass-heath found locally in northern England and southern Scot-

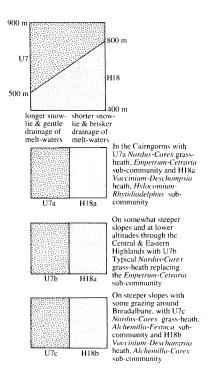
land, where temperatures are somewhat warmer, are usually of this type. The shift in climatic and edaphic conditions is marked here by a floristic move towards the grassier kind of *Vaccinium-Deschampsia* heath, Arctic-Alpines generally having their patchiest representation. It is in such situations, too, that grazing may have some effect on the composition of the community. Over higher ground, the predations of larger herbivores such as sheep and deer are probably negligible, though McVean & Ratcliffe (1962) noted how mice and voles could congregate beneath the snow on *Nardus-Carex* vegetation, heaps of chopped up grass and droppings marking their activity after the thaw.

Zonation and succession

The Nardus-Carex grass-heath is characteristically found with sub-shrub vegetation, snow-bed communities and mires in the low- and middle-alpine zones of our higher mountains, where vegetation patterns are influenced mostly by differences in exposure and soil moisture, themselves in turn much dependent on topography. Towards higher altitudes, the community often gives way to summit moss-heath or fell-field, while below it usually passes to heaths and grasslands among which anthropogenic factors become of increasing importance.

Essentially, the *Nardus-Carex* vegetation can be seen as an extension downwards of grass- and sedge-dominated heath into the zone of sub-shrub communities where there is locally prolonged snow-lie through the winter and spring, and it is usually associated towards its lower levels with some kind of moderately chionophilous bilberry vegetation. Most often, this is the Vaccinium-Deschampsia heath which, throughout the range of the Nardus-Carex heath but especially in the Grampians, tends to replace it whenever snow melts a little earlier and the waters drain away rather more sharply (Figure 33). The zonation between the two communities is partly a broad altitudinal one, with the Vaccinium-Deschampsia heath becoming increasingly important over sheltered ground towards the transition to the subalpine, the Nardus-Carex community petering out generally below around 600 m, the Vaccinium-Deschampsia heath often extending down to 400 m. But, within the low-alpine zone, mostly between 600 and 800 m, the vegetation types frequently occur together, disposed over ground that is sheltered to varying degrees or where differences in slope affect the readiness with which melt-water drains away. One community can thus give way to the other with shifts in aspect, north- and eastfacing slopes providing sufficient shelter and shade for the Nardus-Carex grass-heath to replace the Vaccinium-Deschampsia vegetation, or with changes in slope, a pattern well seen over the treads and risers of terraced ground on the Cairngorms (Burges 1951) and, of course, around distinct snow-beds, several examples of which were illustrated by McVean & Ratcliffe (1962). In the Cairngorms, which has a greater range of chionophilous vegetation than any other mountain system in Britain, a moderately late snow-bed in the low-alpine zone characteristically has a central patch of Nardus-Carex vegetation, usually of the Empetrum-Cetraria type, but with Scirpus often thickening up on the wettest ground towards the base, with an arch of Vaccinium-Deschampsia heath on the steeper back face. Essentially similar patterns occur on Monadhliath and right down through the east-central Highlands, particularly on Beinn a'Ghlo, and then more locally in the western Highlands, over the Fannich and Monar hills, on Ben Wyvis and Beinn Dearg, though from Breadalbane to Clova, and at lower altitudes to the west, the Typical sub-community increasingly replaces the *Empetrum-Cetraria* type. The absolute differences in length of snow-lie and soil wetness which control the switch from the Nardus-Carex to the Vaccinium-Deschampsia vegetation are still unknown but, floristically, the major change is in a move from Nardus dominance to an abundance of sub-shrubs, the low canopy of the heath being particularly rich in V. myrtillus and E. nigrum, with ssp. nigrum appearing at lower altitudes, and V. vitis-idaea also occurring fre-

Figure 33. Relationships between U7 Nardus-Carex grass-heath and H18 Vaccinium-Deschampsia heath on snow-bound slopes through the montane zone, with variations at different localities.



quently. C. bigelowii becomes just occasional, R. lanuginosum is much less abundant and plants like J. squarrosus and S. cespitosus hardly ever appear in the heath but there is often strong continuity through the grasses and other cryptogams. The two vegetation types come especially close in the Empetrum-Racomitrium subcommunity of the heath, but the Hylocomium-Rhytidiadelphus type grades into Typical Nardus-Carex heath and the Alchemilla-Carex sub-community into the Alchemilla-Festuca sub-community here, and zonations can be found with each of these pairs. In some places, too, the patterns are complicated by the occurrence of the Vaccinium-Rubus heath, a community which seems to be about as chionophilous as the Vaccinium-Deschampsia heath, but where the substrate is generally sodden peat and where R. chamaemorus, Cornus suecica and Sphagna provide a diagnostic element.

On moving up through the low-alpine zone, and especially towards the wetter west, on Creag Meagaidh, Bidean Nam Bian, around Glen Affric, on the Fannich Hills, Ben Hope and Ben More Assynt, the *Nardus-Carex* grass-heath is quite often found among mixtures of the above vegetation types and the *Deschampsia-Galium* grassland, this latter often also extending up to 800 m or more and marking out slopes with moderately long snow-lie and, more particularly, sustained irrigation by the trickling of melt-water and rain. Here again, there can be marked continuity among the grass and pleurocarp elements of the vegetation but the change from *Nardus* to *D. cespitosa* as the dominant is usually obvious enough.

With the shift to snowier slopes at higher altitudes, locally through the western Highlands, as around Beinn Dearg, the Monar Forest and the Affric-Cannich Hills, but more widely over Monadhliath and particularly the Cairngorms, the proportion of more strikingly chionophilous vegetation increases and here the Nardus-Carex grass-heath is most commonly represented by the Empetrum-Cetraria sub-community, frequently forming a surround to various kinds of very late snow-bed vegetation. Through the central Highlands, this is often the Carex-Polytrichum sedge-heath, where plants such as C. bigelowii, Polytrichum alpinum, Cetraria islandica, Cladonia arbuscula and C. uncialis maintain a strong qualitative continuity, but where Nardus becomes very sparse and the sedge generally dominant with much Dicranum fuscescens, a moss that is only occasional and usually of low cover in the Nardus-Carex grass-heath. Quite frequently, in the Cairngorms, there is some slight difference between the Empetrum-Cetraria vegetation above the snow-bed and that, some 100-150 m downslope, on the gentler ground below. It is in the former situation that lichens such as Cladonia bellidiflora and Cetraria delisei tend to be better represented, with Scirpus more prominent in the latter, but this variation is not so

striking as that implied by McVean & Ratcliffe's (1962) separation of a higher *Nardetum medio-alpinum* from their *Nardus-Trichophorum* nodum.

In other places, where snow lies longest of all, it is the moss-dominated vegetation of the Polytrichum-Kiaeria or Salix-Racomitrium communities that occurs within a surrounding zone of the Nardus-Carex heath. Here, the boundaries between the less and more chionophilous vegetation are usually well marked by a reduction in the abundance of C. bigelowii, increased frequency of such plants as Salix herbacea, Saxifraga stellaris and Omalotheca supina, and prominence of snow-tolerant bryophytes like Racomitrium heterostichum, Kiaeria starkei, Conostomum tetragonum, Polytrichum sexangulare, Oligotrichum hercynicum and Gymnomitrium concinnatum. McVean & Ratcliffe (1962) provide a sketch of a snow-bed complex from over 1200 m in the Cairngorms where lichen-rich Empetrum-Cetraria vegetation forms a fringe around a nivation hollow, with the Polytrichum-Kiaeria community marking out the patches of deepest and longest snow-lie and running along the relatively stable dry watercourses. There is also Salix-Racomitrium vegetation on stone-striped ridges running down between the snow patches where there is intermittent irrigation and downwash. In some localities, where stabilised block scree, tumbled boulders or ledges occur in those beds where snow lies longest, the Cryptogramma-Athyrium community can be found in close juxtaposition with the Nardus-Carex grass-heath, its clumps of ferns benefiting by the protection that the snow cover provides, usually marking out the stands clearly.

In the Cairngorms, and less extensively over high ground elsewhere through the east-central Highlands, the context for these late snow-beds is usually Juncus-Racomitrium fell-field which extends up, on gentlysloping and flat areas, over the summits of these mountains where exposure can be severe. The floristic differences between this and the Nardus-Carex heath are not always very marked, particularly where, in the fell-field vegetation, both C. bigelowii and R. lanuginosum are abundant with scattered grasses and a rich and extensive lichen flora. Moreover, extensive tracts of Juncus-Racomitrium vegetation are the exception, the usual picture being of a network of erosion surfaces, among which gentle hollows and shallow basins which accumulate a little snow can have patches of Nardus-Carex grass-heath, the boundaries between the communities being often complex and sometimes diffuse. But, as a general guide, Nardus is scarce in the fell-field and Juncus-trifidus is typically at least co-dominant.

Even at some sites within the east-central Highlands, then down through the Grampians, on Carn Gorm, Ben More and Ben Alder, and increasingly with the shift to the more oceanic mountains of the western Highlands, flat and gently-sloping ground of this kind, with moderate exposure over summits and spurs, has some kind of Carex-Racomitrium moss-heath. This occurs through roughly the same altitudinal zone as the Nardus-Carex grass-heath, replacing it wherever a combination of lack of shelter with reasonably sharp drainage gives R. lanuginosum a strong, competitive advantage in the cool, humid climate. It can thus run up, around and beyond low-alpine snow-beds, on to higher ground, occurring very extensively over the tops of more rounded mountains of north-west Scotland such as Beinn Dearg and Ben Wyvis, or provide a general context for Nardus-Carex and Deschampsia-Galium snow-fields over slopes that are too freely draining to have blanket mire, as can be seen through the Kintail-Glen Affric district. In their floras, the Carex-Racomitrium and Nardus-Carex communities show great continuity, with C. bigelowii, V. myrtillus, D. flexuosa, G. saxatile, R. lanuginosum, Cladonia uncialis and Cetraria islandica occurring very commonly through both, but Nardus is only very occasional in the former vegetation type, where dominance almost always lies with R. lanuginosum or mixtures of this with C. bigelowii and V. myrtillus. Nonetheless, Typical sub-communities of each come very close in their composition and the Galium type of Carex-Racomitrium heath can intergrade with the Alchemilla-Festuca sub-community of the Nardus-Carex vegetation.

With the shift on to exposed situations over gentlysloping spurs and summits at lower altitudes, dwarfed sub-shrub heaths with abundant mosses or lichens tend to replace these communities in patterns with the Nardus-Carex grass-heath. In the more oceanic west, R. lanuginosum and bulky pleurocarps are very prominent in such vegetation and through the low-alpine zone there, particularly where the ground becomes rough and rocky, the Vaccinium-Racomitrium heath characteristically replaces the *Nardus-Carex* community where the slopes are less sheltered and snow-bound. V. myrtillus and/or E. nigrum ssp. hermaphroditum and the mosses are usually co-dominant in the heath, but plants like C. bigelowii, D. flexuosa, G. saxatile and Nardus can all occur very commonly and, in the widespread Cetraria sub-community, a variety of lichens enhances the floristic continuity between the vegetation types. Moving down into the sub-alpine zone in the western Highlands, Calluna becomes increasingly important in such dwarfed heaths, with Arctostaphylos spp. figuring more locally, and then the Nardus-Carex grass-heath gives way over very exposed brows to some kind of Calluna-Racomitrium or Calluna-A. alpinus vegetation, subshrubs again becoming an abundant element in the cover, though the canopy is often very stunted and patchy in the wind-blasted conditions. Through the east-central Highlands, directly comparable zonations and mosaics can be seen where moderately late snowbeds occur, among exposed spurs, although here it is lichens that have uncompromising dominance in the ground layer, the *Vaccinium-Cladonia* heath running up with the *Nardus-Carex* vegetation to the middle-alpine, the *Calluna-Cladonia* heath extending right down among the lower altitude snow-beds to the sub-alpine. The *Racomitrium* sub-community of the former and the *Cladonia* sub-community of the latter can be seen as floristic transitions to *Nardus-Carex* vegetation where slight hollows or a shift in aspect provide a modest amount of shelter.

In large-scale altitudinal zonations, the low-alpine sub-shrub communities and snow-beds give way below to heaths and grasslands which are strongly modified by anthropogenic activities, being maintained essentially by grazing and burning. Among the varied patchworks of vegetation types clothing these lower slopes, the Nardus-Galium grassland makes the closest approach to the Nardus-Carex grass-heath, particularly where it runs on to sunless aspects at rather higher altitudes than is usual, where, in its Racomitrium sub-community, R. lanuginosum, and S. cespitosus become common with occasional C. bigelowii, E. nigrum, and Cetraria among the abundant Nardus surrounding the more obviously chionophilous vegetation. In other situations, patches of wetter grassland with Nardus and J. squarrosus, usually some kind of Juncus-Festuca vegetation, can occur on wetter peaty soils transitional to blanket peat mantling the shelving slopes at lower altitudes. Indeed, in the east-central Highlands, ombrogenous bog of the Calluna-Eriophorum type is quite a common context for snow-beds over gentle peat-bearing slopes at even very high altitudes and, where melt-water emerges in springs from patches of Nardus-Carex grass-heath and runs into such vegetation, a stand of the Philonoto-Saxifragetum often marks the spring and its vigorous rills.

Distribution

Apart from a few outlying stands scattered through the Southern Uplands and northern England, the community is confined to the higher mountains of Scotland, occurring widely through the central and western Highlands. The Typical sub-community is the most extensively distributed form, with the *Empetrum-Cetraria* type more strongly restricted to wetter regions and more obviously chionophilous situations. The *Alchemilla-Festuca* sub-community is the commonest kind of *Nardus-Carex* grass-heath outside the Highlands.

Affinities

The Nardus-Carex community includes most of the kind of high-level Nardetum referred to in the studies of the altitudinal zonation of the Cairngorms (Watt & Jones 1948, Metcalfe 1950, Burges 1951) and subsumes a variety of moderately chionophilous Nardus noda subsequently described from a number of mountain ranges in Scotland (Poore 1955c, Poore & McVean 1957, McVean & Ratcliffe 1962, Birks 1973, Huntley 1979, Birse 1980), these latter rather peculiar when looked at in isolation, but integrating quite well into this single somewhat diverse community of snow-bed vegetation.

Stands of the Alchemilla-Festuca type, with their A. alpina and Carex pilulifera, provide a link with the subalpine Nardo-Galion swards, among which Nardusdominance is essentially an anthropogenic phenomenon, but the overall affinities of the Nardus-Carex grassheath are clearly with the Nardeto-Caricion bigelowii, an alliance among the generally chionophilous vegetation of the Salicetea herbaceae (Nordhagen 1936, Dahl 1956). Here, an abundance of *Nardus* is associated with but a slim contribution from sub-montane plants, and high frequencies of such Arctic-Alpines as C. bigelowii, Diphasium alpinum, Empetrum nigrum ssp. hermaphroditum, Polytrichum alpinum and Cetraria islandica, species tolerant of the short and cool growing season, with soils being maintained in a suitably moist condition for the grass by moderately long snow-lie or irrigation from its melt or heavy rain. As in the particular case of this British Nardus-Carex vegetation, it is a feature of the alliance in general that the direct effects of snow cover are hard to distinguish from its influence on drainage (Dahl 1956, McVean 1958), something which is evident in related communities described from the Faroes (Böcher 1937) and from the low-alpine of Scandinavia, particularly from the western districts (Nordhagen 1928, 1943, Knaben 1950, Gjaerevøll 1956). Among these, the Sub-alpine Nardus Association of Nordhagen (1928), with its abundance of pleurocarpous mosses, bears the closest resemblance to Typical Nardus-Carex heath, with the various alpine Nardus communities (Nordhagen 1928, Gjaerevøll 1956) and Nardeta chionophila (Nordhagen 1943, Dahl 1956) corresponding more with our *Empetrum-Cetraria* type, though Scandinavian equivalents are generally more species-rich, containing some species which, in Britain, occur in later snow-bed vegetation. The abundance of R. lanuginosum in some stands of the Nardus-Carex heath also knows no real counterpart in the less oceanic Scandinavian Nardeto-Caricion vegetation.

Floristic table U7

| | a | b | c | 7 |
|--------------------------------|------------------------|-----------|------------------------|-----------|
| Nardus stricta | V (1–10) | V (1-10) | V (1-4) | V (1-10) |
| Carex bigelowii | V (1-4) | V (1-6) | V (1-4) | V (1-6) |
| Vaccinium myrtillus | V (1-4) | V (1-6) | V (1-4) | V (1-6) |
| Racomitrium lanuginosum | V (1-9) | IV (1–8) | V (1-6) | V (1-9) |
| Cladonia uncialis | V (1-3) | III (1–4) | V (1-3) | IV (1-4) |
| Galium saxatile | III (1–4) | V (1-6) | V (1-4) | IV (1-6) |
| Cetraria islandica | V (1-3) | III (1–4) | III (1-3) | III (1-4) |
| Empetrum nigrum hermaphroditum | IV (1–6) | I (1-6) | I (1) | II (1-6) |
| Cladonia bellidiflora | III (1-3) | I (1-3) | I (1) | II (1-3) |
| Scirpus cespitosus | III (1–4) | I (1–8) | | II (1–8) |
| Vaccinium uliginosum | III (1–4) | I (4) | | II (1–4) |
| Cladonia gracilis | III (1–3) | I (1-3) | | I (1–3) |
| Juncus squarrosus | II (1–3) | I (1–6) | I (1–4) | I (1–6) |
| Anastrepta orcadensis | II (1-4) | I (1–4) | I (1–3) | I (1-4) |
| Diplophyllum albicans | II (1–4) | • , | I (1-4) | I (1-4) |
| Narthecium ossifragum | II (1–3) | | , | I (1–3) |
| Cladonia pyxidata | II (1–4) | | | I (1–4) |
| Solidago virgaurea | II (1–3) | | | I (1–3) |
| Anastrophyllum donianum | I (1-3) | I (1) | | I (1–3) |
| Lophozia sudetica | I (1–3) | - (-) | | I (1-3) |
| Cetraria delisei | I (1-3) | | | I (1-3) |
| Pleurozia purpurea | I (1-3) | | | I (1–3) |
| Bazzania tricrenata | I (1–4) | | | I (1–4) |
| Cladonia leucophaea | I (1-3) | | | I (1-3) |
| Scapania nemorosa | I (1-3) | | | I (1-3) |
| Cladonia tenuis | I (1-3) | | | I (1-3) |
| Rhytidiadelphus squarrosus | | II (1–4) | I (1-3) | I (1-4) |
| Kiaeria starkei | I (1-3) | II (1–4) | , , | I (1–4) |
| Eriophorum vaginatum | , , | I (1–3) | | I (1–3) |
| Polytrichum alpestre | | I (1–3) | | I (1-3) |
| Rumex acetosa | | I (1-3) | | I (1-3) |
| Alchemilla alpina | I (1) | I (1-6) | IV (1-4) | II (1–6) |
| Festuca ovina/vivipara | I (1) | II (1–4) | IV (1-6) | II (1-6) |
| Carex pilulifera | I (1-3) | II (1–4) | III (1–3) | II (1–4) |
| Agrostis canina | I (1-3) | II (1–4) | III (1–4) | II (1–4) |
| Luzula multiflora | | I (1-3) | II (1–3) | I (1-3) |
| Polytrichum juniperinum | I (1) | • • | II (1–3) | I (1–3) |
| Polytrichum piliferum | | | II (1–3) | I (1-3) |
| Deschampsia flexuosa | III (1-3) | III (1–6) | III (1–6) | III (1–6) |
| Potentilla erecta | III (1-3) | II (1–4) | III (1–4) | III (1–4) |
| Dicranum scoparium | III (1 -4) | II (1–4) | III (1 -4) | III (1–4) |
| Diphasium alpinum | III (1-4) | II (1-4) | III (1–4) | III (1-4) |
| Cladonia arbuscula | III (1–3) | II (1-4) | III (1–4) | III (1-4) |
| Rhytidiadelphus loreus | III (1-3) | II (1-3) | III (1–4) | III (1-4) |

| Ptilidium ciliare | III (1–4) | II (1–4) | III (1 -4) | II (1–4) |
|--------------------------|-----------------------|-----------------------|------------------------|--------------|
| Pleurozium schreberi | II (1 -4) | III (1-4) | III (1-3) | II (1–4) |
| Huperzia selago | II (1–3) | II (1 -4) | II (1-3) | II (1–4) |
| Hypnum cupressiforme | II (1-3) | II (1-3) | II (1–3) | II (1-3) |
| Dicranum fuscescens | II (1–6) | II (1–6) | II (1–4) | II (1–6) |
| Barbilophozia floerkii | II (1–3) | I (1–4) | II (1-3) | II (1–4) |
| Polytrichum alpinum | I (1–3) | II (1–4) | II (1–4) | II (1–4) |
| Vaccinium vitis-idaea | I (1–3) | II (1–4) | II (1-3) | II (1–4) |
| Polytrichum commune | I (1) | II (1–4) | II (1-3) | II (1–4) |
| Hylocomium splendens | I (1-3) | II (1–6) | II (1-3) | II (1–6) |
| Agrostis capillaris | I (1–3) | II (1–6) | II (1-3) | II (1–6) |
| Juncus trifidus | I (1–4) | I (1–4) | I (1) | I (1–4) |
| Salix herbacea | I (1-3) | I (1–6) | I (1–3) | I (1–6) |
| Cladonia rangiferina | I (1–3) | I (1–6) | I (1–4) | I (1–6) |
| Luzula sylvatica | I (1-3) | I (1–3) | I (1) | I (1-3) |
| Plagiothecium undulatum | I (1-3) | I (1–3) | I (1-3) | I (1-3) |
| Cladonia coccifera | I (1-3) | I (1-3) | I (1-3) | I (1-3) |
| Deschampsia cespitosa | I (1) | I (1-6) | I (1–3) | I (1-6) |
| Cladonia impexa | I (4) | I (1) | I (1-3) | I (1–4) |
| Viola palustris | I (1-3) | I (1-3) | I (1) | I (1-3) |
| Calluna vulgaris | I (1–4) | I (1-3) | I (1) | I (1-4) |
| Cornus suecica | I (1-3) | I (1–3) | | I (1-3) |
| Sphagnum capillifolium | I (1-3) | I (1-4) | | I (1–4) |
| Carex panicea | I (1–4) | I (1-3) | | I (1-4) |
| Scapania gracilis | I (1–3) | | I (1) | I (1-3) |
| Omalotheca supina | | I (4) | I (1-4) | I (1-4) |
| Barbilophozia hatcheri | | I (1–4) | I (1-3) | I (1-4) |
| Thymus praecox | | I (1–4) | I (1–4) | I (1-4) |
| Campylopus paradoxus | | I (1–4) | I (1) | I (1-4) |
| Carex nigra | | I (1–3) | I (1–4) | I (1–4) |
| Number of samples | 37 | 45 | 14 | 96 |
| Number of species/sample | 20 (7–31) | 17 (9–33) | 25 (21–31) | 19 (7–33) |
| Vegetation height (cm) | 8 (2–15) | 12 (2–25) | 8 (3–20) | 10 (2–25) |
| Vegetation cover (%) | 97 (60–100) | 97 (70–100) | 92 (60–100) | 97 (60–100) |
| Altitude (m) | 810 (133–1220) | 716 (8–1068) | 755 (530–1006) | 756 (8–1220) |
| Slope (°) | 4 (0–10) | 8 (0–35) | 20 (5–55) | 8 (0-55) |
| | | | | |

a Empetrum nigrum hermaphroditum-Cetraria islandica sub-community

b Typical sub-community

c Alchemilla alpina-Festuca ovina sub-community

⁷ Nardus stricta-Carex bigelowii grass-heath (total)

