A NEW APPROACH TO SCOTTISH MOUNTAIN VEGETATION

BY M. E. D. POORE* AND D. N. MCVEAN
(The Nature Conservancy, Edinburgh)

(With seven Figures in the Text)

CONTENTS

I. INTRODUCTION

Since Watt and Jones drew attention in 1948 to the scarcity of information about vegetation at higher altitudes in Britain there have been several contributions to this subject (Metcalfe, 1950; Pearsall, 1950; Burges, 1951; Poore, 1955). As these are either detailed regional studies, or parts of works of wider scope, there seems to be room for a review of some of the general problems posed by Scottish mountain vegetation. We hope to describe in this paper some of the variation which is evident over the whole of the Scottish Highlands, and discuss the factors responsible, at the same time trying to fit the communities so distinguished into the known pattern of vegetation in north-west Europe.

II. REVIEW OF LITERATURE

In Smith's classification, reproduced in Tansley (1939), vegetation which is above the potential tree-line and rich in Arctic-Alpine species, is divided into two zones, the Arctic-Alpine and the Upper Arctic-Alpine. The lower limit of the former is placed at *c*. 2000 ft. (612 m.) in the central Highlands, but descends almost to sea level in the west. It contains the climax association of Arctic-Alpine grassland and certain unspecified heath associations. In the Upper Arctic-Alpine zone are grouped the *Rhacomitrium* heath association, the moss-lichen associes of mountain-top detritus, and certain snow-patch communities, in addition to scree and chomophyte

* At present working with Hunting Aero Surveys, Elstree Way, Boreham Wood, Herts.

vegetation. The communities are differentiated by maturity, by the exposure-snow cover complex and by the chemical composition of the rock.

Pearsall (1950), in discussing the Arctic-Alpine zones, is mainly concerned with soil characteristics to which he attributes the main differentiation of communities. He distinguishes four types of vegetation; *Rhacomitrium* heath, montane grassland, summit-heath vegetation and flush vegetation; and concludes 'the normal trend of vegetational development on the mountain-top detritus with increasing stability of surface thus follows the sequence: *Rhacomitrium* heath – summit grassland – summit heath (dry or wet) and is associated with the leaching of the humus which follows the stabilization of the surface'.

Crampton (1911) distinguishes three associations on the mountains of Caithness: the *Rhacomitrium* carpet association, the *Calluna*-lichen mat association, and the *Arctostaphylos* mat association. In the geologically uniform terrain in which he worked he considered that the plant associations were differentiated chiefly by the degree of exposure to which each locality was subjected.

Watt and Jones (1948) are more systematic and detailed in their treatment. They distinguish four zones above the present tree-line: the *Calluna* zone, the *Empetrum-Vaccinium* zone, the *Juncus* zone, and snow-patch vegetation. In Fig. 6 (p. 297) of their paper, the relationships of these zones, and of the associations occurring in them, are represented in a diagram showing altitude as one variable, and the exposure-snow cover complex as the other.

Each of these contributions represents part of a system which might be applied more generally, but in none of them is the scope wide enough to relate the parts to the whole. In particular it is unfortunate that so little reference is made to the extensive and relevant Scandinavian publications.

The scheme which is produced here is complete but tentative. It is based on vegetation studies carried out by the methods described by Poore (1955a), supplemented by extensive observations. In particular we have traced certain communities over much of their range and have observed how their floristics, organization and reaction to habitat may change. From this, preliminary hypotheses have been formed about the principal causal influences. As the importance of some of the factors has not previously been stressed in the British literature, and as some of the communities used in illustration have not previously been described, some space is also devoted to these topics.

III. The ecological framework

A general scheme for the arrangement of Scottish mountain vegetation should be based on floristics and synecology; for, although it is more convenient to distinguish noda by floristics (Poore, 1955b), it is easier and more satisfactory to arrange these noda in ecological series. In the present state of our knowledge this can best be done by using the factor complexes which govern the main variation in vegetation, and only later splitting them into their components.

Communities which are undoubtedly seral (e.g. screes) are omitted from the scheme. We consider that most mountain communities (heaths, snow beds, flushes and springs) are part of a climax mosaic, each being maintained by the action of powerful habitat factors. Within each community there is often cyclical change, or a small-scale pattern of micro-succession, as the work of the Cambridge Cairngorm party has demonstrated abundantly; but the distribution of most of them and their position relative to one another are so closely correlated with the present pattern of habitat factors that they are unlikely to stand in a developmental relation to each other. Alterations of the boundaries of communities caused by small climatic fluctuations are more evident than signs of seral development (contrast Pearsall, 1950).

Most of the Scottish mountain communities will fit into a framework made up of the following five factor complexes:

A. *Altitudinal zonation*

The climatic forest limit, which is a convenient datum line in the zonation of mountain vegetation, is difficult to employ in Scotland because of the general scarcity of native forest and the modification of its upper limit by grazing and burning. Some confusion arises in assigning to the correct category certain vegetation types which may have been derived either from the upper forest or from the region immediately above (Fig. 1, *a* to *c*).

The scraps of evidence remaining (unpublished material – D. McV.) indicate that the natural forest limit in Scotland, if it could be realized, would be determined largely by exposure and might, therefore, be expected to show considerable altitudinal variation and attain surprisingly high levels locally in sheltered sites.

The highest natural forest limit (pine) to be seen at the present day lies at 2100 ft. (640 m.) on an exposed western shoulder of the Cairngorms (Watt and Jones, 1948), and it is bordered above by a narrow band of juniper scrub. In Scandinavia the belt of birch scrub (*Betula tortuosa*) above the upper limit of pine, spruce, or mixed deciduous wood, is known as the Sub-Alpine zone. Within it there are areas of juniper and willow, or even of grassland where the establishment of saeters has been followed by clearing and grazing. Burning of scrub is not customary here. If the local topography is irregular there may also be clearings caused by greater exposure or sustained snow cover.

The birch belt is fragmentary in Scotland and the picture still further confused by the replacement of pine and oak by secondary birch woods at lower altitudes. The juniper scrub mentioned above, some of the upper birch scrub in the west and central Highlands and the most northern birch woods of the mainland, beyond the limit of oak and pine, may belong to the Sub-Alpine zone. The lower limit of the zone might be set at 2300 to 2500 ft. (690 to 750 m.) in the east and central Highlands and about 300 to 500 ft. (91 to 135 m.) in the west, although the artificiality of the present tree-line and of the communities immediately above make it difficult to fix with any precision.

Following Du Rietz (1925), Nordhagen (1943) has divided the Norwegian mountains above the birch-line into three regions,* the Low Alpine, the Middle Alpine and the High Alpine (Fig. 2). In Scandinavia the Low Alpine zone is predominantly one of the dwarf shrubs, of which the most important in continental Norway are juniper (*Juniperus communis* ssp. *nana*), dwarf birch (*Betula nana*) and various Arctic willows (*Salix glauca*, *S. hastata*, *S. lanata*, *S. lapponum*, *S. myrsinites* and

* The term 'region' is used in English translations of the Scandinavian literature. As this usage may lead to confusion, we propose to use 'zone' instead.

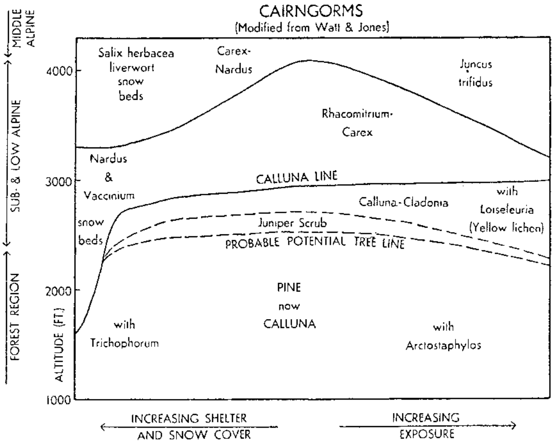

Fig. 1a. Vegetation diagram – Cairngorms. Modified from Watt and Jones.

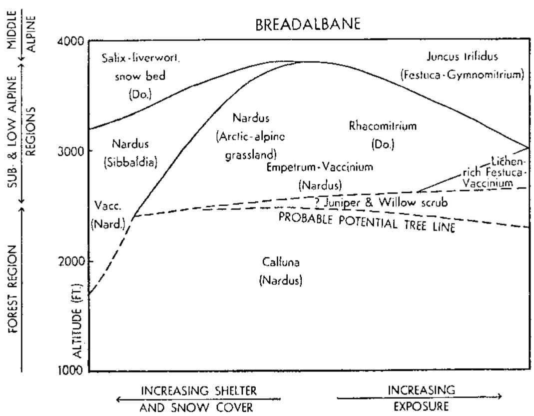

Fig. 1b. Vegetation diagram – Breadalbane.

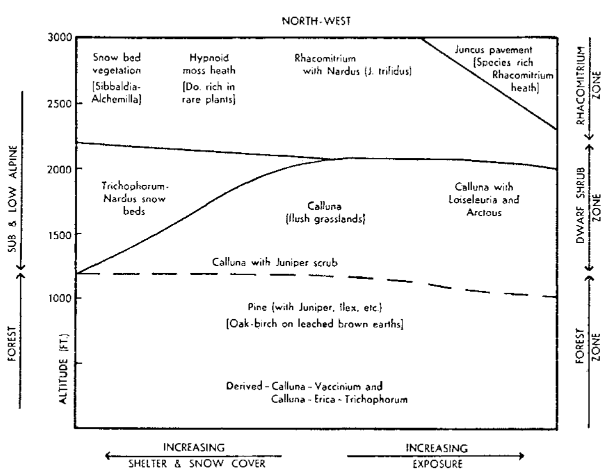

Fig. 1c. Vegetation diagram – North-west Highlands.

S. phylicifolia). Juniper and birch favour dry, poor soils and the willows thrive on wetter or richer spots, especially where flushed from above by snow water.

This is also the region of dominance of the ericoid dwarf shrubs (*Vaccinium* spp., *Empetrum* spp., *Arctous*, *Arctostaphylos* and *Calluna*). In Sogn (Knaben, 1950) juniper ceases at about 900 m. and the vegetation above this is composed of *Empetrum*, *Vaccinium*, *Arctostaphylos* and *Nardus* communities up to about 1100 m. where the Low Alpine passes into the Middle Alpine zone, which contains snow beds and heaths of *Juncus trifidus*, *Festuca ovina* and *Carex bigelowii*.

Continuity can be traced between the Scandinavian zones and those distinguishable in the mountains of Scotland (Fig. 2). The passage from the Low to the Middle Alpine zone corresponds well with the transition in Scotland from dwarf shrub heaths, with abundant *Calluna*, *Empetrum*, *Vaccinium* and *Loiseleuria* to snow-bed vegetation or communities dominated by grasses and grass-like hemicryptophytes

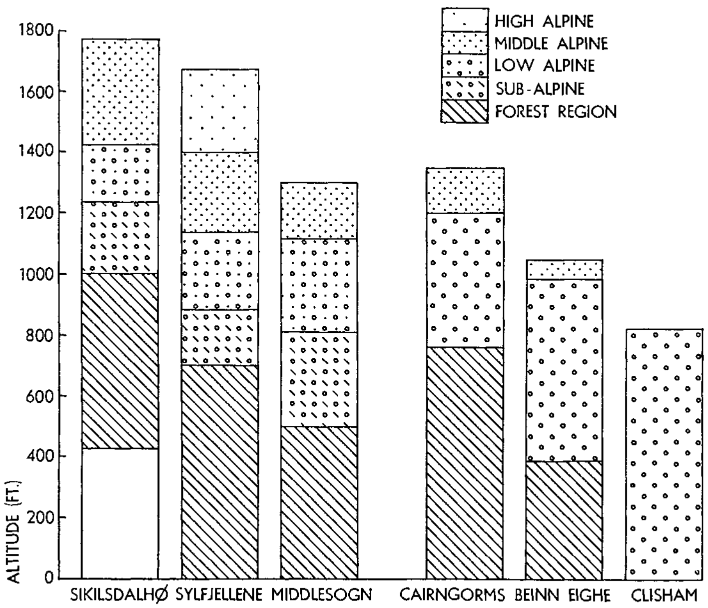

Fig. 2. Altitudinal variation in the alpine regions of Norway and Scotland.

such as *Juncus trifidus*, *Festuca vivipara*, *Luzula spicata*, *Deschampsia flexuosa* and *Carex bigelowii*. In this zone communities which are characteristic of moderately exposed ground are virtually squeezed out (Fig. 1b). The division falls at about 3800 to 4000 ft. (1160 to 1215 m.) in the Cairngorms and at about 3500 ft. (1065 m.) in Breadalbane; but the exact level is dependent on exposure and snow-lie, as communities of the Middle Alpine zone extend downwards where either of these is excessive. In Scotland the Low Alpine zone may again be subdivided into a lower sub-zone of dwarf shrub heaths in which *Calluna* is the most important dominant and an upper zone of *Rhacomitrium* heaths or, where some shelter is afforded by snow, of *Empetrum-Vaccinium* heaths.

Few mountain ranges in Scotland have large areas of vegetation assignable to the Middle Alpine zone, and it is doubtful if any reach the true High Alpine zone although exposure on the highest Scottish tops limits continuous vegetation in the same way as raw soil parent material plus low temperature in continental regions, and produces High Alpine conditions locally in the Ben Nevis range, the Cairngorms and elsewhere.

These zones can be schematized as follows:

Sub-Alpine zone		(Potential birch wood) *Calluna* moors, blanket bogs, *Trichophorum-Molinia*, *Nardus* and *Agrostis-Festuca* grassland.
Low Alpine	*a*. Dwarf shrub zone	Ericoid dwarf shrub heaths. Rarely willow, juniper and dwarf birch scrub.
	b. Moss zone (dwarf shrubs still present)	*Rhacomitrium* heaths. *Nardus* grassland. *Empetrum-Vaccinium* communities.
Middle Alpine		*Juncus trifidus* heaths. *Festuca vivipara-Gymnomitrium* communities. Snow-bed communities.

As *Empetrum-Vaccinium* communities are clearly limited to areas with slight snow cover, and as *Rhacomitrium* heaths are such a widespread and characteristic feature of the Upper Low Alpine zone, it is suggested that '*Rhacomitrium* zone' should be substituted for '*Empetrum-Vaccinium* zone' as a term of general application to the Scottish Highlands. In Fig. 2 the altitudinal distribution of these zones in a transect from continental Norway to the west of Scotland is represented diagrammatically. The various stations are Sikilsdalhø in the eastern Jotunheim, the Sylfjellene west of Trondheim, the mountains of middle Sogn, the Cairngorms, Beinn Eighe (Wester Ross) and Clisham (Harris). No attempt has been made to maintain a firm distinction between the Sub- and Low Alpine zones in Scotland.

It can be seen that in Norway the boundaries of the various zones are steadily depressed towards the more maritime stations and that there is a simultaneous tendency for the zones to widen. The Cairngorms correspond more closely to Sylene than to Sogn, their lower latitude perhaps compensating for their probably greater oceanicity (pp. 412-13). The vegetational parallels between the Cairngorms and the more acid parts of the Sylene national park are striking (Poore, 1955c). Within Scotland the lower position of all zones than that of their counterparts in Norway is evident. Particularly noteworthy is the much increased importance of the Low Alpine zone. This is probably due to the depression of the tree-line caused by exposure, the great extension of bog-covered ground, and to the relatively higher altitude at which temperature becomes critical for dwarf shrub growth.

Juniper, willow and dwarf birch scrub

The abundance of woodland and scrub in the Norwegian mountains affords a striking contrast to the typical landscapes of the Scottish Highlands. In Sikilsdal, for instance, *Betula tortuosa* extends to 1238 m. on south-facing slopes, and scrub continues for another 200 m. (Nordhagen, 1943). In relatively continental areas willow and juniper scrub reach the lower limit of communities which show the influence of exposure, while in the cold oceanic climate of Mjølfjell, below the Hardangervidda, and Middle Sogn, on the western side of the Jotunheim, snow-bed communities occur as enclaves in the birch wood. This scrub is partly primary, belonging to the Low Alpine zone, and partly secondary, derived from birch wood by cutting and grazing. It is only in the neighbourhood of the saeters that human interference is so intense that the vegetation begins to look like the better Scottish mountain pasture.

This profound contrast makes one consider how far the absence of a willow-juniper-dwarf birch belt in Scotland is due to climatic differences, or to the absence of suitable ecotypes, and how much it is due to the different pattern of land use in the two countries. Evidence of relict scrub in Scotland, and of the course of degradation in Scandinavia, is strongly in favour of the latter view. It is to be expected, however, that the Scottish scrub, although not identical with the Norwegian, would have showed strong similarities to it as do some other communities which have escaped the full weight of man's activities (e.g. *Carex saxatilis* sociation, Poore, 1950c). With the exception of *Salix herbacea* the Arctic willows are rare in Scotland and such populations as do occur are mainly confined to cliffs. That this is due to grazing is clear from the absence of willows on suitable soils away from the cliffs and from their undoubted palatability to animals. Occasional grazed specimens may be found in Sub-Alpine grassland as, for example, a 10 cm. high shrub of *S. lapponum* in *Nardus* grassland in Breadalbane. Poore (1955c) cites good indirect evidence for the occurrence of willow scrub in Scotland in discussing the *Carex saxatilis* sociation in Breadalbane, a sociation which shows close affinities in floristics and habitat with two sociations in Sylene and Sikilsdal but which differs principally in the absence of the willows. Other sociations show the same effect.

Where conditions are suitable small patches of 'willow scrub' do develop in Scotland. The small groups of *Salix lapponum* on screes and steep ground in Glen Doll might qualify for this term. These probably owe their presence to the inaccessibility of the ground together with the relatively high seeding potential of bushes on the surrounding cliffs. Over most of the Highlands the number of individuals left is so small, and the sexes often so widely separated, that reconstitution of this vegetation type in the absence of grazing would be a long process.

The most remarkable area of willow scrub yet found in Scotland is on limestone pavement in Inchnadamph. On a plateau lying between 700 and 900 ft. (210 to 274 m.) outcrops of the Durness limestone alternate with peat-covered hollows. The exposed rock shows the characteristic clints and grikes of limestone pavement but there are no large continuous areas of this formation. Blanket peat may formerly have covered much of the limestone that is now exposed, though suitable refugia for basiphilous species will always have existed on the steep sides of the nearby Traligill burn. About 300 acres (121 ha.) of this ground are partially covered by low willow scrub, mainly of *S. myrsinites*, but also containing *S. repens*, *S. aurita* and their hybrids. Individual bushes are from 6 in. (15 cm.) to 18 in. (46 cm.) tall and have a prostrate habit. They are well established and are even invading thin peat over limestone.

Five samples of the scrub (intervening areas of Callunetum on deep peat deliberately avoided) revealed considerable floristic uniformity (Table 1), five species being constant. The mat of hypnoid mosses is usually co-extensive with the shoots of willow, though it may extend beyond them in a few places, and contains the same assemblage of species as certain low willow scrubs in *Festuca ovina* sociations of central Norway which also show this phenomenon. Tall Norwegian scrubs, however, develop a different ground and field layer as light intensity decreases.

Dryas is abundant on the drier limestone and the crevices have a flora which has some affinities with northern woodland, e.g. *Cirsium heterophyllum*, *Trollius europaeus*, *Sanicula europaea*, *Polystichum lonchitis*, *Primula vulgaris*, *Rubus saxatilis*, *Galium boreale*. The scrub is within the potential woodland zone (a few small trees of *Betula* *pubescens* and *Sorbus aucuparia* are present) so that it may partly be of secondary origin following the removal of the primary woodland and deep peat cover. It is, therefore, analogous to the secondary scrub of the Sub-Alpine zone (p. 406).

This evidence, scanty though it is, favours the view that there was once a region above the tree-line which contained scrub of Arctic willows on the damper and more

Table 1. Salix myrsinites *scrub*

	1	2	3	4	5
Plot area (sq. m.)	4	4	4	8	6
Calluna vulgaris	+	—	—	+	1
Empetrum nigrum	2	1	—	—	—
Rubus saxatilis	—	+	—	—	—
Salix myrsinites	8	8	8	8	7
Vaccinium myrtillus	—	—	—	—	3
Blechnum spicant	+	—	—	—	—
Agrostis tenuis	3	4	—	2	3
Anthoxanthum odoratum	5	—	—	—	—
Festuca ovina	4	3	3	3	3
Deschampsia caespitosa	—	—	2	—	—
Nardus stricta	—	—	1	—	—
Carex binervis	—	—	1	2	—
Luzula campestris	—	—	1	—	—
Cirsium heterophyllum	+	—	—	—	—
Galium hercynicum	—	1	3	3	3
Oxalis acetosella	+	4	—	—	3
Potentilla erecta	3	2	3	2	3
Primula vulgaris	1	—	—	—	2
Ranunculus acris	1	—	—	—	—
Thymus drucei	2	3	3	1	—
Trifolium repens					
Viola riviniana	3	3	2	5	3
Breutelia chrysocoma	—	4	—	—	—
Ctenidium molluscum	3	1	—	—	—
Dicranum scoparium	—	—	—	4	1
Ditrichum flexicaule	—	1	—	—	—
Hylocomium splendens	2	4	8	5	7
Mnium undulatum	—	1	—	3	2
Pleurozium schreberi	—	3	—	3	5
Pseudoscleropodium purum	2	2	—	1	—
Rhytidiadelphus loreus	—	—	—	—	1
R. squarrosus	2	1	3	—	2
R. triquetrus	4	1	3	—	4
Thuidium tamariscinum	5	3	—	—	3
Tortella tortuosa	—	1	—	—	—
Frullania tamarisci	—	+	—	—	—
Cladonia impexa	—	—	—	—	1
C. pyxidata	—	—	—	1	—
Peltigera aphthosa	1	—	—	—	—
P. canina	1	—	1	2	—

base-rich soils. It is likely that willows have also played a role in the vegetation of the Sub-Alpine birch woods, and that a scrub of *Salix atrocinerea* and *S. aurita* may have replaced alder wood at various altitudes on acid soils of impeded drainage, as it still does in suitable habitats in the north of Scotland.

Above the upper limit of pine on Creag Fhiaclach, already mentioned, there is a discontinuous band of juniper scrub which has so far escaped destruction by moor fires. This scrub is dense in places and about 4 ft. (>1 m.) tall, formed of spreading shrubs with low branches which turn upward at the tips. In leaf characters this juniper is more closely related to the ssp. *communis* than to the prostrate ssp. *nana*. The scrub flora is different from that of the surrounding *Calluna* heaths and the principal feature of the ground layer is the continuous carpet of hypnoid mosses (*Hylocomium splendens, Hypnum cupressiforme, Pleurozium schreberi, Rhytidiadelphus loreus, Thuidium tamariscinum*), *Plagiothecium undulatum* and *Dicranum scoparium*.

Analyses have not yet been made of this community, but the following species have been seen on different occasions: *Blechnum spicant, Lycopodium annotinum, Vaccinium myrtillus* and *V. vitis-idaea, Anthoxanthum odoratum, Holcus mollis, Oxalis acetosella, Rumex acetosa, Veronica officinalis* and, occasionally, *Listera cordata, Pyrola ?media, Thalictrum alpinum* and *Platysma lacunosum*.

It is uncertain whether the juniper scrub at the upper forest limit in the eastern Highlands carried a proportion of birch, but, whether it did or not, we can probably

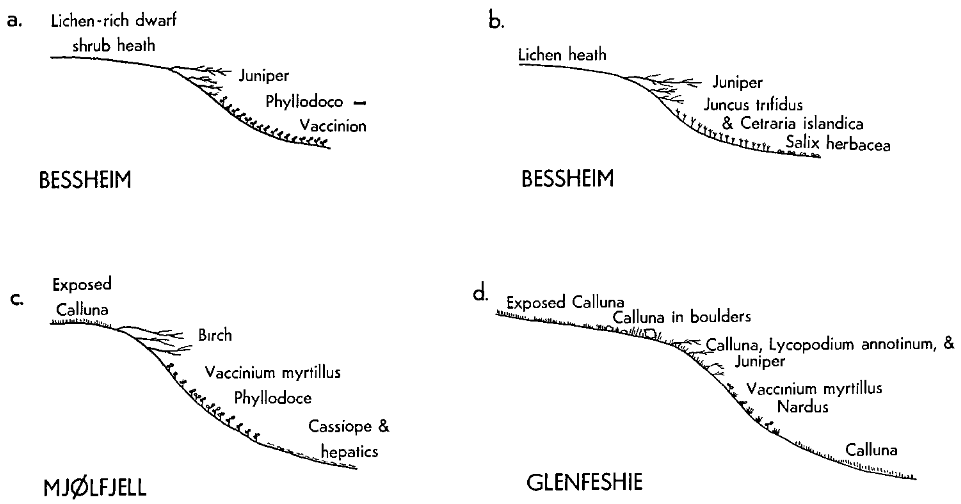

Fig. 3. Relation of Sub-Alpine scrub to snow cover. For explanation see text.

assign most of it to the Sub-Alpine zone. Evidence that primary juniper scrub was an important constituent of the Low Alpine zone is very scanty, because most suitable ground at these altitudes has been regularly burnt for over a century and sporadically for a much longer period. However, occurrences such as the following are suggestive.

Near the limit of scrub in Norway juniper often forms an 'eyebrow' round the upper edge of a snow bed between the exposed communities above and the snow-bed communities (usually Phyllodoco-Vaccinion) below. Fig. 3 shows two situations observed near Bessheim in the eastern Jotunheim, and a similar zonation from within the birch woods at Mjølfjell in western Norway (Fig. 3, *a*, *b* and *c*); cf. also McVean (1955). Traces of this situation, with juniper occupying the same place in the zonation, but not forming scrub, can be found in the Cairngorms and central Perthshire where exposed communities border *Vaccinium* snow beds (Fig. 3, *d*). The following list gives the composition of such a community:

Calluna vulgaris	6
Empetrum hermaphroditum	5
Juniperus communis	4
Sorbus aucuparia	+
Vaccinium myrtillus	5
V. vitis-idaea	3
Lycopodium annotinum	2
Carex bigelowii	1
Deschampsia flexuosa	2
Nardus stricta	1
Melampyrum pratense	1
Dicranum scoparium	2
Hylocomium splendens	6
Pleurozium schreberi	4
Cladonia rangiferina	1
C. sylvatica	3

Small patches of such juniper scrubs, at and above the tree-line, are frequent in the Monadhliath to the west of Strathspey. Juniper scrub below the tree-line is also widespread in this part of the country, especially in Glen Dulnan and on the hills of the Aberdeenshire-Banffshire border. The Glen Dulnan scrub covers large areas of alluvial flats as well as parts of the surrounding slopes.* Fire seems to be the main enemy of the juniper, but where the scrub has once been opened up, grazing can effectively check regeneration. Many of the bushes are of great age, and the scrub seems to be receding almost everywhere.

The extensive juniper scrub on headlands coming under the influence of blown shell sand near Bettyhill, Sutherland, can probably be assigned to this nodum also.

There is no evidence that mixed scrubs of juniper and dwarf birch, such as can be found in central Norway, ever occurred in Scotland. The somewhat different behaviour of *Betula nana* in the two countries would be sufficient to account for this (p. 425).

A scrub of *Juniperus nana*, which undoubtedly belongs to the dwarf shrub communities of the Low Alpine zone, will be described below. We shall have to wait for more detailed stratigraphical and pollen analytical studies before we can know for certain whether these scrub types did in fact play a part as important as is assigned to them here, although certain sub-fossil finds in the north-west Highlands are significant (p. 421).

On the basis of vegetational evidence at present at our disposal it seems reasonable to suppose that a scrub zone succeeded the tree zone at higher altitudes over much of the Scottish Highlands. This scrub zone was probably of juniper on the well-drained and acid hills of east and central Scotland, of willows (*Salix lanata, S. lapponum. S. nigricans, S. myrsinites, S. repens* and *S. aurita*) on the wetter and more eutrophic soils, and of *Juniperus nana* on the Cambrian quartzite, Torridonian sandstone and granites of the west.

Betula nana may have been an important constituent of scrub bogs in this zone, but it is unlikely that it has been a dominant within historical times (p. 423).

At higher altitudes the effect of human activities becomes very much reduced and the variation of vegetation can usually be explained in terms of physical factors alone.

* Characteristic lichens growing on the twigs of this juniper are *Cetraria pinastri* S. F. Gray and *C. sepincola* Wain.

B. *Oceanicity*

The notable differences, both in climate and vegetation, between the western European seaboard and parts of the European continent distant from the sea have long been recognized by ecologists. Watt (1936), in his studies of the Breckland region of East Anglia, has drawn attention to the continental characteristics of this area. No attempt has been made so far to gauge the importance of this factor in controlling the communities of the Scottish mountains or in placing them in the series from 'oceanic' to 'continental' recognized in the mountains of Scandinavia.

The communities which make the greatest contribution to the vegetation above the potential tree-line in Scotland have already been mentioned (p. 406). It is only in the coastal regions of Norway that the most important species of these communities, *Calluna* and *Rhacomitrium*, play any part. Instead, extensive areas are covered with *Empetrum*, *Arctostaphylos*, *Betula nana* and lichen heath (*Alectoria ochroleuca*, *A. divergens*, *Cetraria nivalis*, *C. islandica*, *C. cucullata* and *Cladonia alpestris*). The Norwegian communities dominated by juniper and willows have already been discussed.

The trend from oceanic to continental climate involves a number of factors which are important in the understanding of plant distribution. Various attempts have been made to combine them in Indices of Oceanicity. Before considering these, what are the climatic variables involved?

Precipitation is higher in oceanic regions, and there is a marked increase of the precipitation/evaporation ratio associated with the large number of wet days and sustained high humidity. Insolation is also reduced. This has the effect of increasing the rate of growth and the competitive power of the bryophytes, especially *Sphagnum*, *Rhacomitrium* and the hypnoid mosses, and there are also marked secondary effects in the leaching of soils, and the development of impeded drainage.

Another important consequence for vegetation, and especially mountain vegetation, is the form of the annual temperature curve. Characteristic of a continental climate are a high summer maximum and low winter minimum with rapid transitions in spring and autumn. The curve for an oceanic climate is flattened; in Poore (1955c) a characteristic curve for Scotland is compared with that from a relatively oceanic part of Norway.

The growth period is reduced in oceanic regions but the indirect effects may be even more important. Because of the continuously low winter temperatures in continental regions snow cover is both deeper and more persistent from year to year. Furthermore, low summer rainfall and high temperatures are less efficient removers of snow than low summer temperatures and high rainfall. This was well illustrated in Scotland by the late snow-lie in the hot dry summer of 1955, compared with the early disappearance of snow in the cool wet summer of 1954.

One effect of this oceanic feature may well have been the severe restriction of the range of frost-sensitive montane species. In a continental climate snow melt is usually rapid and followed by warm weather; in Scotland most of the snow may be stripped from the hills in the middle of winter or early spring by a warm air stream, and this may be followed immediately by hard frost (cf. Poore, 1955c).

Another feature of the oceanic climate is the prevalence of high winds. It cannot fail to impress the British ecologist in Norway that the evidences of wind cutting of trees and damage to mountain plants by high winds and blizzards are relatively rare compared with what he sees at home.

Godske (1944) has discussed the distribution in Norway of various Indices of Oceanicity which are calculable from standard meteorological measurements. He finds that the best correlation with biological phenomena is given by modifications of Kotilainen's Index of Oceanicity. Kotilainen's original index is given by the formula

$$K = \frac{N.dt}{100\ \triangle}$$

where N is the precipitation in millimetres, dt is the number of vernal or autumnal days (i.e. days with mean temperature between 0° and 10° C.) and $\triangle$ is the difference between the mean temperature of the warmest and coldest month. The various modified indices ($K_{0\cdot 0}$, $K_{0\cdot 1}$, $K_{1\cdot 0}$) are made by substituting for N the values $N_{0\cdot 0}$, $N_{0\cdot 1}$

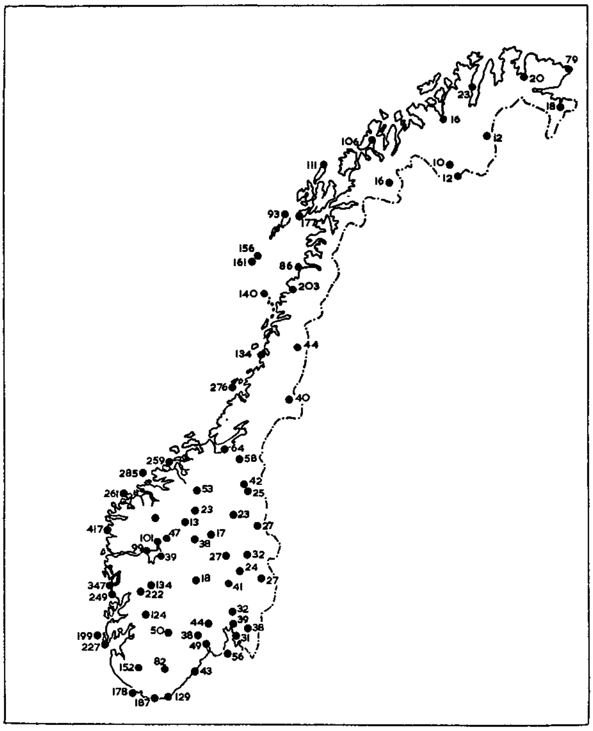

Fig. 4. Indices of Oceanicity – Norway. Modified from Godske.

and $N_{1\cdot 0}$ which are respectively the number of days with precipitation, 'measurable' or not, of days with precipitation of 0.1 mm. and of 1.0 mm. The best correlation with biological phenomena was obtained with $K_{0\cdot 0}$. As exact equivalents cannot be calculated from British meteorological data for these modified indices, values have been calculated for K and the results are presented in Figs. 4 and 5.

It can be seen from these maps that higher figures are registered for Glenbranter and Achnashellach than for any station on the west coast of Norway, where the highest value is 417 at Florø, north of the Sognefjord. Furthermore, as one would expect, the index is lower in the islands (Lewis, Shetlands, Orkneys, Coll, etc.) than it is on the west coast itself. It is significant that no values for the index of over 100 are recorded from inland stations in Norway except from Svandalsflona at 1065 m.

and that stations in the Jotunheim and Dovrefjell give low values (e.g. Dombås, 13), while the lowest value in Scotland is at Nairn, 118 (cf. also Nordhagen, 1943, and Knaben, 1950).

It is clear that these figures support the hypothesis that much of the difference between Scottish and Norwegian mountain vegetation, where undisturbed by man, is due to the very oceanic climate of the Scottish mountains. This is supported also by data from the distribution of individual species. In a discussion of the flora of the

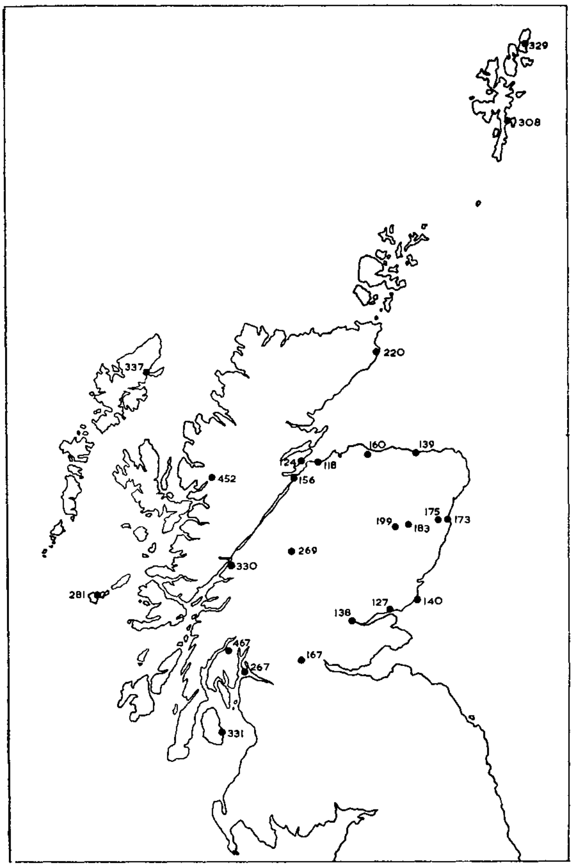

Fig. 5. Indices of Oceanicity – Scotland.

Sogn district of western Norway Knaben (1950), cites as oceanic the following species, which occur in our mountains:

Blechnum spicant	Holcus mollis
Carex pulicaris	Hypericum pulchrum
Digitalis purpurea	Juncus squarrosus
Dryopteris oreopteris	Luzula sylvatica
Galium hercynicum	Narthecium ossifragum

Of these, *Carex pulicaris* and *Holcus mollis* occur very rarely as far east as Vik in the Sognefjord. *Luzula sylvatica* and *Hypericum pulchrum* reach Balestrand (K, 256) and only *Blechnum* and *Dryopteris oreopteris* stretch farther to the east. In contrast it is clear that there is no climatic restriction on the general distribution of these species in the Scottish mountains. *Carex pulicaris, Hypericum pulchrum, Narthecium* *ossifragum* and *Juncus squarrosus* occur at considerable altitudes wherever edaphic conditions permit. *Dryopteris oreopteris, Luzula sylvatica, Galium hercynicum* and *Blechnum spicant* show a dependence on snow cover in the central and eastern Highlands, but not in the west. The two last species, for instance, are almost confined to snow beds in the Cairngorms, but *Galium hercynicum* occurs on relatively exposed *Rhacomitrium* heaths in Breadalbane. More specific evidence of the oceanicity of the Scottish mountain climate will be dealt with later.

C. *Snow cover*

Within a mountain area which is climatologically and geologically uniform the principal causes of local differences in vegetation are the snow cover-exposure com-

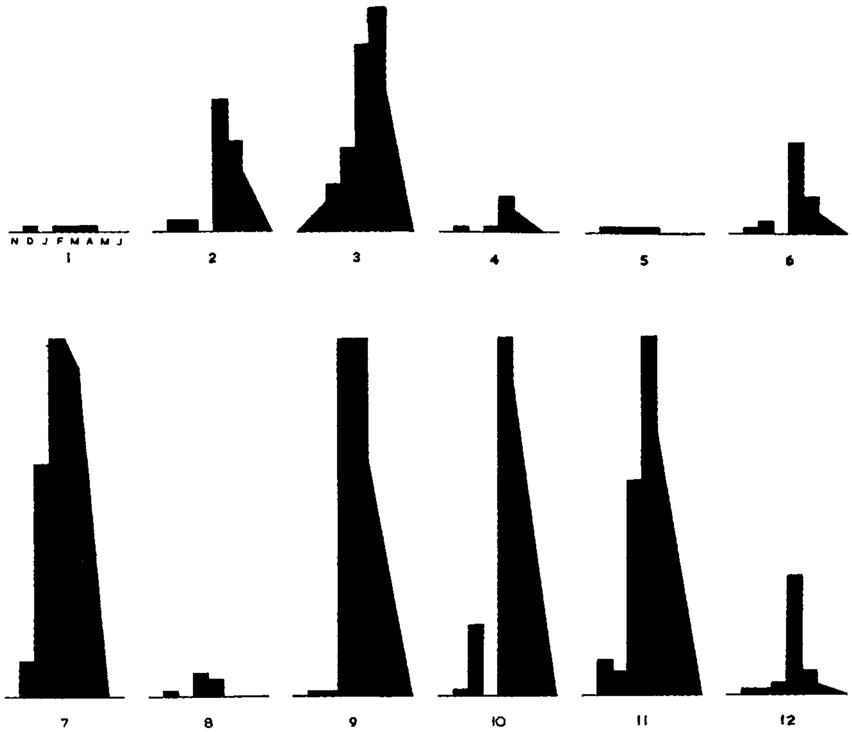

Fig. 6. Snow depth records for some Breadalbane plant communities. For explanation see text.

The stands in question were:

1. *Rhacomitrium-Carex bigelowii* sociation: Ben Ghlas: 3100 ft. (945 m.): ground level.
2. High altitude *Nardus stricta* soc.: Ben Ghlas: 3100 ft. (945 m.): N.E. aspect.
3. High altitude *Nardus stricta* soc.: Ben Lawers: 3250 ft. (990 m.): S.S.W. aspect.
4. Lichen-rich *Vaccinium-Alchemilla* soc.: Ben Lawers, 2550 ft. (777 m.): S. aspect.
5. Middle Alpine *Festuca vivipara* soc.: Ben Lawers: (provisional constants of this sociation are *Festuca vivipara, Luzula spicata, Oligotrichum, Pohlia nutans, Polytrichum piliferum, Rhacomitrium lanuginosum, Diplophyllum albicans, Gymnomitrium concinnatum* and *G. coralloides, Nardia scalaris* and various lichens including *Cerania vermicularis*).
6. *Vaccinium-Alchemilla* grassland: Ben Lawers: 3250 ft. (990 m.): S.E. aspect.
7. *Sibbaldia* nodum: Ben Lawers: 3250 ft. (990 m.): S.E. aspect.
8. *Sibbaldia* nodum: Ben Lawers: 2800 ft. (853 m.): N. aspect.
9. *Salix herbacea* nodum: Ben Lawers: 3750 ft. (1143 m.): E. aspect.
10. *Salix herbacea* nodum: Ben Lawers: 3300 ft. (1006 m.): N.W. aspect.
11. *Carex saxatilis* sociation: Ben Lawers: 3000 ft. (914 m.): S.S.E. aspect.
12. *Carex saxatilis* sociation: Ben Lawers: 2800 ft. (853 m.): N. aspect.

Fig. 6 shows the depth in inches of the snow on the dates mentioned below.

plex and soil moisture. There are other factors which are locally important, but broad trends can be explained in terms of these two.

The scheme of Watt and Jones has drawn attention to the importance of snow cover and exposure, but it has been less stressed than it deserves, probably because most vegetational studies are concentrated in the summer months. Poore (1955b and c) has also mentioned its importance, and has predicted the probable snow regime of a number of communities. These predictions have been generally justified by more intensive winter observations.

At the beginning of November 1954 twelve stands were chosen in representative communities on Ben Lawers and Ben Ghlas, and a graduated pole six feet (2 m.) long was driven into each. The depth of the snow was read on these posts at the beginning of each month throughout the winter. Readings could not be made in May and all snow had disappeared by June 1st.

These observations confirm that the communities thought to be chionophobous (the *Rhacomitrium-Carex bigelowii* soc. (1) and the Middle Alpine *Festuca* soc. (5)), undoubtedly remain uncovered except just after snow-fall on a windless day, a sufficiently rare occurrence to be ignored. In exceptional circumstances such a fall may thaw and freeze again before drifting. These conditions were found in February 1954 when a deep snow-fall was followed by hail and sleet which then froze to produce a surface like frozen sago pudding. Usually, however, these communities are blown clear of snow and have only banners of rime on stones and projecting vegetation, or a thin skin of verglas. The lichen-rich *Vaccinium-Alchemilla* soc. (4) sometimes collects a little snow, but usually remains clear. At the other extreme are communities (7), (9), (10) and (11). All of these had a cover of over 5 ft. (152 cm.) for a period of at least four weeks, but the cover is not necessarily so deep throughout the entire winter. The reason for this is sufficiently clear on the ground. Each deep drift is built up round a centre of accumulation; even on November 1st there was a small patch of drifted snow less than 1 ft. (30.5 cm.) square near Post (9) which had already taken on the hard compacted texture of névé. Later accumulation occurs round and over initial centres of this kind, although of course the pattern may be far from regular. In the early stages the ground round the forming drift is usually bare and exposed to extremely severe conditions.

Cornices and deep drifts are usually formed in the lee of a ridge. Exposure reaches its height immediately on the windward side, and the wind lashes back in violent eddies just under the lee crest. To give some idea of the severity of weather experienced it may be sufficient to say that on only one visit between November and April was it physically possible, even on hands and knees, to cross the north ridge of Ben Lawers at Post (9).

At lower elevations and in less exposed situations deep drifts may form without such violent marginal conditions; here too the snow does not last so long, and a continuous cover of vascular plants helps to collect a small sheltering cover of rime and snow. The distinction between conditions in the snow bed and in its environs is thus not so sharp.

The observations in the *Carex saxatilis* nodum (11 and 12) illustrate the same point. Post (11) was nearer the centre of accumulation than (12), although neither coincided with it exactly. These sites differ from the others because the first snow or frost produces a crust of ice an inch or two thick, which covers the whole flush, but is slightly raised above the vegetation level, only the upper parts of the *Carex* leaves being frozen into the ice sheet. Drifting snow accumulates over the ice but, because this is an unfavourable holding surface, the centre of accumulation is usually slightly upslope from the flush.

The *Vaccinium-Alchemilla* grassland appears to be intermediate in its snow regime; and the *Nardus* sociation is, as predicted, consistently different from the *Rhacomitrium-Carex bigelowii* soc.

Although the exposure-snow cover factor is complex, and the ways in which it may influence the vegetation are numerous and insufficiently understood, yet its visible effects are consistent and effectively differentiate the communities within the Low and Middle Alpine regions. In any attempt to schematize the variation in the vegetation of a mountain region, this is one of the key factors.

D. *Base status*

Enough has been written about the influence of the chemical composition, and especially the base content, of soils on the distribution of vegetation to make it unnecessary to develop this theme. It is now accepted that base status is a fundamental factor differentiating plant communities, although its operation is once again little known.

E. *Moisture*

A further fundamental distinction can be made on the water content of the soil from well-drained to permanently waterlogged. Community variation can be broadly explained in terms of variation in this factor, although smaller differences may be due to additional variables such as oxygenation of the water supply, whether it is perennial or seasonal, and so on.

It is true that the effects of moisture and snow cover cannot be entirely separated. Snow beds are often (although not always) in less well-drained situations; drifting leads to a redistribution of winter precipitation, and irrigation by melt water is important in determining the distribution of hygrophilous communities. In the Middle Alpine zone and the *Rhacomitrium* zone there is a close correlation between the exposure-snow cover complex and drainage; but at lower altitudes they are more independent.

Summary

Even if the number of master factors of a satisfactory ecological framework can be reduced to five (and this will necessarily exclude many specialized communities), it is impossible to represent the whole situation diagrammatically. Nor is a hierarchical classification any more satisfactory, although the critical consideration required in making such a classification, and the resulting classification itself, may be of the greatest value, as has been shown by the use to Scottish vegetation studies of the admirable works of Nordhagen. The only complete answer appears to be a vegetation key as suggested by Gams (1917 and 1939).

Diagrams may, however, be invaluable for representing parts of the variation in vegetation. Thus, taking that reproduced in Watt and Jones (1948, Fig. 6) as a model, Figs. 1, *a-c*, show the variation of vegetation with altitude and with the exposure-snow cover complex in three areas, the continental Cairngorms, the Breadalbane hills, and the oceanic hills of north-west Scotland. More base-rich variants of common communities are inserted in square brackets. By using different variables in diagrams such as these, the whole situation may be simply presented. If the diagrams for these three areas are compared, it can be seen that the situation in Breadalbane is very similar to that in the Cairngorms, although there are differences in the composition of the various communities which can only be seen by inspection of tables; the main difference between these two lies in the presence in Breadalbane of large areas of base-rich rock forming soils with larger silt and clay fractions. The differences between them and the third are more definite, although the arrangement of the different types follows much the same pattern. Among the differences are: the replacement of *Nardus*, *Carex* snow beds by hypnoid moss heath; the presence of the species-rich moss heath in the base-rich series of the *Juncus trifidus* zone, which may be due in part to the particular characteristics of the dolomitic mudstones, and in part to the greater solifluction effects of the north-western hills; the association of *Nardus* with the *Rhacomitrium* heaths; and the disappearance of the snow-bed communities below the potential tree-line.

IV. COMMUNITIES DISTINGUISHED

The communities described below have been chosen partly for their intrinsic interest, and partly to illustrate how the pattern of variation of Scottish mountain vegetation can be fitted into the ecological framework. Two main groups can be distinguished; those which, like the *Rhacomitrium* heaths, have part of their principal distribution in Britain, and those which are typically Scandinavian, and are local in Scotland. The localized communities may be restricted to relatively small areas within well-known British vegetation types. It is thought that the principle, useful in autecology, that the general distribution of the species can be valuable in interpreting its local behaviour, and *vice versa*, may be equally useful in the field of phytosociology (cf. Boyko, 1947).

A. *Dwarf shrub heaths*

Within the Calluneta of the Sub-Alpine and Low Alpine zones, there is great diversity, communities of very different tolerances being included. The designation of these by the name of the common dominant has helped to conceal interesting details of distribution and of affinities to communities elsewhere in which *Calluna* plays only a subordinate part or is entirely absent. Although the two sociations which follow, and the *Betula nana* bogs and lichen heaths of the next sections, might all be classed as Calluneta, they have been named instead after other constant species which are thought to give a better expression of their ecology.

Loiseleuria-Arctous *sociation* (*Table* 2)

Some exposed habitats of intermediate altitude in the north-west of Scotland are occupied by a dwarf shrub heath which is somewhat richer in species than the *Calluna* heaths occupying this habitat elsewhere. Seven lists are set out in Table 1, two from Ben Clibreck, two from the Coulin forest, Wester Ross, one from Beinn Dearg, east of Loch Broom, and one from Beinn Eighe. The distribution of the community, as known at present, is a narrow discontinuous band stretching from Loch Torridon in the south-west to Ben Clibreck in the north-east. The *Arctostaphylos*-mat association described by Crampton (1911) from Morven, Caithness, almost certainly belongs to this sociation.

The community forms a thick-set mat of dwarf shrubs and lichens up to 5 cm. deep, broken occasionally by stones. In exceptionally exposed places it may be banded and interrupted by patches of erosion pavement liable to solifluction. From the data so far available, it is distinguished by the constancy of *Loiseleuria procumbens*, *Arctous alpina*, *Calluna vulgaris* (which usually has a cover of over 50 per cent), *Empetrum* (both species), *Rhacomitrium lanuginosum* (small cover), *Cetraria islandica*, *Cladonia sylvatica*, *C. uncialis*, *Ochrolechia tartarea*, *Platysma glaucum* and *Sphaerophorus globosus*. It is also distinguished by the occurrence of the lichen *Platysma lacunosum* and of certain species which are characteristic of exposed heaths in the north-west Highlands, e.g. *Solidago virgaurea*, *Antennaria dioica*, *Euphrasia frigida* and *Lotus corniculatus*.

Table 2. Arctous-Loiseleuria *nodum*

	1	2	3	4	5	6
Cover	100	95	100	100	100	100
Altitude (ft.)	1780	1700	2000	2300	1800	2000
Slope (deg.)	1	2-3	0	2	2	2
Aspect	SW	W	—	N	E	W
Area of plot (sq. m.)	4	4	4	1	4	1
Arctostaphylos uva-ursi	—	—	—	+	1	—
Arctous alpina	4	4	4	5	4	5
Calluna vulgaris	8	8	7	7	6	7
Empetrum (both spp.)	5	4	4	3	4	2
Erica cinerea	2	—	—	—	—	—
Juniperus communis	—	—	—	2	3	4
Loiseleuria procumbens	4	4	+	+	4	4
Salix repens	—	—	+	—	—	—
Vaccinium myrtillus	1	2	1	—	3	—
V. uliginosum	—	—	+	—	—	+
V. vitis-idaea	3	1	—	—	—	—
Lycopodium alpinum	+	+	—	+	—	+
L. selago	1	1	+	—	—	—
Agrostis tenuis	—	—	1	—	—	—
Deschampsia flexuosa	3	3	—	1	3	—
Festuca vivipara	2	2	—	2	—	3
Carex bigelowii	+	2	—	3	2	—
C. panicea	4	—	3	—	—	3
Juncus squarrosus	—	—	—	—	+	—
Luzula multiflora	—	—	1	—	—	—
Trichophorum caespitosum	+	—	1	—	—	1
Antennaria dioica	2	1	+	—	—	—
Euphrasia frigida	1	+	+	—	—	—
Galium hercynicum	—	—	—	2	—	1
Hieracium alpinum	—	—	—	—	—	+
Lotus corniculatus	+	+	—	—	—	—
Pinguicula vulgaris	+	+	—	—	—	—
Potentilla erecta	—	—	+	—	—	1
Solidago virgaurea	—	—	—	—	1	1
Thymus drucei	—	+	—	—	—	—
Pleurozium schreberi	—	—	1	—	—	—
Rhacomitrium lanuginosum	1	3	5	2	2	1
Pleurozia purpurea	—	—	—	3	—	2
Alectoria nigricans	—	2	1	—	—	—
Cetraria aculeata	1	2	3	—	—	1
C. islandica	2	1	1	2	1	1
Cladonia bellidiflora	—	—	—	1	1	—
C. coccifera	—	—	—	—	1	—
C. gracilis	—	1	—	—	—	—

C. pyxidata	1	—	—	1	—	—
C. subcervicornis	—	—	—	—	—	1
C. sylvatica	—	5	5	5	4	3
C. uncialis	—	3	1	1	1	1
Cerania vermicularis	—	1	—	—	—	—
Ochrolechia tartarea	—	3	1	1	1	1
Parmelia omphalodes	—	1	—	—	—	—
Platysma glaucum	3	3	+	3	3	3
P. lacunosum	+	1	2	—	—	1
Psoroma hypnorum	1	—	—	—	—	—
Sphaerophorus globosus	1	3	3	2	1	2
Stereocaulon vesuvianum	—	—	—	+	—	—

Map reference

1. Ben Clibreck 29/553270
2. Ben Clibreck 29/550270
3. Ben Dearg 28/248780
4. Coulin 18/975540
5. Coulin 18/988545
6. Drum Grudie, Beinn Eighe 18/971642

This sociation is confined to exposed bluffs and ridges between the altitudes of 1700 and 2300 ft. (518 to 701 m.) where it may be extensive. The parent material is usually morainic and composed of smallish stones of Torridonian sandstone or quartzite mixed with Moine schists or Serpulite grits. It has not yet been found on moraine of pure quartzite, and this is probably too mineral-deficient a substratum to support it. The soil is a thin skin of peat over sandy humus-rich gravel and is shallow (20 to 30 cm. in depth). The habitat is well drained and usually blown clear of snow in winter. The community is replaced at higher altitudes in similar habitats by *Rhacomitrium* heaths and at lower altitudes by the dry facies of the *Calluna-Trichophorum-Molinia* complex of deforested ground. From its floristics it would appear to be northern and oceanic in affinity. Analogues in other parts of the Highlands are *Calluna-Arctostaphylos* and *Calluna-Loiseleuria* communities in the eastern and central Highlands, and the rare *Calluna*-lichen heaths (see below). On Beinn Eighe there is a transition to *Nardus* associated with increased snow cover.

Juniperus-Arctostaphylos *sociation* (*Table* 3)

Juniper scrub of the composition presented in Table 3 is very restricted in distribution, having so far been found only on the north and north-east slopes of Beinn Eighe, and in the Coulin forest, both in Wester Ross. It is confined to quartzite morainic material, generally coarser than that described for the previous sociation, between the altitudes of about 1200 and 1800 ft. (366 to 549 m.). Where well developed (lists 1 to 5) it survives as islands having total vegetative cover in a landscape of quartzite erosion pavement with rather scanty vegetation. Lists 6 to 8 are examples of semi-degraded juniper scrub; complete degradation leaves only a few scattered individuals of the constant species with a cover of 5 to 10 per cent. Closed scrub forms a carpet about 5 to 10 cm. deep of *Juniperus nana*, *Arctostaphylos*, *Calluna*, and sometimes *Arctous* and *Empetrum hermaphroditum*. Associated with these are various sporadic herbs and grasses. A constant and notable feature is the abundance in the ground layer of the liverworts *Herberta adunca* and *Pleurozia purpurea*, the former sometimes attaining a cover of 20 to 25 per cent. *Cladonia impexa* and forms of *C. uncialis* are also constant. In contrast slightly degraded forms have a broken dwarf shrub cover and a richer lichen flora; the alga *Gloeocapsa magna* (mountain dulse) is often abundant.

Table 3. Juniperus-Arctostaphylos *nodum*

	1	2	3	4	5	6	7	8	9
Cover (per cent)	100	100	100	100	100	90	75	80	75
Altitude (ft.)	1350	1350	1350	1650	1850	1250	1400	1800	1500
Slope (deg.)	2	2	2	2	2	0	0	7	5
Aspect	N	N	N	SE	W	—	—	—	NE
Area of plot (sq. m.)	4	4	4	2	4	4	2	2	4
Arctostaphylos uva-ursi	3	4	5	4	2	4	+	5	+
Arctous alpina	2	—	—	4	3	+	4	4	4
Calluna vulgaris	5	5	5	4	6	6	7	6	5
Erica cinerea	2	4	—	—	—	4	3	2	—
Empetrum hermaphroditum	—	—	—	4	1	—	—	—	—
Juniperus communis	7	7	8	7	7	3	2	3	3
Sorbus aucuparia	—	—	—	—	—	—	—	—	+
Vaccinium myrtillus	—	—	—	2	—	—	—	—	—
V. uliginosum	—	—	—	—	3	—	+	—	—
Lycopodium selago	2	2	—	—	1	1	2	2	2
Deschampsia flexuosa	3	3	3	3	2	—	3	—	—
Festuca vivipara	—	—	—	—	—	—	3	2	+
Molinia caerulea	—	2	1	—	—	4	+	—	+
Carex bigelowii	—	—	—	—	—	—	—	3	—
Juncus trifidus	—	—	—	—	—	—	—	+	—
Trichophorum caespitosum	3	3	1	—	2	3	+	2	3
Orchis ericetorum	2	—	—	2	2	—	—	—	—
Antennaria dioica	—	—	—	—	—	—	3	3	+
Euphrasia brevipila	—	1	3	—	—	—	2	1	—
Pedicularis sylvatica	—	—	—	—	—	1	—	—	—
Potentilla erecta	—	2	—	—	2	3	+	+	+
Solidago virgaurea	—	—	—	—	1	+	+	+	—
Succisa pratensis	—	—	2	—	—	—	2	—	—
Campylopus flexuosus	—	—	1	—	1	—	—	—	—
Hylocomium splendens	—	—	1	—	—	—	—	—	—
Hypnum cupressiforme	1	3	1	2	2	—	1	—	—
Pleurozium schreberi	—	—	—	1	—	—	—	—	—
Rhacomitrium lanuginosum	3	3	2	+	2	3	3	3	2
Sphagnum acutifolium agg.	—	—	2	—	2	—	—	—	—
Diplophyllum albicans	1	1	—	—	—	+	—	—	1
Herberta adunca	5	4	4	1	2	+	—	+	—
Pleurozia purpurea	4	4	3	1	2	2	1	2	1
Frullania tamarisci	—	—	—	—	1	—	—	—	—
Ptilidium ciliare	—	—	—	1	—	—	—	—	—
Scapania gracilis var. laxifolia	—	—	—	—	—	—	1	—	—
Cetraria aculeata	—	—	—	—	—	+	2	2	—
C. islandica	—	—	—	—	—	2	1	—	—
Cladonia bellidiflora	—	—	—	—	—	—	1	—	—
C. gracilis var. chordalis	—	—	—	1	1	—	1	—	—
C. impexa	4	5	4	4	3	2	—	—	4
C. leucophaea	—	—	—	—	—	+	—	—	—
C. pyxidata	—	—	—	—	1	—	—	—	—
C. squamosa	—	—	—	—	—	+	—	—	—
C. subcervicornis	—	—	—	—	—	—	—	—	+
C. sylvatica	—	—	—	—	—	2	2	3	—
C. tenuis	—	—	—	—	—	1	1	—	—
C. uncialis	3	3	3	3	3	1	2	2	4
Ochrolechia tartarea	—	—	—	—	—	—	1	—	—
Platysma glaucum	—	—	—	—	—	1	—	—	—
Sphaerophorus globosus	1	2	—	—	2	+	2	2	—
Gloeocapsa magna	—	—	—	—	—	3	+	—	—

Map reference

1. 18/992618
2. 18/992618
3. 18/992618
4. 18/973336
5. 18/984615
6. 18/995623
7. 18/992626
8. 18/990598
9. 18/988530

The soil consists of a few inches of juniper and bryophyte peat over quartzite rubble. The actual depth of the peat varies from place to place, and it is very liable to erosion when the scrub mat is broken. As there is no evidence that there is any difference in habitat between the areas covered by juniper scrub and those of erosion pavement, it seems probable that the extensive areas of quartzite moraine above the forest limit on Beinn Eighe and Coulin once bore closed or nearly closed scrub of this kind. Indeed the similarity in floristics of this type of ground throughout the whole area of quartzite in the north-west Highlands suggests that the *Juniperus-Arctostaphylos* scrub may once have been a widespread and common community. Its disappearance may be attributed partly to the upward extension of those fires which have reduced the former pine woods at lower altitudes to an erosion pavement sparsely vegetated with *Molinia* and *Trichophorum*.

Sub-fossil stems of dwarf juniper are often exposed in deep peat by erosion and they also are found in abundance lying loose on quartzite and Torridon sandstone erosion pavement throughout the Torridon-Loch Maree area. It therefore seems likely that the juniper scrub is a community of some antiquity, and that it has been restricted in area by a period of more active bog growth.

In floristics and habitat this scrub is very closely related to the *Calluna-Arctous* sociation described above, but it differs in the poorer and coarser substratum and in reduced exposure indicated by the absence of, for example, *Loiseleuria procumbens* and the replacement of lichens by hepatics.

B. Betula nana *bogs*

It has been mentioned above that the vegetation in southern Norway in which *Betula nana* plays a prominent role is essentially continental and that this species replaces *Calluna vulgaris* as distance from the coast increases. It is, therefore, of great interest to find that *Betula nana* is an important constituent of certain bogs in the north and central Highlands. At present (December 1955) examples have been found on Ben Clibreck and Ben Dearg which cover several hundred acres; but on Ben Wyvis and the Monadhliath above Dunachton almost all suitable ground is covered with *B. nana* bog. The farthest south that this community has been found is on the north side of Cam Creag above Camghouran, Loch Rannoch. Relict patches on deeply eroded peat occur south of Loch Droma in the Fannich forest. The floristic composition is presented in Table 4. The remaining constants are *Eriophorum* (either species), *Calluna vulgaris*, *Vaccinium myrtillus*, *Hylocomium splendens*, *Pleurozium schreberi* and *Sphagnum capillaceum*.

From a distance these bogs are indistinguishable from ordinary *Calluna-Eriophorum* communities; the *Betula* grows as an undershrub, the shoots rarely reaching the surface of the *Calluna* canopy when the two are closely associated, although it may be conspicuous where the *Calluna* is sparse. *Sphagnum* growth is usually rapid, and the branches of the dwarf birch spread widely with their bases buried in the accumulating moss remains.

The community appears on flat or gently sloping terrain between 1500 ft. (457 m.) and 2400 ft. (731 m.). In the north-west its range appears to be rather lower (1500 to 1800 ft.) (457 to 550 m.) than in the Monadhliath (2000 to 2300 ft.) (608 to 700 m.). At its upper limit it adjoins the communities of exposed ridges (*Loiseleuria-Arctous* sociation on Beinn Dearg and Ben Clibreck, exposed *Calluna* at Rannoch and in the Monadhliath); below it grades into eroded *Calluna-Eriophorum vaginatum* bogs.

Table 4. Betula nana *bogs*

	1	2	3	4	5	6	7
Cover (per cent)	100	100	100	100	80	70	70
Altitude (ft.)	1500	1700	1500	1800	1650	2300	2250
Slope (deg.)	0	3	2-3	2	5	1	2
Aspect	—	E	W	SW	NE	S	NE
Plot area (sq. m.)	4	4	4	4	4	4	4
Arctous alpina	4	2	4	4	—	—	—
Betula nana	4	3	4	3	3	4	4
B. pubescens	—	—	—	+	—	—	—
B. verrucosa	—	—	—	+	—	—	—
Calluna vulgaris	6	6	9	7	8	6	7
Chamaepericlymenum suecicum	+	—	—	—	—	—	—
Empetrum nigrum	3	3	3	3	4	—	—
E. hermaphroditum	—	—	—	—	—	3	3
Erica tetralix	2	—	1	1	1	—	—
Oxycoccus microcarpus	—	—	—	—	1	3	—
Rubus chamaemorus	1	—	1	3	3	3	3
Vaccinium myrtillus	—	2	3	2	3	2	1
V. uliginosum	—	—	—	—	—	—	3
V. vitis-idaea	—	—	—	—	2	2	—
Carex binervis	—	—	—	+	—	—	—
Eriophorum angustifolium	—	3	4	—	—	—	—
E. vaginatum	5	—	—	6	7	6	5
Juncus squarrosus	7	6	4	1	—	—	—
Trichophorum caespitosum	2	—	3	+	—	—	—
Listera cordata	—	+	—	—	—	—	—
Pinguicula vulgaris	—	—	1	—	+	—	—
Potentilla erecta	—	—	1	—	—	—	—
Aulacomnium palustre	—	1	—	—	—	—	—
Campylopus flexuosus	1	—	1	—	—	—	—
Dicranum scoparium	—	1	—	—	—	—	1
Eurhynchium praelongum	1	—	—	—	—	—	—
Hylocomium splendens	3	5	—	6	6	2	1
Hypnum cupressiforme	—	1	3	—	4	—	1
Plagiothecium undulatum	—	3	—	2	—	—	—
Pleurozium schreberi	1	—	2	4	4	2	2
Rhytidiadelphus loreus	—	2	—	4	3	—	3
R. squarrosus	3	—	—	—	—	—	—
Sphagnum palustre	—	+	—	—	—	—	—
S. fuscum	—	—	—	+	—	—	—
S. cf. **capillaceum**	3	4	7	4	8	9	5
Calypogeia trichomanis	—	—	—	1	—	—	—
Diplophyllum albicans	1	1	—	—	—	—	—
Lepidozia setacea	1	—	—	—	—	—	—
Leptoscyphus taylori	1	—	—	—	—	—	—
Lophozia ventricosa	—	—	—	1	—	—	—
Mylia anomala	—	1	—	—	—	1	1
Ptilidium ciliare	—	—	—	1	2	1	3
Cladonia gracilis	—	—	—	—	—	—	1
C. impexa	—	3	+	3	—	—	—
C. leucophaea	—	+	—	—	—	—	—
C. rangiferina	—	—	—	—	1	3	2
C. sylvatica	—	+	3	—	—	6	6
C. uncialis	—	2	—	—	—	—	1

Map reference

1. 29/559271
2. 28/250778
3. 28/258778
4. 28/448652
5. 27/550525
6. 28/788090
7. 28/790092

The surface of the bog is gently undulating, and shows no signs of localized growth, or 'regeneration complex', and the community, except in its eroded form, may be influenced to some extent by ground water.

Three distinct facies are apparent in the Table. In the stands from north of the Great Glen (1, 2, 3, and 4), *Arctous* is constant, whereas it is absent from those to the south, which tend to be outside the range of the species. Lists 6 and 7 are from a lichen-rich facies widespread in the Monadhliath.

The community occurs always on what appear to be 'flushed' areas of blanket bog, and is absent from the poorer rocks. For instance it does not appear on the quartzite and Torridon sandstone of Ross-shire and Sutherland, and avoids the granite of the Cairngorms and Monadhliath (Geall Charn Mor, Geall Charn Beag), although it is present a mile or two away on the Moine schists. The country rocks of the listed sites are quartzite schists, and, on Ben Wyvis, pelitic schists. There is much suitable ground adjacent to these bogs, similar but for the absence of the birch, and it is possible that the community was once much commoner and that its range has been reduced by burning and peat erosion.

Scandinavian affinities

The Scottish *Betula nana* bogs are so similar to the associations described by Nordhagen (1928 and 1943), and placed in the provisional Alliance Oxycocco-Empetrion hermaphroditi, that they may be assigned with some confidence to this alliance – but to an oceanic phase distinguished by the presence of such species as *Erica tetralix, Juncus squarrosus, Carex binervis* and by the prominence of *Calluna*. This alliance has been divided into three associations:

a. Oxycocco-Empetrum herm. – sphagnetosum
b. Oxycocco-Empetrum herm. – cladinosum
c. Oxycocco-Empetrum herm. – hylocomiosum

of which the first two have been described from Sylene and Sikilsdal, and the last from Sylene alone. In contrast to our bogs they occur as hummocks in fens or bogs which may be base-rich and belong to the Alliance Caricion atrofuscae-saxatilis. In the Rondane district of central Norway they form a smooth carpet in wet hollows of the lichen heath (Dahl, in press).

In Table 5 the constants in these various sociations are compared with the provisional constants in the two facies of the Scottish bogs.

Sub-fossil evidence

The species composition of the present-day *Betula nana* bogs is strongly reminiscent of that of several peat layers described as 'Arctic beds' by Lewis (1905-11) in his study of the plant remains in Scottish peat mosses. A full discussion might well provide the material for a separate paper, but it seems worth while to make one or two comments at this stage. The flora of the lowest Arctic bed is somewhat different, and cannot be discussed here.

Lewis's record of *Salix arbuscula* from the upper of the two main beds, and from the 'Arctic' intercalation in the 'Upper Forestian', in association with *Sphagnum* and *Arctous alpina*, is ecologically unlikely. *Salix repens* and *S. aurita* have been noted on the bogs described above, although they do not occur in the floristics tables, but Lewis does not record any of the more acid-tolerant *Salices* among his sub-fossil finds.

If it is accepted that these Upper Arctic beds on *Sphagnum-Trichophorum-Eriophorum* peat represent communities that were substantially the same as the existing bogs then it seems unnecessary to postulate, as Lewis does, a climatic deterioration of sufficient magnitude to bring about corrie glaciation in the Highlands in order to explain their occurrence.

The lowest appearance of Lewis's second Arctic bed is at 150 ft. (46 m.) O.D. in Shetland, at 500 ft. (150 m.) near Cape Wrath, at 750 ft. (228 m.) in the southern Uplands and at 1500 ft. (457 m.) in east Sutherland and the central Highlands. His

Table 5. *Comparison between Scottish and Scandinavian* Betula nana *bogs*

	Lichen-Rich			*Sphagnum-Rich*			*Pleurozium-Rich*	
	1	2	3	4	5	6	7	8
Andromeda polifolia	100	100	0	100	100	0	93	0
Calluna vulgaris	100	0	100	4	0	100	43	0
Betula nana	100	100	100	100	100	100	100	×
Empetrum hermaphroditum	94	100	100	100	100	100	100	×
Vaccinium myrtillus	63	70	100	52	8	100	100	0
V. uliginosum	24	80	50	100	100	0	100	×
Oxycoccus microcarpus	47	100	50	100	92	20	97	0
Rubus chamaemorus	100	100	100	100	96	80	100	×
Carex pauciflorus	0	0	0	100	0	0	0	0
Eriophorum vaginatum	41	100	100	100	100	60	100	×
Dicranum bergeri	0	100	0	20	20	0	?100	0
Hylocomium splendens	0	0	100	0	0	80	0	×
Pleurozium schreberi	94	100	100	88	68	80	100	0
Pohlia nutans	0	100	0	16	88	0	100	0
Polytrichum strictum	53	100	0	84	96	0	97	0
Sphagnum angustifolium	0	0	0	92	0	0	73	0
S. capillaceum	77	0	100	0	0	100	0	0
S. fuscum	18	100	0	100	100	20	87	0
S. russowii	0	0	0	100	0	0	97	0
Mylia anomala	94	100	100	100	100	100	97	0
Cetraria islandica	0	100	0	8	12	0	27	0
Cladonia alpestris*	65	100	0	0	40	0	3	0
C. coccifera	59	100	0	0	12	0	23	0
C. deformis	94	100	0	0	0	0	47	0
C. impexa	0	0	0	0	0	60	0	0
C. rangiferina	100	100	100	20	52	20	70	0
C. sylvatica	100	100	100	28	64	40	97	0

(Microhepatics are omitted: constancy – per cent.)

* The plant named as *Cladonia impexa* in these Scottish bogs is in many features intermediate between lowland *C. impexa* and *C. alpestris*.

Key:
- 1, 4, 7, Sylene.
- 2, 5, Sikilsdal.
- 3, 6, Scotland.
- 8, Rondane (× = presence only).

later intercalation in the upper forest layer occurs at 300 ft. (91 m.) O.D. in Sutherland, and at 2000 ft. (608 m.) in the central Highlands.

At the present day the *Betula-Arctous* bogs of Sutherland extend down to 1500 ft. (457 m.) and the central Highland facies of the community to just under 2000 ft. (608 m.); there are indications that in the absence of moor burning they would be found lower still. At any rate they extend to just above or a little below the present potential forest limit.

It should also be noted that the *Salix myrsinites* scrub at Inchnadamph can be found at 700 ft. (640 m.) above sea level.

Lewis appears to have underestimated the profound influence that man has had upon Scottish vegetation, and also the importance of local edaphic factors, when making the following statements: 'In short the distribution of pine and birch forest and sub-arctic moorland is well defined, and the two associations are not now found intermixed under precisely the same climatic conditions' and 'No change in drainage or peat characteristics would cause a forest of *P. silvestris* to replace a close growth of *B. nana*, etc.'. He also fails to appreciate the rapid drop in the lower limit of Arctic-Alpine species towards the north of Scotland.

All this leads to the conclusion that the Upper Arctic beds could have been laid down under climatic conditions little different from those of today; perhaps somewhat cooler and wetter to the extent of depressing the tree-line by several hundred feet, but certainly not 'Sub-Arctic'. The *Betula nana-Salix* horizons could thus be of later date than he implies.

It would be instructive to carry out an examination of the peats below the present *Betula nana* communities.

Ecology of Betula nana

The behaviour of *Betula nana* differs considerably in Scotland and Norway. In the continental districts of Norway it is often a dominant even on well-drained soils, spreading into exposed communities of morainic ridges where it mingles with such species as *Cetraria nivalis* and *Alectoria ochroleuca*. Knaben's remarks on the ecology of *Betula nana* in Sogn may be significant. She attributes its scarcity in this oceanic region to its high heat requirement and sensitivity to exposure since she finds it only in sheltered localities with relatively strong insolation.

Its behaviour in Iceland is more like that of the Scottish than of the Norwegian type, and the ecological or genetical reasons for this restriction of habitat would be worth investigating.

C. *Lichen heaths*

Of somewhat similar interest are the lichen heaths of the Scottish mountains. They resemble the Norwegian heaths in composition, and are found in much the same habitat, so that they can be considered as extensions of the Scandinavian series.

In Table 6 are presented lists from the *Calluna*-lichen heath (1 to 5), *Vaccinium myrtillus*-lichen heath (6 to 10) and an exposed facies of the former which is rich in 'yellow lichens' (11 and 12). *Empetrum*-lichen heaths also occur in a habitat similar to that of the *Vaccinium* sociation.

In all of these the lichens are so abundant that they can be described as the physiognomic dominants, and the communities can readily be distinguished from some distance by the characteristic grey-green and yellow colour. The dwarf shrubs are in the same layer as the lichens, and hold the mat together so that it can be rolled off the ground like a carpet. In wet weather the mat is slippery under foot, and in dry weather the crisp and brittle lichens are easily destroyed by trampling.

The lichen heaths are restricted in their distribution, being known only from between 2400 ft. and 2600 ft. (731 to 791 m.) on the western spurs of Geall Charn, Carn Ban Mor and Carn Ban Beag above Glenfeshie and from the area of Carn Dearg Mor and Geall Charn Mor in the Monadhliath, all localities being on the granite although apparently suitable habitats exist close at hand on the schists.

From information supplied by Mr. A. Macdonald it seems likely that a similar heath may occur on Moine schist in the Glen Strathfarrar district.

The sociations are zoned according to exposure. That rich in yellow lichens (*Alectoria ochroleuca* and *Cetraria nivalis*) occurs only in the most exposed sites, where the dwarf shrub is low (1 to 2 cm.), and intermittent. *Alectoria ochroleuca* is confined to these sites although it does not attain such luxuriance as in Scandinavia where its

Table 6. *Lichen heaths*

	1	2	3	4	5	6	7	8	9	10	11	12
Cover (per cent)	100					100					100	100
Altitude (ft.)	2500					2500					2600	2600
Slope (deg.)	20					10					1	0
Aspect	N					N					N	—
Area of plot (sq. m.)	1					1					4	4
Calluna vulgaris	7	7	7	7	7	—	—	—	—	—	7	6
Empetrum hermaphroditum	4	2	4	4	3	—	—	—	3	4	2	3
Loiseleuria procumbens	—	—	—	2	—	—	1	—	—	—	2	3
Vaccinium myrtillus	2	1	3	3	3	4	4	4	3	3	3	—
V. vitis-idaea	—	—	—	—	—	—	—	—	—	—	2	3
Lycopodium alpinum	—	1	1	—	—	—	—	—	—	—	—	—
L. selago	1	—	—	—	—	—	—	—	—	—	1	+
Carex bigelowii	1	—	—	—	2	2	3	1	3	3	3	+
Deschampsia flexuosa	3	2	3	3	3	3	3	3	3	3	1	1
Juncus trifidus	—	1	—	—	—	—	—	—	—	—	3	3
Alicularia scalaris	—	—	—	—	—	—	1	—	—	—	—	—
Diplophyllum albicans	—	1	—	—	—	—	—	—	—	—	—	+
Lophozia alpestris	—	—	—	—	—	—	—	—	—	—	—	+
Microhepatics	—	1	—	—	—	—	—	—	—	—	—	2
Dicranum scoparium	—	—	—	—	—	—	1	1	1	2	—	—
Hypnum cupressiforme	2	—	—	—	1	—	—	—	—	—	—	—
Pleurozium schreberi	—	—	—	—	—	2	2	2	2	3	—	—
Polytrichum piliferum	—	—	—	—	—	—	—	—	—	—	1	—
Rhacomitrium lanuginosum	1	1	3	2	2	2	—	1	—	—	+	—
Rhytidiadelphus loreus	—	—	—	—	—	—	1	1	—	—	—	—
Alectoria nigricans	—	1	1	—	—	—	—	—	—	—	3	3
A. ochroleuca	—	—	—	—	—	—	—	—	—	—	3	—
Cerania vermicularis	—	—	—	—	—	—	—	—	—	—	1	1
Cetraria aculeata	2	2	2	1	1	—	—	—	—	—	4	3
C. islandica	3	2	3	3	3	3	2	2	2	3	2	1
C. nivalis	3	2	1	1	3	2	—	3	—	—	—	2
Cladonia bellidiflora	1	—	1	—	—	—	—	—	—	—	2	2
C. floerkeana	—	1	—	—	—	—	—	—	—	—	—	—
C. gracilis	—	—	—	3	2	3	2	—	1	—	3	2
C. pyxidata	—	—	—	—	—	—	—	—	—	—	1	—
C. rangiferina	4	2	3	4	4	3	4	3	3	3	—	—
C. sylvatica	7	6	7	7	7	9	9	9	9	9	5	4
C. uncialis	3	3	3	3	3	3	3	—	1	—	4	3
Ochrolechia frigida } O. tartarea }	—	—	—	—	—	—	—	—	—	—	4	4
Sphaerophorus globosus	—	1	—	—	—	—	—	—	—	—	3	4

Map reference
1-10. 28/888023 11, 12. 27/880976

tangled branches appear to suppress the dwarf shrubs. It may be used as a differential species between this nodum and those which follow. (The other species of chionophobous lichens, *Alectoria divergens* and *Cetraria cucullata*, are not yet known to us in the Scottish mountains, nor is true *Cladonia alpestris*, which is the chief heath former of Scandinavia.)

The lichens of these communities can be arranged in order of increasing tolerance to snow cover – *Cetraria nivalis* – *Cladonia sylvatica* – *Cetraria islandica*. The Norwegian order is – *Cetraria nivalis* – *Cladonia alpestris* – *C. sylvatica* – *Cetraria islandica* (Nordhagen, 1943, p. 211).

Because these lichen communities occur under the same conditions of exposure and on the same rock as similar communities poorer in lichens elsewhere in the Cairngorms their range is unlikely to be determined by exposure and rock type; and, as they represent the extension of a continental vegetation type into an oceanic region, their distribution is probably controlled by microclimate. The explanation is far from established, but it may lie along the following lines. At the junction of the Low Alpine and Middle Alpine zones in Norway lichen heath covers extensive exposed habitats at and above the altitude of our lichen heaths, i.e. much of their potential range in the Cairngorms is occupied by *Rhacomitrium* heath and *Juncus trifidus* communities. It seems possible that the greater force of the winter winds, and absence of snow cover, prevent the colonization by lichens of the ground occupied by *J. trifidus* heath (scattered patches of lichen are present at this altitude); and that, where slight shelter is present, they are excluded by the competitive power of *Rhacomitrium*. Casual observations suggest that the lower limit of the *Rhacomitrium* heath coincides with the average cloud base.

The lichen-rich *Vaccinium-Festuca* sociation in Breadalbane (Poore, 1955c), occupies similar habitats at the same altitude, and is probably a parallel development on more basic rock.

D. *Moss heaths*

Rhacomitrium heaths are characteristic of moderately exposed plateaux and ridges throughout the Scottish mountains, descending to just under 3000 ft. (914 m.) in the east and to somewhat lower elevations in the west.

Rhacomitrium-Carex bigelowii *nodum*

The *Rhacomitrium-Carex bigelowii* nodum has been defined by Poore (1955b), but other noda and their variants do occur, particularly in north-west Scotland, where the moss heaths occupy vast areas of high ground as in the Fannich forest of Ross-shire.

The moss heaths may be floristically impoverished or surprisingly species-rich, according to the base status of the soil and the exposure of the site, so that the constants of the entire complex are few: *Vaccinium myrtillus*, *Carex bigelowii*, *Rhacomitrium lanuginosum* and *Cetraria islandica*.

With increasing exposure they grade into the various open communities of erosion pavements and solifluction soils, and with increasing snow cover they give way to *Nardus* and *Deschampsia caespitosa*-dominated snow beds or to dwarf shrub heaths at lower elevations. Abrupt transitions from Callunetum to *Rhacomitrium* heath occur at 2500 ft. (760 m.) on Ben Wyvis and from *Calluna*-lichen heath to *Rhacomitrium* at 2900 ft. (882 m.) on Carn Ban Mor (Cairngorms.) These are not exposure effects but may rather be related to increasing precipitation/evaporation ratio associated with increasing mist cover at higher altitudes.

Where the summit soils are deep and sandy, as on the Torridonian formation of the north-west, there often appears to be a cyclical alternation between *Rhacomitrium* heath and erosion pavement according to the vagaries of the wind in producing local erosion or deposition. All the Scottish evidence, on the other hand, is opposed to the sequence suggested by Pearsall (1950, p. 90). An appearance of successional relationships may be given by the effect of winter snow cover in favouring peat development and the growth of certain species such as *Nardus stricta, Deschampsia caespitosa* and *Trichophorum caespitosum,* but in an oceanic climate *Rhacomitrium* has immense competitive power and its communities great stability over the favoured range of exposure. It does not play a prominent part in the open communities of erosion pavement owing to the extreme exposure and frost movement in the soil, although it may colonize rock detritus on level ground or scree where the fragments are large enough to have stability. Subsequent development of the vegetation on this substratum will depend on the exposure of the site and not on autogenous succession alone.

Rhacomitrium heaths have been described from Iceland (Hansen, 1930; Steindørsson, 1951; McVean, 1955) and the Faeroes (Ostenfëld, 1908). They are also known for western Norway, and are thus markedly oceanic in distribution. In continental Norway they are hygrophilous communities occupying flush areas of the lichen heath (Dahl, in press).

In Table 7 the twelve examples of the *Rhacomitrium-Carex bigelowii* nodum described by Poore (1955b), have been combined with seven examples of the same nodum from northern Scotland and the constancy of the species indicated in col. 1. Column 2 distinguishes those species which occur only in Breadalbane lists (B) or the northern lists (N). The remaining columns are devoted to analyses of other moss heaths from northern Scotland.

Empetrum hermaphroditum *facies of the* Rhacomitrium-Carex *nodum* (*Table* 7; 3 *and* 4)

Only two examples of this variant have so far been analysed and its relationships with *Empetrum*-hypnoid moss heath have yet to be examined.

Nardus stricta *facies* (*Table* 7; 5, 6 *and* 7)

Nardus stricta heath is so far known only from the north-west where it can be distinguished from *Nardus*-dominated snow beds by topographical features and floristically, by the almost complete absence of hepatics. Isolated colonies of *Nardus* in moss heath tend to encourage a little snow accumulation in their vicinity and, through the extra shelter and moisture, influence the environment in their favour; but lasting snow beds are never built up in this way (see also Poore, 1955c, pp. 623-4).

Polygonum viviparum-Salix herbacea *facies* (*Table* 7; 10 *and* 11) *and hypnoid moss facies* (*Table* 7; 12 *and* 13)

These interesting variants are again of limited distribution in Scotland, and so far known only from the north-west where dolomitic mudstones and shales of the Cambrian formation outcrop at about 3000 ft. (914 m.).

Floristic affinities are with the Icelandic *Rhacomitrium* heaths (McVean, 1955) and with those of the Faeroes (Ostenfëld, 1908) rather than with the *Rhacomitrium-Carex bigelowii* nodum.

The soil is a rich, brown, stony mud, circum-neutral in reaction, and the community is a somewhat open one because of the moderately severe exposure.

In the angles of the terraces, where a little snow accumulates, *Rhacomitrium* is replaced by the hypnoid mosses *Hylocomium, Pleurozium* and *Rhytidiadelphus.* The exposed terrace flats are never protected by more than a coating of rime or verglas.

Cochlearia micacea, Solidago virgaurea, Coeloglossum viride, Selaginella selaginoides, Sagina saginoides, Juncus trifidus, Luzula spicata and *Aulacomnium turgidum* are characteristic of the *Rhacomitrium* phase, while *Oxalis acetosella, Saxifraga hypnoides, Rumex acetosa, Cerastium vulgatum, Achillea millefolium, Plagiothecium undulatum* and *Rhytidiadelphus triquetrus* are confined to the hypnoid moss mat. This species-rich hypnoid moss community may also be regarded as a facies of the *Rhytidiadelphus-Deschampsia caespitosa* nodum described below.

Juncus trifidus-Salix herbacea *facies* (*Table* 7; 8 *and* 9)

The few examples of this variant that have been analysed are closer in their affinities to the *Rhacomitrium-Polygonum-Salix herbacea* facies than to the *Rhacomitrium-Carex bigelowii* nodum itself. The *Juncus trifidus* variant in Poore (1955) should be compared with this. Soils are developed from a mixed parent material of mudstones and quartzites so that they are probably of intermediate base status.

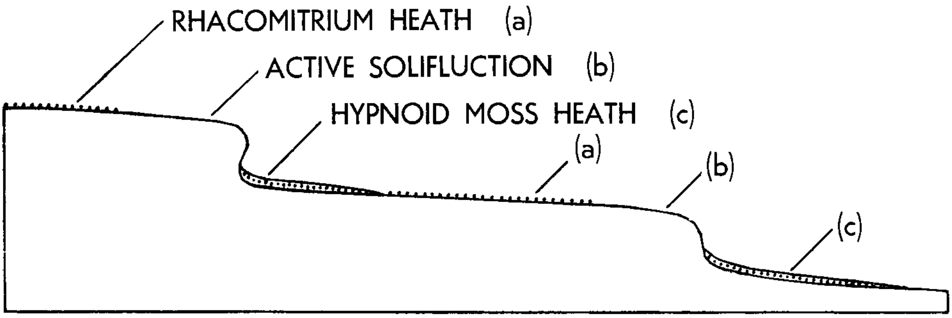

Fig. 7. Relationship of the moss heaths to exposure on the solifluction terraces of Ruadh Stac Beag, Beinn Eighe.

Rhytidiadelphus-Deschampsia caespitosa *nodum* (*Table* 7; 14)

Small areas dominated by *Hylocomium, Pleurozium* and *Rhytidiadelphus* are found throughout the *Rhacomitrium* heaths of the northern Highlands. The relation of the two types is well seen on Fionn Bheinn, a western outlier on the Fannich hills, where hypnoid mosses occupy all depressions in the *Rhacomitrium* mat not sufficiently deep to encourage *Nardus* dominance. The status of the nodum is not yet certain but it has been named provisionally as above.

Soil profiles reveal a deeper and damper layer of surface humus under the hypnoid mat than under the *Rhacomitrium* but the extent of podzolization is variable in both types.

On Ben Clibreck an *Empetrum*-hypnoid moss community corresponds to the *Empetrum-Rhacomitrium* of Beinn Eighe. It forms patches in the *Rhacomitrium* heath and the change in moss dominance is abrupt and corresponds to the edge of the *Empetrum* mat and not to any variation in topography.

Hypnoid mosses sometimes dominate the *Rhacomitrium* in Icelandic moss heaths (McVean, 1955, p. 334).

E. Nardus *snow beds*

Depressions dominated by *Nardus stricta* are one of the commonest signs of late snow-lie throughout the Scottish mountains between the altitudes of 2000 ft. and 3000 ft. (608 to 914 m.) although the lower limit in the central Highlands is 500 or 600 ft. (150 and 180 m.) higher than in north-west Scotland.

Poore (1955b) has already defined the high altitude *Nardus stricta* sociation as a *Nardus*-dominated community which also contains *Galium hercynicum, Carex bigelowii, Pleurozium schreberi* and *Rhytidiadelphus squarrosus*. Table 8 shows the composition of this sociation in the Beinn Eighe district of Ross-shire; and the combined constancy of each species when these lists are added to Poore's Breadalbane and Cairngorm analyses. Only *R. squarrosus* has had to be dropped from the list of constants and *R. loreus* has almost replaced it there. Species limited to central or northern Highlands are indicated as in the previous table.

It will be noticed immediately that the northern lists resemble the Cairngorm *Nardus* grassland of the '*Empetrum-Vaccinium*' zone (Burgess, 1951) in the presence of *Vaccinium uliginosum* and *Empetrum hermaphroditum*. They are also richer in species, particularly hepatics, than any of the Scottish lists previously published, and thus approach more closely the *Nardus* sociation of Scandinavia.

A notable feature of the Beinn Eighe lists is the abundance of *Rhacomitrium* and scarcity of the hypnoid mosses, although *R. loreus* and *Hypnum cupressiforme* are constants. This is rather surprising in view of the fact that a small amount of snow accumulation on the *Rhacomitrium* heath is sufficient to reverse moss dominance. No. 6, however, which is the only example from the summit ridge of Beinn Eighe, has *Rhytidiadelphus* more abundant than *Rhacomitrium*.

In the north the soils are again podzolic with a tendency to peat accumulation, and the *Trichophorum* variant (*Trichophorum-V. uliginosum* variant of Beinn Eighe) in wetter situations is even more distinct than in Breadalbane; deep peat snow beds on Beinn Eighe may be dominated by *T. caespitosum*.

The northern examples of the *Nardus* sociation are associated with a maximum period of snow cover of about five months, two months less than that of the most permanent beds.

The *Nardus* snow beds of Iceland, which occur at low altitudes on the coast, differ in the abundance of forbs and grasses and the reduced role of the mosses, particularly *Rhacomitrium* and *Pleurozium* (McVean, 1955).

F. Vaccinium *snow beds*

The effects of winter and spring snow-lie on vegetation stretch down into the Sub-Alpine zone and even below the potential altitudinal limit of pine forest. In the central and eastern Highlands these habitats are occupied by *Vaccinium* and *Nardus* communities. The most characteristic of the *Vaccinium* snow beds has been provisionally named the *Vaccinium-Chamaepericlymenum* nodum and a few lists are presented as a basis for discussion, although further study is necessary before it can be defined accurately. Lists 1 and 2 (Table 9) are taken at altitudes of 2500 ft. (750 m.) and 2400 ft. (720 m.) on Meall Dubhag and Craig an Dail Beag respectively; lists 3 to 7 come from a large stand at 1800 ft. (540 m.) near the head of Loch Einich in the Cairngorms. This is within the limit of historical pine forest and represents the lowest extension of the nodum, where the snow does not lie sufficiently long to inhibit

Table 7. *Moss heaths*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cover (per cent)			100	100	100	100	99	100	100	90	90	100	100	100
Altitude (ft.)			2800	2800	2200	2300	2200	3100	2600	3000	2900	3100	2900	2800
Slope (deg.)			2	10	0	2	0	0	5	2	3	1	3	3
Aspect			NW	E	—	S	—	—	NW	E	NW	E	W	N
Plot area (sq. m.)			4	4	1	4	4	4	4	4	4	2	2	4
Empetrum hermaphroditum	25	—	6	7	5	3	4	—	—	—	—	—	—	—
E. nigrum	10	—	—	—	—	—	—	—	—	—	—	—	—	—
Salix herbacea	20	—	—	—	—	+	—	2	1	3	6	—	—	—
Vaccinium myrtillus	75	—	2	3	3	3	3	1	4	—	2	—	—	—
V. vitis-idaea	35	—	—	—	—	—	—	—	—	—	—	—	—	—
V. uliginosum	—	—	2	5	—	—	3	+	—	—	—	—	—	—
Lycopodium alpinum	—	—	—	—	3	1	1	—	—	—	—	—	—	—
L. selago	15	—	—	—	1	—	—	—	—	—	—	—	—	—
Agrostis canina	25	—	—	3	—	—	—	—	—	—	—	—	—	—
A. tenuis	35	—	—	—	—	—	—	—	2	—	—	—	4	3
Deschampsia caespitosa	5	N	—	—	—	—	—	—	2	2	—	6	6	2
D. flexuosa	40	—	2	1	—	—	2	3	1	—	—	—	—	—
Festuca ovina agg.	70	—	1	—	—	—	—	—	4	—	—	—	—	—
F. rubra	15	N	—	—	—	—	—	—	—	—	—	—	—	2
F. vivipara	55	—	—	—	1	—	—	3	—	3	3	3	2	—
Nardus stricta	15	—	—	3	6	5	6	+	—	—	—	—	—	—
Carex bigelowii	100	—	3	2	2	2	+	5	3	4	4	2	+	3
C. panicea	—	—	—	—	4	—	—	—	—	—	—	—	—	—
C. pilulifera	5	N	—	—	—	—	—	—	—	—	—	—	—	—
Juncus squarrosus	—	—	—	—	—	1	—	+	—	—	—	—	—	—
J. trifidus	5	—	—	1	—	—	—	6	6	3	+	—	—	—
Luzula multiflora	5	B	—	—	—	—	—	—	—	—	—	—	—	—
L. spicata	10	B	—	—	—	—	—	2	1	2	2	—	—	—
Trichophorum caespitosum	—	—	—	+	—	—	2	—	—	—	—	—	—	—
Coeloglossum viride	—	—	—	—	—	—	—	—	—	—	+	—	—	—
Narthecium ossifragum	—	—	—	—	2	—	3	—	—	—	—	—	—	—
Achillea millefolium	—	—	—	—	—	—	—	—	—	—	—	—	2	—
Alchemilla alpina	20	—	—	—	—	—	—	—	—	+	—	3	—	—
Armeria maritima	5	N	—	—	—	—	—	+	+	2	2	2	1	—
Cerastium vulgatum	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Chamaepericlymenum suecicum	—	—	—	+	—	—	—	—	—	—	—	—	—	—
Cochlearia micacea	—	—	—	—	—	—	—	—	—	+	1	—	—	—
Euphrasia frigida	—	—	—	—	—	—	—	—	—	2	2	—	—	—
Galium hercynicum	60	—	—	—	—	—	—	2	1	3	—	4	3	3
Oxalis acetosella	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Polygonum viviparum	—	—	—	—	—	—	—	—	+	3	3	—	—	—
Potentilla erecta	20	N	—	1	—	—	—	—	—	—	—	—	—	—
Ranunculus acris	—	—	—	—	—	—	—	—	—	—	+	—	2	—
Rumex acetosa	—	—	—	—	—	—	—	—	—	—	—	1	3	+
Saussurea alpina	—	—	—	—	—	—	—	—	—	—	4	—	+	—
Saxifraga hypnoides	—	—	—	—	—	—	—	—	—	—	—	—	+	—
Sedum roseum	—	—	—	—	—	—	—	—	—	—	+	—	—	—
Sibbaldia procumbens	—	—	—	—	—	—	—	—	—	—	—	2	+	—
Silene acaulis	—	—	—	—	—	—	—	—	2	2	2	—	2	—
Solidago virgaurea	5	N	—	+	—	—	—	—	—	—	1	—	—	—
Succisa pratensis	5	N	—	—	—	—	—	—	—	—	—	—	—	—
Thalictrum alpinum	—	—	—	—	—	—	—	—	—	—	+	—	—	—
Thymus drucei	5	N	—	—	—	—	—	—	—	1	+	+	4	—
Aulacomnium turgidum	—	—	—	—	—	—	—	—	—	1	1	—	—	—
Dicranum fuscescens	60	—	1	—	—	—	—	2	—	—	1	3	—	—
D. scoparium	25	—	—	—	+	—	—	—	—	—	—	1	—	—
Oligotrichum hercynicum	10	B	—	—	—	—	—	—	—	—	—	—	—	—
Plagiothecium undulatum	—	—	—	—	—	—	—	—	—	—	—	—	2	—
Pleurozium schreberi	20	—	2	—	—	—	—	—	2	1	1	2	—	—

H J.E.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Pohlia ?annotina	5	B	—	—	—	—	—	—	—	—	—	—	—	—
Polytrichum alpinum	65	—	—	—	—	—	—	1	1	1	3	2	—	2
P. commune	—	—	—	—	1	—	—	—	—	—	—	—	2	—
P. gracile	5	N	—	—	—	—	—	—	—	—	—	—	—	—
P. urnigerum	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Rhacomitrium lanuginosum	100	—	8	7	6	8	7	8	8	8	8	2	—	—
Rhytidiadelphus loreus	10	—	1	—	—	—	—	—	—	1	1	3	7	9
R. triquetrus	—	—	—	—	—	—	—	—	—	—	—	—	3	—
Anastrepta orcadensis	—	—	1	—	—	—	—	—	—	—	—	—	—	—
?Aplozia sphaerocarpa	5	B	—	—	—	—	—	—	—	—	—	—	—	—
Diplophyllum albicans	15	B	—	—	—	—	—	1	—	—	—	—	—	—
Nardia scalaris	5	B	1	—	—	—	—	—	—	—	—	—	—	—
Lophozia alpestris	—	—	—	—	—	—	—	—	—	—	2	—	—	—
L. hatcheri	—	—	—	—	—	—	—	—	—	—	1	—	—	—
L. ?ventricosa	5	B	—	—	—	—	—	—	—	—	—	—	—	—
Ptilidium ciliare	5	B	1	—	—	—	—	—	—	—	2	—	—	1
Alectoria nigricans	20	—	+	—	—	—	—	—	—	—	—	—	—	—
Cerania vermicularis	40	—	—	—	—	—	—	—	—	+	—	—	—	—
Cetraria aculeata	50	—	1	—	—	—	—	—	—	+	—	—	—	—
C. islandica	90	—	3	2	+	2	3	—	—	+	1	—	—	—
Cladonia alpicola	10	B	—	—	—	—	—	—	—	—	—	—	—	—
C. bellidiflora	35	—	—	—	—	—	1	—	—	1	1	—	—	—
C. coccifera	10	B	—	—	—	—	—	+	—	—	—	—	—	—
C. crispata	5	B	—	—	—	—	—	—	—	—	—	—	—	—
C. furcata	5	B	—	—	—	—	—	—	—	—	—	—	—	—
C. gracilis	30	B	1	—	—	—	—	—	—	—	—	—	—	—
C. leucophaea	—	—	2	—	—	—	—	—	—	—	—	—	—	—
C. pyxidata	10	B	—	—	—	—	—	—	1	—	—	—	—	—
C. rangiferina	10	B	—	—	—	—	—	—	—	—	—	—	—	—
C. subcervicornis	—	—	—	—	—	—	1	—	—	—	—	—	—	—
C. sylvatica agg.	40	—	—	3	+	—	—	—	—	—	+	—	—	—
C. squamosa	25	B	—	—	—	—	—	—	—	—	—	—	—	—
C. tenuis	—	—	3	—	—	—	—	—	—	—	—	—	—	—
C. uncialis	70	—	1	3	2	+	3	1	—	2	2	—	—	—
Coriscium viride	10	B	—	—	—	—	—	—	—	—	—	—	—	—
Icmadophila ericetorum	5	B	—	—	—	—	—	—	—	—	—	—	—	—
Ochrolechia tartarea	35	—	—	—	—	—	—	1	1	—	—	—	—	—
Peltidea aphthosa var. leucophlebia	—	—	—	—	—	—	—	—	—	+	1	—	—	—
Peltigera canina	—	—	—	—	—	—	—	—	—	—	1	2	1	1
Sphaerophorus globosus	25	—	1	—	—	—	—	—	2	2	2	—	—	—
Stereocaulon evolutoides	5	N	2	—	—	—	—	—	—	+	—	—	—	—
S. vesuvianum	—	—	—	—	—	—	—	1	—	—	—	—	—	—

Map reference

3. 18/975634	9. 18/972618
4. 18/985604	10. 18/955598
5. 18/902609	11. 18/973617
6. 18/895580	12. 18/953605
7. 18/973603	13. 18/973618
8. 18/952599	14. 28/148622

the growth of *Calluna*. The first pair should probably be regarded as the type and the second as a variant. Nevertheless, there are a number of constants for the entire group: *Chamaepericlymenum suecicum*, which shows high fidelity to this habitat, *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *Blechnum spicant*, *Galium hercynicum* and several bryophytes. Lichens are comparatively scarce.

These *Vaccinium* communities characteristically occur as a band below the crest on the lee side of ridges in the Low Alpine zone, or in small depressions in *Calluna* moors, habitats which correspond in topography to the longer-lasting snow beds at higher altitudes. The centre of the *Vaccinium* patches may be occupied by *Nardus* if the snow is persistent (Figs. 1*b*, 3*d*).

Table 8. Nardus stricta *snow beds*

	1	2	3	4	5	6	7	8
Cover (per cent)			100	100	100	100	100	100
Altitude (ft.)			2300	2200	2200	3200	2700	2750
Slope (deg.)			0	1	2	5	1	2
Aspect			—	N	N	SW	SE	NW
Plot area (sq. m.)			4	4	4	4	4	4
Calluna vulgaris	7	N	+	—	—	—	—	—
Empetrum hermaphroditum	35	N	1	4	4	—	2	3
Juniperus nana	7	N	—	—	+	—	—	—
Vaccinium myrtillus	70	—	3	3	2	1	2	1
V. uliginosum	28	N	+	—	3	—	4	4
Lycopodium alpinum	25	—	1	—	—	—	3	+
L. selago	7	N	—	—	—	2	—	—
Agrostis stolonifera	7	B	—	—	—	—	—	—
A. tenuis	56	—	—	3	3	3	2	—
Deschampsia caespitosa	7	N	—	—	—	+	—	—
D. flexuosa	49	—	—	—	—	—	3	+
Festuca ovina agg.	7	B	—	—	—	—	—	—
F. vivipara	35	B	—	—	—	—	—	—
Nardus stricta	100	—	8	9	8	9	8	9
Carex bigelowii	100	—	2	3	3	4	2	1
C. flacca	7	N	—	—	—	—	1	—
C. pilulifera	7	B	—	—	—	—	—	—
Juncus squarrosus	28	N	+	—	+	—	1	2
Luzula sylvatica	14	N	—	—	+	+	—	—
Trichophorum caespitosum	35	—	2	—	4	—	5	2
Narthecium ossifragum	7	N	—	—	—	—	2	—
Alchemilla alpina	7	B	—	—	—	—	—	—
Chamaepericlymenum suecicum	7	N	—	—	—	+	—	—
Euphrasia frigida	7	N	—	—	—	—	1	—
Galium hercynicum	80	—	4	1	2	4	—	—
Melampyrum pratense	7	N	—	—	1	—	—	—
Potentilla erecta	49	—	1	3	2	3	3	3
Rumex acetosa	35	—	—	—	—	+	—	—
Solidago virgaurea	14	N	—	2	1	—	—	—
Dicranodontium unciatum	7	N	1	—	—	—	—	—
Dicranum fuscescens	7	B	—	—	—	—	—	—
D. scoparium	56	—	—	2	—	—	1	—
Hylocomium splendens	7	N	—	—	—	5	—	—
Hypnum cupressiforme	35	N	1	1	1	—	+	1
Plagiothecium undulatum	7	B	—	—	—	—	—	—
Pleurozium schreberi	80	—	3	—	—	2	+	1
Polytrichum alpinum	35	B	—	—	—	—	—	—
P. commune	35	—	—	+	1	—	—	—
P. formosum	7	B	—	—	—	—	—	—
P. gracile	14	N	1	—	—	3	—	—
P. juniperinum	7	N	—	—	—	—	1	—
Rhacomitrium lanuginosum	63	—	5	5	4	3	5	4
Rhytidiadelphus loreus	75	—	2	1	1	4	1	1
R. squarrosus	49	B	—	—	—	—	—	—
Sphagnum quinquefarium	14	N	2	2	—	—	—	—
S. tenellum	7	N	—	—	—	—	1	—
Anastrepta orcadensis	28	—	—	1	—	4	3	—
Anastrophyllum donianum	7	N	—	—	—	—	—	4
Aplozia sphaerocarpa	7	N	—	—	—	—	1	—
Bazzania triangularis	14	N	—	3	4	—	—	—
Diplophyllum albicans	14	—	—	—	—	—	—	1
Leptoscyphus taylori	7	N	—	—	—	—	—	1
Lophozia alpestris	7	N	—	—	—	—	1	—
Orthocaulis floerkii	35	—	—	—	—	—	1	—
Pleurozia purpurea	14	N	—	2	3	—	—	—

	1	2	3	4	5	6	7	8
Ptilidium ciliare	63	—	1	—	—	3	+	3
Scapania gracilis	7	N	2	—	—	—	—	—
S. nemorosa	14	N	3	3	—	—	—	—
Cerania vermicularis	7	B	—	—	—	—	—	—
Cetraria aculeata	7	N	—	+	—	—	—	—
C. islandica	56	—	3	3	2	—	3	3
Cladonia bellidiflora	35	—	—	1	1	—	2	2
C. gracilis	28	—	—	1	1	—	—	3
C. impexa	14	N	—	4	4	—	—	—
C. leucophaea	21	N	—	2	2	—	—	1
C. pyxidata v. chlorophaea	28	—	—	—	4	—	+	1
C. rangiferina	7	B	—	—	—	—	—	—
C. sylvatica	21	B	—	—	—	—	—	—
C. tenuis	14	N	—	—	—	—	3	1
C. uncialis	56	—	2	1	2	—	3	2
Ochrolechia frigida	7	N	—	—	—	—	—	+
Sphaerophorus globosus	7	N	—	+	—	—	—	—

Map reference

3. 18/932639 6. 28/946600
4. 18/985598 7. 18/978635
5. 18/985598 8. 18/975636

The nodum corresponds to an extension of the Scandinavian alliance Phyllodoco-Vaccinion with which it has a number of features in common in addition to habitat.

The Scottish localities of *Phyllodoce caerulea,* a species faithful to the alliance in Norway, lie within the nodum whose preference corresponds exactly to Nordhagen's diagnosis 'humus-loving, acidophilous, chionophilous and mesophilous to weakly xerophilous'.

Although the alliance is represented in continental Norway, it assumes most importance in oceanic and sub-oceanic regions where a large proportion of the high precipitation falls as snow. That relatively small areas are covered by this nodum in Scotland is probably due to the warmth of our oceanic climate and the particularly erratic snow cover at low altitudes. It is notable that three of the four Norwegian associations of the alliance are covered with wood or scrub of juniper, *Betula nana* or *B. tortuosa*. Sociations analogous to these were no doubt once present in Scotland.

G. Dryas *heaths*

Base-rich mountain heaths are rare in Scotland partly because of the scarcity of limestone or calcareous schist outcrops on fairly level terrain in Low and Sub-Alpine regions and partly because of the formidable rate of soil leaching in an oceanic climate. Any potential sites of base-rich heath are exposed to strong leaching, and base-rich communities are confined to the slopes and crag ledges below as a variety of flush associations. On hard limestone peat may form directly on the rock, and acid communities become dominant as at Loch Daimh, Perthshire, and at Durness and Inchnadamph in Sutherland. Even in the east and central Highlands the only level and well-drained habitats which have a rich vegetation are those on soft rocks where the rate of weathering can keep pace with leaching, and where the physical structure of the soil favours frost movement. This is even more pronounced in the west and north. (Cf. Coombe and White, 1951.)

Nordhagen (1943) divides the Class Elyno-Seslerietalia into two alliances, the damper and more chionophilous Potentillo-Polygonion vivipari and the drier more exposed Elyno-Dryadion. Poore (1955) compares the *Sibbaldia* nodum and some of the richer communities of 'Arctic-Alpine grassland' in Breadalbane with sociations of the former. Well-drained localities which might support *Dryas* in this region do not do so, but the occurrence of *Dryas* on the cliffs nearby suggests that this may be in part a grazing effect. One fragment of a community allied to *Dryas* heaths has been found in Glen Lochay with the following composition:

Salix reticulata	Polygonum viviparum	Carex bigelowii
Selaginella selaginoides	Saxifraga aizoides	C. pulicaris
Alchemilla alpina	S. oppositifolia	Festuca vivipara
Armeria maritima	Silene acaulis	Ditrichum flexicaule
Cerastium alpinum	Thalictrum alpinum	Pleurozium schreberi
Dryas octopetala	Thymus drucei	Tortella tortuosa

The nearest approach to the Scandinavian alliance is found on the Durness limestone and on the extensive deposits of blown shell sand along the north coast of Sutherland. These areas naturally form excellent grazings and have been used so intensively that they are now covered with a close grass sward from which many of the more interesting species have been eliminated. Small patches of *Dryas* heath have been preserved by their inaccessibility.

Lists 1 and 2 (Table 10) were made on the shell sand at Druim Chuibhe near Bettyhill and list 3 from limestone near Borralie. The second list is from an exposed site and much poorer in species, but clearly belongs to the same nodum as the others, (provisionally named *Dryas-Carex flacca*). All are probably primary communities although scrub woodland of birch, juniper and hazel may have been widespread along this coast at one time.

Nordhagen (1943) expresses the view that the Irish *Dryas* communities on the Burren do not belong to the same alliance as the mountain *Dryas* heaths. This is arguable in view of the connecting links now established between them.

The *Dryas-Carex rupestris* nodum (lists 4 and 5) occurs only on steep (30 to 60 degrees) slopes on skeletal soils, and has been identified so far only at Durness and at Heilam on the east shore of Loch Eriboll. It forms a close turf alternating with the *Dryas-Carex flacca* nodum on moister sites. Fragments also occur at 1000 ft. (304 m.) above Loch Mhaolach-Coire near Inchnadamph, at Knockan and on epidiorite in Breadalbane where *Sesleria caerulea* is added to the list of species.

V. SUMMARY

The methods of vegetation analysis and description developed in the Breadalbane district of Perthshire (Poore, 1955) have been applied more widely to the mountain vegetation of the Highlands.

The principal ecological factors at work in determining vegetation development in the Scottish mountains are first described, with particular emphasis on hitherto neglected aspects such as the influence of snow cover and the degree of oceanicity. Comparisons are also made with the situation in Scandinavia. The inter-relationship of altitude and exposure is shown in the form of diagrams for three key areas of the Highlands.

Examples of Sub-Alpine scrub, dwarf shrub heaths and bogs, moss heaths, *Dryas* heaths and snow-bed communities are then described in detail. These can be divided into two categories; communities which, like the *Rhacomitrium* heaths, have part of their principal range in Scotland, and which are well enough represented to show a

Table 9. Vaccinium-Chamaepericlymenum *nodum*

	1	2	3	4	5	6	7
Cover (per cent)	—	70-90					
Altitude (ft.)	2500	2400					
Slope (deg.)	45	10-15					
Aspect	N	SSE					
Area of plot (sq. m.)	1	4	1	1	1	1	1
Calluna vulgaris	—	—	4	5	3	5	3
Chamaepericlymenum suecicum	3	3	3	3	3	3	3
Empetrum hermaphroditum	3	2	5	4	1	2	5
Rubus chamaemorus	—	—	2	2	1	1	2
Vaccinium myrtillus	5	7	8	7	9	8	7
V. uliginosum	—	7	—	—	—	—	—
V. vitis-idaea	—	—	3	3	3	3	3
Blechnum spicant	3	3	—	2	1	1	1
Dryopteris austriaca	—	—	—	—	+	—	—
Lycopodium annotinum	1	—	—	—	—	—	—
Agrostis tenuis	3	+	—	—	—	—	—
Carex bigelowii	3	—	—	—	—	—	—
C. binervis	—	+	—	—	—	—	—
C. echinata	—	—	1	1	—	—	1
Deschampsia flexuosa	—	—	4	3	4	3	3
Molinia caerulea	—	2	—	—	—	—	—
Nardus stricta	5	4	—	—	—	—	—
Alchemilla alpina	—	2	—	—	—	—	—
Galium hercynicum	2	2	—	2	3	3	1
Melampyrum pratense	1	2	1	1	—	—	—
Oxalis acetosella	—	—	—	—	+	—	—
Potentilla erecta	—	3	—	—	—	—	—
Trientalis europaea	—	2	—	—	—	—	—
Viola palustris	—	+	—	—	—	—	—
Dicranum scoparium	—	+	4	4	3	3	3
Hylocomium splendens	—	—	4	4	5	4	4
Hypnum cupressiforme	—	—	1	—	3	—	—
Leucobryum glaucum	—	+	—	—	—	—	—
Pleurozium schreberi	3	8	3	3	3	1	3
Polytrichum commune	3	—	2	2	4	3	2
Ptilium crista-castrensis	—	—	1	—	—	—	—
Rhytidiadelphus loreus	2	—	6	3	4	6	4
Sphagnum spp.	7	+	6	6	6	4	7
S. capillaceum	+	—	+	+	+	+	+
S. quinquefarium	+	—	—	—	—	—	—
Microhepatics	—	—	3	1	1	1	3
Cetraria islandica	—	3	—	—	—	—	—
Cladonia bellidiflora	—	1	—	1	1	—	—
C. gracilis	—	+	—	—	—	—	—
C. sylvatica	1	2	—	1	—	—	—
Icmadophila ericetorum	—	—	—	1	—	—	—

Map reference

1. 28/883023
2. 37/154974
3. }
4. }
5. } 27/90–97–
6 }
7. }

Table 10. Dryas *heaths*

	1	2	3	4	5
Cover (per cent)	100	100	100	80	85
Altitude (ft.)	200	175	200	50	100
Slope (deg.)	5	2	5	40	30
Aspect	N	S	SE	W	W
Area of plot (sq. m.)	4	4	4	4	4
Arctostaphylos uva-ursi	—	—	3	—	—
Calluna vulgaris	—	—	—	—	1
Dryas octopetala	9	9	6	4	8
Empetrum nigrum and hermaphroditum	3	3	4	—	—
Juniperus communis	—	—	4	—	—
Salix repens	3	2	1	—	—
Thymus drucei	3	3	3	3	3
Selaginella selaginoides	+	—	3	+	—
Agrostis tenuis	—	—	3	+	1
Carex cf. bigelowii	+	—	—	—	—
C. flacca	6	6	5	3	4
C. panicea	—	—	+	—	—
C. rupestris	—	—	—	6	5
Festuca ovina	2	—	6	5	5
F. rubra	—	—	—	2	—
Helictotrichon pratense	—	—	1	—	—
Sieglingia decumbens	—	—	—	4	2
Koeleria gracilis	+	—	1	2	3
Luzula campestris	—	—	1	—	—
Schoenus nigricans	—	—	2	—	+
Epipactis atrorubens	—	—	—	+	—
Listera ovata	—	—	1	—	—
Orchis mascula	—	—	2	—	—
Antennaria dioica	+	—	2	+	2
Anthyllis vulneraria	—	—	1	1	—
Bellis perennis	+	1	—	+	2
Campanula rotundifolia	2	—	2	1	—
Cerastium vulgatum	—	1	—	—	—
Daucus carota	—	—	—	+	—
Euphrasia agg.	—	—	—	—	2
Galium hercynicum	—	—	—	—	1
G. verum	1	2	—	—	—
Gentianella amarella	—	—	—	—	2
Hieracium pilosella	—	—	—	2	2
Hypericum pulchrum	—	—	+	1	3
Hypochaeris radicata	—	—	—	—	+
Lathyrus montanus	—	—	—	+	—
Linum catharticum	1	—	3	3	3
Lotus corniculatus	1	+	—	1	1
Plantago lanceolata	+	+	3	2	3
P. maritima	1	—	2	3	3
P. media	+	—	—	—	—
Polygonum viviparum	2	—	—	—	—
Polygala cf. vulgaris	1	+	2	1	—
Potentilla erecta	—	—	—	—	2
Prunella vulgaris	—	—	—	2	3
Saxifraga aizoides	—	—	—	2	—
Senecio jacobaea	—	—	—	+	—
Succisa pratensis	—	—	3	2	3
Thalictrum alpinum	—	—	3	—	—
Viola riviniana	+	+	3	1	2
Camptothecium lutescens	1	2	—	—	—
Ctenidium molluscum	—	—	2	1	+
Ditrichum flexicaule	3	3	3	1	+
Fissidens decipiens	1	1	—	—	1
Hylocomium splendens	2	—	—	—	—
Hypnum cupressiforme	—	—	3	—	1
Mnium sp.	1	—	—	—	—

	1	2	3	4	5
Neckera crispa	—	—	—	1	—
Pleurozium schreberi	—	—	4	—	—
Pseudoscleropodium purum	1	1	1	—	—
Rhacomitrium lanuginosum	—	—	—	1	—
Rhytidiadelphus triquetrus	4	—	1	—	—
Thuidium sp.	3	—	3	—	—
Tortella tortuosa	—	—	—	3	+
Lochocolea sp.	1	—	—	—	—
Plagiochila asplenioides	—	+	—	—	—
Scapania undulata	+	—	+	—	—
Cladonia rangiformis	—	—	+	1	—
Peltigera canina	+	—	—	—	—
Solorina saccata	—	—	—	1	—

Map reference

1. 29/705605
2. 29/696612
3. 29/388652
4. 29/421676
5. 29/453604

response to change in the ecological factors in different parts of the country, and those such as *Dryas* heath, which occur in Scotland only as the scattered fragments of well-known vegetation types of Scandinavia.

Salix myrsinites scrub, *Betula nana* bog, lichen heath, *Dryas* heath and certain moss and dwarf shrub heaths are here described for the first time from Scotland.

Addendum

Since this paper was submitted further progress has been made with the survey of Scottish montane vegetation carried out by the Nature Conservancy, Edinburgh. The floristic lists presented above have been incorporated in the more extensive data now available so that some reshuffling of the communities and nomenclatural changes have been necessary.

In particular, further examples of lichen heath, *Dryas* heath, and the species-rich facies of *Rhacomitrium-Carex bigelowii* heath have been analysed and their status is now better known. A chionophilous Athyrietum alpestris has been recognized in the central and northern Highlands and communities of late snow areas dominated by *Dicranum falcatum*, *D. starkei*, *Polytrichum norvegicum*, *Rhacomitrium* spp. and *Gymnomitrium* spp. (*Salix herbacea* nodum of Breadalbane, Poore, 1955c) have been described from the Cairngorms, Ben Wyvis, the Fannich forest and Kintail.

The majority of Poore's Breadalbane noda have been found to be widespread in the Highlands with minor, but often significant, variations in floristic composition.

A final classification must await completion of the entire survey.

REFERENCES

Boyko, H. (1947). On the role of plants as quantitative climate indicators and the geo-ecological law of distribution. *J. Ecol.*, **35**, 138.

Burges, A. (1951). The ecology of the Cairngorms. III. The *Empetrum-Vaccinium* zone. *J. Ecol.*, **39**, 271.

Coombe, D. E. and White, F. (1951). Notes on calcicolous communities and peat formation in Norwegian Lappland. *J. Ecol.*, **39**, 33.

Crampton, C. B. (1911). *The Vegetation of Caithness Considered in Relation to the Geology*. Edinburgh.

Dahl, E. (In press). Vegetation of Rondane.

Du Rietz, G. E. (1925). *Die regionale Gliederung der skandinavischen Vegetation*. Upsala.

Godske, C. L. (1944). The geographical distribution in Norway of certain indices of humidity and oceanity. *Bergens Mus. arb.* Faturvit. Rekke. **8.** Bergen.

Hansen, H. M. (1930). *Studies on the Vegetation of Iceland.* Copenhagen.

Knaben, G. (1950). Botanical Investigations in the Middle Districts of Western Norway. *Universitetet i Bergen Årbok.*, Naturvit. Rekke. **8.**

Lewis, F. J. (1905-11). The Plant Remains in the Scottish Peat Mosses. *Trans. Roy. Soc. Edin.*, **41,** 45-70.

McVean, D. N. (1955). Notes on the vegetation of Iceland. *Trans. Bot. Soc. Edin.*, **36,** 320-38.

Metcalfe, G. (1950). The ecology of the Cairngorms. II. The mountain Callunetum. *J. Ecol.*, **38,** 46.

Nordhagen, R. (1928). *Die Vegetation und Flora des Sylenegebiets.* Oslo.

Nordhagen, R. (1943). *Sikilsdalen og Norges Fjellbeiter, en Plantesosiologisk Monografi.* Bergens Mus. Skr., **22.**

Ostenfëld, C. H. (1908). *The Land-Vegetation of the Faeroes.* London.

Pearsall, W. H. (1950). *Mountains and Moorlands.* London.

Poore, M. E. D. (1955a). The use of phytosociological methods in ecological investigations. I. The Braun-Blanquet system. *J. Ecol.*, **43,** 226.

Poore, M. E. D. (1955b). The use of phytosociological methods in ecological investigations. II. Practical issues involved in an attempt to apply the Braun-Blanquet system. *J. Ecol.*, **43,** 245.

Poore, M. E. D. (1955c). The use of phytosociological methods in ecological investigation. III. Practical application. *J. Ecol.*, **43,** 606.

Steindórrson, S. (1941). *Skrá um Islensk Grodurhverfi* (*A list of Icelandic Plantsociations examined and defined*). Akureyri.

Tansley, Sir A. G. (1939). *The British Islands and their Vegetation.* Cambridge University Press.

Watt, A. S. (1936). Studies in the ecology of Breckland. I. Climate, soil and vegetation. *J. Ecol.*, **24,** 117.

Watt, A. S. and Jones, E. W. (1948). The ecology of the Cairngorms. I. The environment and the altitudinal zonation of the vegetation. *J. Ecol.*, **36,** 283.

(*Received March 8th,* 1956)