
H19

Vaccinium myrtillus-*Cladonia arbuscula* heath

Synonymy

Empetreto-Vaccinetum Burges 1951 *p.p.*; *Vaccinium myrtillus*-lichen heath Poore & McVean 1957; *Empetrum*-lichen heath Poore & McVean 1957; *Cladineto-Vaccinetum* McVean & Ratcliffe 1962; *Festuceto-Vaccinetum rhacomitrosus* McVean & Ratcliffe 1962 *p.p.*; *Vaccinium myrtillus*-*Empetrum hermaphroditum* nodum Huntley 1979; *Festuceto-Rhacomitrietum lanuginosi* (Birse & Robertson 1976) Birse 1980 *p.p.*; *Carex bigelowii*-*Festuca vivipara* Association (Birse & Robertson 1976) Birse 1980 *p.p.*

Constant species

Carex bigelowii, *Deschampsia flexuosa*, *Vaccinium myrtillus*, *V. vitis-idaea*, *Racomitrium lanuginosum*, *Cetraria islandica*, *Cladonia arbuscula*, *C. uncialis*.

Rare species

Loiseleuria procumbens, *Kiaeria starkei*.

Physiognomy

Like its heather-dominated counterpart, the *Vaccinium myrtillus*-*Cladonia arbuscula* heath consists essentially of a very low mat of sub-shrubs with an abundance of lichens, which again often mark out stands from a distance with a yellowish or grey-green tinge. Indeed, if anything, the lichens tend to be more extensive throughout this vegetation, and their dominance over the other components is more frequent and more extreme than in the *Calluna*-*Cladonia* heath. And, among the sub-shrubs, *Calluna* itself is uncommon overall: it increases in frequency in one sub-community but it is typically of low cover even there and of little structural importance, so the kind of wind-waved canopy associated with an abundance of flattened heather bushes is not usual here. The mat is still, however, very short, usually only 5–10 cm thick, but it is *Vaccinium myrtillus* that provides its most consistent element and, although this becomes sparse and noticeably lacking in vigour in more exposed situations, it is quite often abundant and a fairly regular

co-dominant in what can be a dense and springy cover. *V. vitis-idaea* is somewhat less common and generally not so extensive and, in certain kinds of *Vaccinium*-*Cladonia* heath, it becomes distinctly patchy. *V. uliginosum* very occasionally shows local prominence, but overall it is scarce.

The other important sub-shrub in the community is *Empetrum nigrum*, almost always ssp. *hermaphroditum* and, in some of the vegetation included here (what McVean & Ratcliffe (1962) recognised as *Cladineto-Vaccinetum*), it becomes very frequent and often rivals or exceeds the *Vaccinia* in its cover. *Alchemilla alpina* can also be found, but it is nothing like so common or abundant as among the grassier stands of the *Vaccinium*-*Deschampsia* heath. The rare Arctic-Alpine *Loiseleuria procumbens* is very occasionally recorded, although neither it, nor the *Arctostaphylos* spp., play the sort of role here that they have in the *Calluna*-*Cladonia* or *Calluna*-*A. alpinus* heaths.

As in both those lichen-rich communities, vascular associates of the sub-shrubs in the *Vaccinium*-*Cladonia* heath are few in number, although they can be somewhat more extensive in their cover. This is especially true of *Carex bigelowii* which is not only more frequent in this community than those heaths but often abundant, indeed, co-dominant with the ericoids and the lichens in many stands, occurring sometimes as numerous small tufts of shoots in intimate mixtures with them, in other cases in large clonal patches forming coarser mosaics. The general prominence of this sedge shifts the composition of the vegetation towards the *Carex*-*Racomitrium* heath somewhat, but, although transitional stands can be widely found, the general balance of the structural elements is different there, with both sub-shrubs and lichens generally playing a subordinate role.

The other common associate, though one which is usually less abundant, is *Deschampsia flexuosa*. *Festuca ovina* (including many records for *F. vivipara*) is also fairly frequent, particularly in one kind of *Vaccinium*-*Cladonia* heath, and it can have moderately high cover

there, along with *Galium saxatile* and, more occasionally, *Potentilla erecta*. *Carex pilulifera*, *Agrostis canina* (usually recorded as ssp. *montana*) and *A. capillaris* can also be found at low frequencies throughout the community, but the rich and extensive assemblages of Nardo-Galion herbs typical of grassier stands of the *Vaccinium-Deschampsia* heath are not found here. *Nardus stricta* itself is fairly infrequent, too, which is one good feature distinguishing this vegetation from the more chionophilous *Nardus-Carex* community, where *V. myrtillus* and *C. bigelowii* maintain a constant presence, but where *Nardus* is usually strongly dominant. Towards the opposite extreme, in moving towards fell-field vegetation, *Juncus trifidus*, which characteristically predominates over bilberry and the sedge in the *Juncus-Racomitrium* heath, is scarce and of low cover here.

One other feature which helps mark off the *Vaccinium-Cladonia* heath from the vegetation of cloud-ridden summits is the restricted role of *Racomitrium lanuginosum*. This is in fact rather more prominent here than in McVean & Ratcliffe's (1962) original *Cladineto-Vaccinetum*, and the community perhaps takes in some of what these authors would have placed in the *Festuceto-Vaccinetum rhacomitrosus* and the more bilberry-rich stands of the *Festuceto-Rhacomitrietum* of Birse (1980). But only in one of the sub-communities is the moss of any great abundance and in much *Vaccinium-Cladonia* heath it is distinctly sparse. And *Polytrichum alpinum*, which commonly accompanies it in the *Carex-Racomitrium* heath, is only occasional in this community.

Other bryophytes, too, are rather inconsistent in their contribution. *Dicranum fuscescens* is quite frequent and it very occasionally shows local abundance: where this coincides with low covers of the *Vaccinia*, the community approaches certain kinds of *Carex-Polytrichum* snow-bed vegetation, although McVean & Ratcliffe (1962) reported such transitions as being problematic only in the Clova region. Then, there are some stands in which *Dicranum scoparium*, *Pleurozium schreberi* and *Ptilidium ciliare* become common, but the rich carpets of bulky pleurocarps characteristic of the *Vaccinium-Deschampsia* heath are not usual here. Often, it is just sparse shoots of *Polytrichum alpestre* and *P. piliferum* that are dotted through the mat.

Much more important throughout the community are the lichens, particularly larger fruticose species such as *Cladonia arbuscula* and *C. uncialis* with, less commonly, *C. rangiferina* and *C. gracilis*, mixtures of which can exceed the sub-shrubs in total cover and which form with them a single layered carpet that can sometimes be peeled away from the substrate intact. *Cetraria islandica* and *Cornicularia aculeata* are also very common, though usually less abundant and there is occasional *Alectoria nigricans*, *Cladonia impexa*, *C. coccifera* and *Thamnolia*

vermicularis. *Ochrolechia frigida* and *Cetraria nivalis* can also be found, though they are preferential for one particular sub-community.

Sub-communities

***Festuca ovina*-*Galium saxatile* sub-community:** *Carex bigelowii*-*Festuca vivipara* Association (Birse & Robertson 1976) Birse 1980 p.p. *V. myrtillus* is often abundant here, but it usually shares dominance among the vascular plants with *C. bigelowii* and, strongly preferential to this kind of *Vaccinium-Cladonia* heath, *F. ovina/vivipara*. Among the other sub-shrubs, *E. nigrum* ssp. *nigrum* is sometimes found but ssp. *hermaphroditum* is scarce, while *V. vitis-idaea* attains its maximum frequency and abundance in this sub-community, though it is even then rarely extensive in its cover. *Deschampsia flexuosa* is likewise only moderately abundant. *Galium saxatile* is a good diagnostic species with *Potentilla erecta* also preferential at low frequency and there is occasionally a little *Carex pilulifera* and *Agrostis canina* ssp. *montana*. Where such mixtures occur with a little *Dicranum scoparium*, *Pleurozium schreberi* and *Hypnum jutlandicum*, all of which are occasional here, the vegetation comes close to the *Vaccinium-Deschampsia* heath.

Other stands, with a little less *V. myrtillus* than usual and locally abundant *R. lanuginosum*, are like the grassier forms of the *Carex-Racomitrium* heath but *R. lanuginosum* is usually of low cover and sometimes distinctly patchy and, from both these communities, this vegetation is distinguished by the lichen element. This is not so overwhelmingly extensive as in the *Empetrum-Cladonia* sub-community but *Cladonia arbuscula* is sometimes co-dominant with the vascular plants, *C. uncialis* is moderately abundant throughout and there is commonly a little *Cetraria islandica* and *Cornicularia aculeata* and occasionally some *C. rangiferina*, *C. gracilis*, *C. impexa* and *C. coccifera*.

***Racomitrium lanuginosum* sub-community:** *Festuceto-Vaccinetum rhacomitrosus* McVean & Ratcliffe 1962 p.p.; *Festuceto-Rhacomitrietum*, *Cladonia arbuscula* subassociation Birse 1980 p.p. In this sub-community, the mat is dominated by various mixtures of *V. myrtillus*, *C. bigelowii*, lichens and, unusually abundant for the *Vaccinium-Cladonia* heath, *R. lanuginosum*. *E. nigrum*, mostly ssp. *hermaphroditum*, is fairly common but *V. vitis-idaea* is very patchy in its occurrence. *F. ovina/vivipara* and *Galium saxatile* can occasionally be found and, where other Nardo-Galion grasses also have sparse representation, the vegetation looks transitional to *Racomitrium*-rich *Vaccinium-Deschampsia* heath, the floristic similarity enhanced by the frequent occurrence in this sub-community of small amounts of *Alchemilla alpina*. Such a trend is exceptional, however, and,

though no other species are strongly preferential, the occasional presence of plants like *Salix herbacea* and, among the mosses, the rare *Kiaeria starkei*, both of which can show local abundance, can lend a more pronounced chionophilous look to the vegetation. *Juncus trifidus* also increases in frequency somewhat and there is very occasionally some *Luzula spicata*, *Antennaria dioica*, *Armeria maritima*, *Silene acaulis* and *Sibbaldia procumbens*. In general, though, such plants are still much scarcer than in the *Carex-Racomitrium* heath.

Apart from *R. lanuginosum* and *K. starkei* other mosses are poorly represented, but the lichen cover is quite varied. *C. arbuscula* is sometimes much the most abundant species but it can become very patchy and mixed carpets are more usual, with moderate amounts of *C. uncialis*, *Cetraria islandica* and *Cornicularia aculeata* and, weakly preferential here, *Sphaerophorus globosus*.

***Empetrum nigrum* ssp. *hermaphroditum*-*Cladonia* spp. sub-community:** *Vaccinium myrtillus*-lichen heath Poore & McVean 1957; *Empetrum*-lichen heath Poore & McVean 1957; *Cladineto-Vaccinetum* McVean & Ratcliffe 1962; *Vaccinium myrtillus*-*Empetrum hermaphroditum* nodum Huntley 1979. Mixed mats of *V. myrtillus* and *E. nigrum* ssp. *hermaphroditum* provide the bulk of the vascular cover here though their proportions and vigour are very variable and they are quite often exceeded in abundance by the lichens: this sub-community thus encompasses most of the floristic and physiognomic differences used to define the sub-associations of McVean & Ratcliffe's (1962) *Cladineto-Vaccinetum*. Other sub-shrubs are of generally low cover, although *V. vitis-idaea* can be moderately abundant, and there is quite often here a little *Calluna*. *C. bigelowii* remains very frequent but it is usually subordinate and *D. flexuosa*, though very common, is distinctly sparse in cover. Other grasses are very scarce and species like *Carex pilulifera* and *Galium saxatile* are at their most infrequent.

Among the bryophytes, *R. lanuginosum* remains frequent and there is preferentially common *Pleurozium schreberi*, *Dicranum scoparium*, *Ptilidium ciliare* and, more occasionally, *Rhytidiadelphus loreus*, but only in exceptional circumstances is any of these abundant and even their total cover contribution is usually small. Lichens, by contrast, can be overwhelmingly extensive here with *C. arbuscula* especially abundant, *C. uncialis* usually less so, but *C. rangiferina* is also strongly preferential and locally prominent. Frequent *C. gracilis* is also diagnostic though this, together with *Cornicularia aculeata* and *Cetraria islandica*, is usually found at low cover. Then there is occasionally some *Ochrolechia frigida* and *Cetraria nivalis* with sparse *Cladonia pyxidata*, *C. bellidiflora* and *C. leucophaea*.

Habitat

The *Vaccinium-Cladonia* heath is typical of base-poor soils on what are usually moderately sheltered and snow-bound slopes at high altitudes, particularly in the more continental mountains of northern Britain. Floristic variation within the community seems to reflect differences in exposure and soil type, but overall the vegetation can be considered a climatic climax.

Geographically, the community has much the same range as the *Calluna-Cladonia* heath, being strongly concentrated in the central and eastern Highlands of Scotland, though with a somewhat better representation through the mountains of the north-west and at scattered localities in the Southern Uplands and northern England, where the community can be seen in such places as Dollar Law, Skiddaw and Cross Fell (McVean & Ratcliffe 1962, Ratcliffe 1977). And there is considerable altitudinal overlap between the two vegetation types, the *Vaccinium-Cladonia* heath being also characteristic of the low-alpine zone (Poore & McVean 1957), though usually pitched a little higher within it, mostly above 650 m and quite often towards 1000 m or even well beyond. At such levels, the climate is generally harsh, with mean annual maximum temperatures usually less than 21 °C (Conolly & Dahl 1970), and particularly through the heart of its range the winters are very bitter, with February minima well below freezing and frequent late frosts (*Climatological Atlas* 1952, Huntley 1979). Through much of the distribution, precipitation is not especially heavy, often not much more than 1600 mm yr⁻¹ (*Climatological Atlas* 1952) with 180–200 wet days yr⁻¹ (Ratcliffe 1968), but through the central and eastern Highlands much of the winter share falls as snow and there are up to 100 days or more with morning snow-lie at the altitudes where the community is found.

These general climatic conditions are reflected in the strongly montane character of the vegetation, with Arctic-Alpines such as *C. bigelowii*, *V. vitis-idaea* and *E. nigrum* ssp. *hermaphroditum* all represented with more consistent frequency than in the *Vaccinium-Deschampsia* heath which replaces it at lower altitudes, and plants like *Erica cinerea* and *Molinia caerulea*, which even find a place in the *Calluna-Cladonia* heath at its lower stations, are quite absent. *Alchemilla alpina* adds a further montane element in some stands, and then there is the common occurrence of upland lichens such as *Cetraria islandica* and *Cladonia rangiferina* and more occasional representation of *Juncus trifidus*, *Polytrichum alpinum* and *P. alpestre*.

Just as important, however, to the character of the vegetation is the fact that, compared with most stands of the *Calluna-Cladonia* heath, the local climatic conditions here often seem fairly sheltered. Sometimes the community can be found over more windswept spurs

and ridges such as are the typical habitat of that kind of lichen-heath, when it is more difficult to see what particular environmental factors differentiate the two, but often the location of the *Vaccinium-Cladonia* heath is not so exposed to the frequent biting gales typical of these altitudes and, in winter, some snow is able to settle and, over north- and east-facing slopes, persist long over this vegetation, affording protection from frost. The most obvious general effects of this difference in topoclimate are on the composition and relative luxuriance of the sub-shrub canopy compared with the *Calluna-Cladonia* heath, particularly the shift from *Calluna* to *V. myrtillus* as the most prominent ericoid throughout, and on the frequency and abundance of *C. bigelowii*, with a more sporadic occurrence of markedly chionophilous plants.

Details of the snow-lie regime for the community are still not available, but McVean & Ratcliffe (1962) noted that its common position in the low-alpine sequences of the east-central Highlands, between the *Nardus-Carex* community of the early snow-beds and the *Calluna-Cladonia* heath over more exposed slopes, suggested an intermediate duration and thickness of snow-cover: perhaps roughly the same as for the *Vaccinium-Rubus* heath and less grassy stands of the *Vaccinium-Deschampsia* heath, typical of sheltered situations in the sub-alpine zone. In this scheme, McVean & Ratcliffe's (1962) *Cladineto-Vaccinetum* is essentially identical to the *Empetrum-Cladonia* sub-community and within it can be seen those floristic trends in relation to variation in snow-cover which they used to define sub-associations. To one extreme, closest to the *Calluna-Cladonia* heath of more exposed situations, are stands with an abundance of lichens, among which *Cetraria nivalis* figures prominently; to the other, more prominent *R. lanuginosum* and pleurocarps among extensive covers of *V. myrtillus* and *C. bigelowii* mark a transition to early snow-beds proper.

A continuation of the trend towards greater humidity of the environment is reflected in the *Racomitrium* sub-community by the increasing abundance of this moss and of *C. bigelowii* with the local occurrence of *Salix herbacea* and *Kiaeria starkei*, assemblages characteristic of later snow-bed vegetation. Again, actual details of the snow-lie regime are lacking but some of the stands included here are from the shaded northern and eastern aspects in the east-central Highlands that would be expected to retain their snow-cover longer. Others, though, occur outside this region, extending the range of the *Vaccinium-Cladonia* heath into the north-west Highlands, where annual rainfall rises to well over 1600 mm (*Climatological Atlas* 1952) with 200 or more wet days yr^{-1} (Ratcliffe 1968). There, *R. lanuginosum* becomes a much more consistently abundant element of low-alpine bilberry and crowberry heaths, and the *Vaccinium-*

Cladonia heath grades to the *Vaccinium-Racomitrium* heath.

Even in the east of Scotland, however, the rainfall is sufficient to produce marked leaching in the soils beneath the *Vaccinium-Cladonia* heath especially where, as is usually the case with the two sub-communities above, the parent materials are lime-poor, weathering to podzolised profiles, strongly humic above and with a superficial pH usually not much above 4. The *Empetrum-Cladonia* type seems characteristic of the most impoverished soils, derived often from the granites which underlie the Cairngorms, Lochnagar and Monadhliath or the quartzites and quartzose mica-schists of the Dalradian assemblage through the Grampians, but the *Racomitrium* sub-community is found widely over the latter too, as well as on soils derived from Lewisian gneiss and Torridonian sandstone in the north-west Highlands.

The distribution of the *Festuca-Galium* sub-community, on the other hand, like the grassier stands of the *Vaccinium-Deschampsia* heath down into the sub-alpine zone, shows a clear correlation with the occurrence of the Dalradian limestone and calcareous mica-schists that run from Breadalbane to Clova and, though the superficial pH does not seem very different from that beneath other kinds of *Vaccinium-Cladonia* heath, the profiles tend towards the brown podzolic type, being less humic and perhaps less oligotrophic. Certainly, the floristic trend among the associates is towards the Nardo-Galion and this sub-community also takes in most of the stands of the *Vaccinium-Cladonia* heath towards the warmer and drier southern fringes of its range, from where McVean & Ratcliffe (1962) noted grassy fragments of their *Cladineto-Vaccinetum*. Even there, however, the continuing prominence of *C. bigelowii* with much *F. vivipara* shows a clear trend from low-alpine heath to fell-field vegetation.

Zonation and succession

The *Vaccinium-Cladonia* heath is a characteristic element in the sequences of sub-shrub communities and snow-bed vegetation of the low-alpine zone of the continental mountains of the east and central Highlands, among which floristic variation is strongly related to exposure and snow-lie. Here, it occurs at the limit of ericoid dominance, marking the altitudinal transition in more sheltered situations from sub-alpine and sub-montane heaths to summit moss-heath, fell-field or mire. Geology and soils affect the particular kinds of communities represented with the *Vaccinium-Cladonia* heath and, towards lower altitudes, treatments have modified the vegetation cover but these are not important in maintaining the community itself.

The broad altitudinal zonations in which the *Vaccinium-Cladonia* heath plays an integral part are most

obvious over the upper slopes of the Cairngorms and on the mountain tops of the Breadalbane-Clova region. On the impoverished granite soils typical of the former area, where there has been relatively little impact of sheep-grazing, sequences of sub-shrub vegetation are extensive, starting with mosaics of the *Calluna-Vaccinium* and *Calluna-A. uva-ursi* heaths with fragments of *Pinus-Hylocomium* woodland and *Juniperus-Oxalis* scrub through the sub-montane and up into the sub-alpine zone. Above these levels, past the present limits of tree growth and beyond the influence of the regular burning employed to regenerate the lower-altitude heaths for grouse-rearing, the particular zonation becomes strongly dependent on exposure. Wind-blasted spurs and ridges have the *Calluna-Cladonia* heath and, though the *Vaccinium-Cladonia* heath finds occasional representation in such situations, it is usually in less exposed places that the community begins to make an obvious contribution to the cover.

Indeed, the effects of local shelter can already be seen at lower altitudes in this region, where the *Hylocomium-Rhytidiadelphus* sub-community of the *Vaccinium-Deschampsia* heath often marks out large shallow snow-beds towards the transition to the sub-alpine zone, with the *Polytrichum-Galium* sub-community of the *Vaccinium-Rubus* heath extending even further below, where easterly or northerly aspects provide shaded and cool conditions. Observation suggests (McVean & Ratcliffe 1962) that each of these vegetation types experiences roughly similar regimes of snow-lie and, among them, the *Empetrum-Cladonia* sub-community of the *Vaccinium-Cladonia* heath can be seen as the high-altitude representative of a mildly chionophilous suite. Quite often, however, mosaics of the *Vaccinium-Cladonia* and *Vaccinium-Deschampsia* heath can be found disposed across hillsides in the low-alpine zone, the enclosed patches of the latter being marked out by a shift from a predominance of lichens among the cryptogamic element to bulky pleurocarps, and by the appearance of species like *Blechnum spicant* and *Cornus suecica*.

Although there are places where the *Vaccinium-Cladonia* heath can be seen in extensive tracts, the more usual picture is for this kind of mosaic to continue, with moves to slopes that are more exposed or less, to the *Calluna-Cladonia* heath on the one hand or to snow-bed vegetation on the other. Transitions to the former are typical of gently undulating hillsides, where the rounded spurs get blown clear of snow, the concavities accumulating a little, and where the move from one community to the other is denoted largely by a replacement of heather by bilberry among a superabundant ground of lichens. Similar transitions can be seen on moving off the exposed tops of the risers on terraced slopes on to the sheltered treads and on shifting round from wind-blasted slopes on to more sheltered aspects and here the

Racomitrium sub-community is sometimes seen as a transition to either *Nardus-Carex* or *Carex-Polytrichum* snow-beds. Moves towards the former involve a reduction in the contribution of *V. myrtillus* and the less snow-tolerant lichens, with an increase in the abundance of *R. lanuginosum* and a marked dominance of *Nardus stricta*. In the latter, *V. myrtillus* and the other sub-shrubs are often absent, but *C. bigelowii* remains prominent with chionophilous bryophytes such as *Polytrichum alpinum* and *Dicranum fuscescens* very common. In such patterns, the patches of the different vegetation types can vary from just a few square metres to hectares in extent.

The greater snow-tolerance of the *Vaccinia* and *E. nigrum* ssp. *hermaphroditum* over *Calluna* means that the *Vaccinium-Cladonia* heath often runs on above the limit of the *Calluna-Cladonia* heath, maintaining a strong sub-shrub representation for a further hundred metres or more and, in such situations, it can replace it in moderately exposed habitats just within the mid-alpine zone. Over the windy and cloud-ridden summits of the Cairngorms, however, the community typically gives way to the *Juncus-Racomitrium* fell-field vegetation or, more locally, the *Carex-Racomitrium* heath. *V. myrtillus* continues with some frequency into such communities, though at low covers, and dominance is usually shared between such plants as *C. bigelowii*, *R. lanuginosum*, *F. ovina* and *J. trifidus*.

Very similar zonations to these can be seen on Monadhliath and Lochnagar but, with the move on to the Dalradian rocks of the Clova area and down to Breadalbane, where lime-rich exposures begin to figure prominently, there are some differences in the vegetation types represented in the various altitudinal zones and, with many of the mountains having small or sloping summits, the upper end of the sequence is often truncated. The *Empetrum-Cladonia* sub-community of the *Vaccinium-Cladonia* heath can be found over quartzose mica-schists and other siliceous rocks through this region but, quite often, it is the *Festuca-Galium* sub-community that is represented over the more base-rich rocks, and here this continues upwards the mildly chionophilous character of the *Alchemilla-Carex* sub-community of the *Vaccinium-Deschampsia* heath. Towards lower altitudes, this in turn can pass to *Festuca-Agrostis-Alchemilla* grassland where sheep-grazing restricts the contribution from the sub-shrubs. Over the less siliceous rocks, the *Calluna-Cladonia* heath tends to be poorly represented, even where there is quite severe exposure, but some kinds of later snow-beds can be seen over ground where there is a little more shelter than with the *Vaccinium-Cladonia* heath, with transitions to certain kinds of *Nardus-Carex* and *Carex-Polytrichum* vegetation.

Towards the north-west of Scotland, the *Vaccinium-Cladonia* heath retains some representation in sequences

that have an altogether more oceanic character, subsuming some of the vegetation which McVean & Ratcliffe (1962) placed in their *Festuceto-Vaccinetum rhacomitrosus*. In this part of Britain, the effects of the greater humidity of climate are felt to some extent on all aspects and *R. lanuginosum*-rich bilberry heaths occur widely between 400 and 1000 m where there is some measure of shelter from winds. The bulk of them can be grouped within the *Vaccinium-Racomitrium* heath where there is a consistent shift away from lichens as the usual co-dominants in the mat, but the *Racomitrium* sub-community of the *Vaccinium-Cladonia* heath is seen locally as a geographical transition to this more western vegetation type. At lower altitudes the sequences among the heaths pass to *Vaccinium-Rubus* and *Calluna-Vaccinium-Sphagnum* heaths, and upwards there is extensive *Carex-Racomitrium* heath over the broader summits, with *Nardus-Carex* snow-beds in sheltered hollows.

Distribution

The range of the *Vaccinium-Cladonia* heath is strongly centred on the Grampians, where the *Empetrum-Cladonia* sub-community is widespread on the granite and quartzitic mountains, with the *Festuca-Galium* sub-community more characteristic of the lime-rich rocks between Breadalbane and Clova. The *Racomitrium* sub-community, too, can be found scattered through the central and eastern Highlands, but it also extends the distribution of the community into north-west Scotland. Each of the sub-communities has some fragmentary representation in the Southern Uplands and/or north-east England.

Affinities

The *Vaccinium-Cladonia* heath is in some senses a parallel community to the *Calluna-Cladonia* heath and, in one of the earliest accounts of this kind of vegetation (Poore & McVean 1957), lichen-heaths rich in either heather or bilberry were grouped together in a single nodum. However, although there are situations within the low-alpine zone where the two vegetation types come very close in their floristics, the difference between them being then largely a matter of the dominance of one sub-shrub rather than the other, the overall characters of the communities present quite a contrast, especially with the somewhat broader definition of the *Vaccinium-Cladonia* heath presented in this scheme as against McVean & Ratcliffe's (1962) understanding of bilberry lichen-heath. Their *Cladineto-Vaccinetum* represents just part of the variation included here, corresponding essentially to the *Empetrum-Cladonia* sub-community, some of the stands of which are from more exposed situations where the floristic and environmental similarities to the *Calluna-Cladonia* heath are most obvious.

In addition to this kind of vegetation, though, the *Vaccinium-Cladonia* heath in this scheme includes many stands which extend the range of the community further towards more sheltered and humid situations. Such a trend is already visible in the *Empetrum-Cladonia* sub-community, the mildly chionophilous character of which was stressed by McVean & Ratcliffe (1962), but it becomes more prominent in the *Racomitrium* sub-community with its local prominence of late snow-bed plants. However, this kind of *Vaccinium-Cladonia* heath also provides greater continuity with the more oceanic bilberry heaths of the low-alpine zone of the north-west Highlands, where it represents a geographical transition to the *Vaccinium-Racomitrium* heath, and perhaps takes in some of the less grassy stands of McVean & Ratcliffe's (1962) *Festuceto-Vaccinetum rhacomitrosus*.

The *Festuca-Galium* sub-community exhibits a different kind of trend towards the vegetation of the *Vaccinium-Deschampsia* heath. Lichen-rich stands of grassy bilberry heaths were noted by both Poore (1955c) and McVean & Ratcliffe (1962), in both cases on the more calcareous rocks of the Breadalbane-Clova region, where this type of *Vaccinium-Cladonia* heath is centred. In both communities, then, there is the same kind of geological and edaphic contrast, the *Festuca-Galium* sub-community being paired with the *Alchemilla-Carex* sub-community of the *Vaccinium-Deschampsia* heath on more base-rich soils, the *Empetrum-Cladonia* sub-community here occurring with the *Hylocomium-Rhytidadelphus* sub-community of the *Vaccinium-Deschampsia* heath on the more acidic profiles of the granites and quartzites. This latter pairing is the one stressed in Burges's (1951) account of the heaths of the Cairngorm terraces, where the two vegetation types were united as lichen-rich and mossy facies of a single *Empetretum-Vaccinetum*. The former parallel is less well described, but can be seen as continuing the floristic variation included in the early-defined 'sub-alpine grassland' of the Breadalbane area (Smith 1911a), where there is a strong similarity among the sub-montane Nardo-Galion swards and the lichen-rich heaths of the low-alpine zone.

More work is needed to provide some sharper environmental differentiation between these higher-altitude heaths, although it is clear that if the chionophilous character of the *Vaccinium-Cladonia* heath is stressed, then it belongs with the *Vaccinium-Deschampsia* and *Vaccinium-Rubus* heaths in what Nordhagen (1943) termed the Phyllodoco-Vaccinon myrtilli alliance. In this he located a number of vegetation types from the Sylene district of Norway, including *C. arbuscula*-rich heaths with much *V. myrtillus* or *E. nigrum*. These, and the *Empetrum*-lichen heaths described from Middle Sogn by Knaben (1950), bear a strong floristic similarity to the *Vaccinium-Cladonia* heath, more especially to the

Empetrum-Cladonia sub-community, though they generally have a more luxuriant cover of sub-shrubs than their Scottish equivalent. McVean & Ratcliffe's (1962) alternative placing of this kind of vegetation among the lichen-heaths and fell-field communities of

the Loiseleurieto-Arctostaphylion (or Arctostaphyleto-Cetrarion) would not be favoured with the broader definition of the *Vaccinium-Cladonia* heath in this scheme.

Floristic table H19

	a	b	c	19
<i>Vaccinium myrtillus</i>	V (1–8)	V (1–8)	V (1–8)	V (1–8)
<i>Carex bigelowii</i>	V (1–10)	V (1–8)	V (1–6)	V (1–10)
<i>Deschampsia flexuosa</i>	V (1–8)	IV (1–8)	V (1–4)	V (1–8)
<i>Cladonia uncialis</i>	IV (1–6)	V (1–5)	V (1–4)	V (1–6)
<i>Racomitrium lanuginosum</i>	IV (1–6)	V (1–10)	IV (1–10)	IV (1–10)
<i>Cetraria islandica</i>	IV (1–4)	IV (1–6)	V (1–6)	IV (1–6)
<i>Cladonia arbuscula</i>	IV (1–8)	III (1–6)	V (1–10)	IV (1–10)
<i>Vaccinium vitis-idaea</i>	IV (1–4)	II (1–4)	IV (1–4)	IV (1–4)
<i>Festuca ovina/vivipara</i>	V (1–8)	III (1–4)	II (1–4)	III (1–8)
<i>Galium saxatile</i>	IV (1–6)	II (1–6)	II (1–3)	III (1–6)
<i>Polytrichum commune</i>	II (1–6)	I (1–3)	I (1–4)	I (1–6)
<i>Potentilla erecta</i>	II (1–4)	I (1–6)		I (1–6)
<i>Hypnum jutlandicum</i>	II (1–8)	I (1–3)	I (1–3)	I (1–8)
<i>Rhytidiadelphus squarrosus</i>	I (1–4)			I (1–4)
<i>Alchemilla alpina</i>	I (1–4)	III (1–8)	I (1–8)	II (1–8)
<i>Kiaeria starkei</i>	I (4)	II (1–8)	I (1–4)	I (1–4)
<i>Huperzia selago</i>	I (1–3)	II (1–3)	I (1–3)	I (1–3)
<i>Salix herbacea</i>	I (1–4)	II (1–6)	I (1–4)	I (1–6)
<i>Sphaerophorus globosus</i>		II (1–3)	I (1–3)	I (1–3)
<i>Armeria maritima</i>		I (1–4)		I (1–4)
<i>Silene acaulis</i>		I (1–3)		I (1–3)
<i>Antennaria dioica</i>		I (1–3)		I (1–3)
<i>Luzula spicata</i>		I (1–3)		I (1–3)
<i>Empetrum nigrum</i>	II (1–6)	III (1–6)	V (1–10)	III (1–10)
<i>Cladonia rangiferina</i>	II (1–4)	II (1–6)	V (1–6)	III (1–6)
<i>Dicranum scoparium</i>	III (1–6)	II (1–3)	IV (1–4)	III (1–6)
<i>Cladonia gracilis</i>	II (1–3)	II (1–4)	IV (1–4)	III (1–4)
<i>Pleurozium schreberi</i>	II (1–8)	I (1–4)	IV (1–6)	III (1–8)
<i>Ptilidium ciliare</i>	II (1–3)	I (1–3)	III (1–3)	II (1–3)
<i>Ochrolechia frigida</i>	I (1–4)	II (1–6)	III (1–4)	II (1–6)
<i>Calluna vulgaris</i>	I (1–4)	I (1–6)	III (1–9)	II (1–9)
<i>Cetraria nivalis</i>	I (1–4)	I (1–3)	II (1–4)	I (1–4)
<i>Cladonia pyxidata</i>	I (1–3)	I (1–3)	II (1–3)	I (1–3)
<i>Rhytidiadelphus loreus</i>	I (1–4)	I (1–3)	II (1–4)	I (1–4)
<i>Cladonia bellidiflora</i>		I (1–3)	II (1–3)	I (1–3)
<i>Cladonia leucophaea</i>			I (1–6)	I (1–6)
<i>Cornicularia aculeata</i>	III (1–6)	III (1–4)	III (1–4)	III (1–6)
<i>Dicranum fuscescens</i>	III (1–6)	II (1–8)	III (1–4)	III (1–8)
<i>Polytrichum alpinum</i>	II (1–4)	II (1–6)	II (1–4)	II (1–6)

<i>Carex pilulifera</i>	II (1–4)	II (1–4)	II (1–3)	II (1–4)
<i>Nardus stricta</i>	II (1–10)	II (1–4)	I (1–3)	II (1–10)
<i>Polytrichum alpestre</i>	II (1–4)	II (1–4)	I (1–3)	II (1–4)
<i>Cladonia coccifera</i>	II (1–3)	II (1–4)	I (1–3)	II (1–4)
<i>Agrostis canina</i>	II (1–6)	II (1–4)	I (1–4)	II (1–6)
<i>Cladonia impexa</i>	II (1–8)	I (1–3)	II (1–6)	II (1–8)
<i>Alectoria nigricans</i>	I (1–4)	II (1–4)	II (1–3)	II (1–4)
<i>Juncus trifidus</i>	I (1–6)	II (1–6)	II (1–6)	II (1–6)
<i>Thamnochloa vermicularis</i>	I (1–3)	I (1–4)	I (1–3)	I (1–4)
<i>Cladonia crispata</i>	I (1–3)	I (1–4)	I (1–3)	I (1–4)
<i>Polytrichum piliferum</i>	I (1–4)	I (1–4)	I (1–3)	I (1–4)
<i>Diphasium alpinum</i>	I (1–3)	I (1–6)	I (1–3)	I (1–6)
<i>Agrostis capillaris</i>	I (1–3)	I (1–4)	I (1–3)	I (1–4)
<i>Cladonia squamosa</i>	I (1–3)	I (1–4)	I (1–3)	I (1–4)
<i>Loiseleuria procumbens</i>	I (1–3)	I (1–4)	I (1–8)	I (1–8)
<i>Juncus squarrosus</i>	I (1–4)	I (1–3)	I (1–3)	I (1–4)
<i>Polytrichum longisetum</i>	I (1–4)	I (1–4)		I (1–4)
<i>Diplophyllum albicans</i>	I (1–3)	I (1–3)		I (1–3)
<i>Luzula multiflora</i>	I (1–3)		I (1–3)	I (1–3)
<i>Anthoxanthum odoratum</i>	I (1–4)		I (1–3)	I (1–4)
<i>Lophozia ventricosa</i>	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Number of samples	65	49	85	199
Number of species/sample	18 (13–28)	18 (10–26)	18 (9–30)	18 (9–30)
Shrub/herb height (cm)	7 (3–14)	4 (1–12)	7 (1–35)	7 (1–35)
Shrub/herb cover (%)	73 (15–100)	60 (15–100)	87 (35–100)	75 (15–100)
Ground layer height (mm)	26 (10–50)	23 (10–50)	27 (10–60)	26 (10–60)
Ground layer cover (%)	71 (25–97)	77 (40–100)	59 (1–98)	71 (1–100)
Altitude (m)	764 (50–970)	773 (8–990)	806 (6–1159)	784 (6–1159)
Slope (°)	6 (0–28)	6 (0–28)	9 (0–45)	7 (0–45)

a *Festuca ovina*-*Galium saxatile* sub-communityb *Racomitrium lanuginosum* sub-communityc *Empetrum nigrum hermaphroditum*-*Cladonia* spp. sub-community19 *Vaccinium myrtillus*-*Cladonia arbuscula* heath (total)

