# H13
# *Calluna vulgaris-Cladonia arbuscula* heath

**Synonymy**
Mountain *Callunetum* Metcalfe 1950 *p.p.*; Lichen heaths Poore & McVean 1957 *p.p.*; *Cladineto-Callunetum* McVean & Ratcliffe 1962, Prentice & Prentice 1975 *p.p.*; *Calluna* heath, dwarf lichen-rich facies Edgell 1969; Dwarf mountain heaths Gimingham 1972 *p.p.*; *Empetrum hermaphroditum-Racomitrium lanuginosum* community Birse & Robertson 1976; *Empetrum hermaphroditum-Cetraria nivalis* nodum Birks & Huntley 1979; *Alectorio-Callunetum vulgaris* (Birse & Robertson 1976) Birse 1980.

**Constant species**
*Calluna vulgaris*, *Empetrum nigrum hermaphroditum*, *Racomitrium lanuginosum*, *Alectoria nigricans*, *Cetraria islandica*, *Cladonia arbuscula*, *C. rangiferina*, *C. uncialis*, *Cornicularia aculeata*.

**Rare species**
*Arctostaphylos uva-ursi*, *Loiseleuria procumbens*.

**Physiognomy**
The *Calluna vulgaris-Cladonia arbuscula* heath has a dwarfed mat of sub-shrubs with few vascular associates but with a prominent contribution from lichens, which form an often co-dominant patchwork and which can be so abundant in total as to give stands a grey or yellowish hue even from a distance. The sub-shrub mat is commonly less than 5 cm thick, only rarely more than 8 cm, and it can form a fairly extensive and uniform cover, but it is usually discontinuous, sometimes very fragmentary and occasionally disposed in rather particular patterns related to exposure to wind and frost, characteristically severe in the places where this community occurs. *Calluna vulgaris* is the most frequent component and generally the most abundant, growing in prostrate fashion and often with its flattened branches orientated downwind. These may thus come to overlie older branches of other heather plants, all having their young leafy shoots knotted together into a tight carpet (Metcalfe 1950), or be arranged in wave-like bands with intervening strips of bare or lichen-covered ground, active shoot growth confined to the sheltered lee faces of the bushes (Crampton 1911, Watt 1947). Over gently-sloping ground, similar vegetated zones may develop on small solifluction terraces, where frost-heave and the filtering downhill of rain water and snow-melt push mineral particles among the distal branches of the heather, building up a riser in which shoots can renew their growth, while behind there forms a bare tread (Metcalfe 1950). Wind can contribute to the formation of this kind of microtopography, blowing often this time against the direction of sub-shrub growth as it whips up and over brows, stunting and trimming the advancing front of the bushes but scouring out the back of each terrace and accentuating the steps (Metcalfe 1950, Prentice & Prentice 1975). Then, over very exposed knolls and summits, wind and frost-heave can reduce the sub-shrub cover to scattered bushes, their contorted wiry stems hugging the ground and being largely bereft of green shoots.

In some stands, *Calluna* is the only sub-shrub but typically other species are present, sometimes finely intermixed with the heather, but often forming a coarse mosaic of patches within the mat. All these associates are rhizomatous or have procumbent rooting branches, so quite far-spread shoots or clumps are frequently found to be joined by straggling stems beneath the heather and these also enable the plants to colonise any sheltered gaps which develop in the mat, often distant from the original point of rooting. Among these other sub-shrubs, *Empetrum nigrum* is the most important overall with ssp. *hermaphroditum* the more characteristic taxon, ssp. *nigrum* partially replacing it towards the lower altitudinal limit of the community, and its shoots can be found intermingled in the mat or aggregated into clumps up to $\frac{1}{2}$ m or so across, often spreading out in the lee of heather bushes on to bare ground.

Of generally similar habit, though of more restricted occurrence in the community, are the Arctic-Alpine rarities *Arctostaphylos uva-ursi* and *Loiseleuria procum-*

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*bens*. *A. uva-ursi* is at most occasional here and it becomes very scarce where this kind of heath spreads on to the highest mountains but, at lower altitudes, it can be locally abundant, even co-dominant with *Calluna* and *Empetrum*, and is particularly striking where it extends out as a sheltered front to heather waves or on to solifluction treads, where it can rapidly colonise bare ground provided lashing by the wind and erosion of the surface are not too severe, only to be smothered again by the *Calluna* where this can follow (Watt 1947, Metcalfe 1950). However, combinations of *A. uva-ursi*, *Calluna* and *Empetrum nigrum* ssp. *nigrum* with *Erica cinerea*, such as are characteristic of the *Calluna-Arctostaphylos uva-ursi* heath, are rare here. Vegetation best placed in that community has sometimes been included within the *Calluna-Cladonia* heath (as in Metcalfe 1950) and transitional stands can be found in the *Cladonia* sub-community, but by and large the distinctions between the two kinds of heath are fairly clear and they show a broad altitudinal separation within eastern Scotland (see below). Likewise, the almost total absence of the other rare Arctic-Alpine bearberry, *Arctostaphylos alpinus*, from the *Calluna-Cladonia* heath serves as an effective separation from the *Calluna-Arctostaphylos alpinus* heath, a rather similar vegetation type, though essentially one of the western Highlands.

*Loiseleuria procumbens*, however, which in the scheme of McVean & Ratcliffe (1962) was very much a characteristic plant of their *Arctoeto-Callunetum*, is again locally quite frequent and abundant within the *Calluna-Cladonia* heath. Indeed, most of the Cairngorm stations of *Loiseleuria* are in this community, a feature well seen in the tables of Birse (1980, where this kind of heath is termed the *Alectoria-Callunetum*), and in the descriptive account of Metcalfe (1950), where *Loiseleuria* can be seen replacing *A. uva-ursi* in some of the higher-altitude stands of the lichen-rich dwarf heaths. It is of much smaller stature than the bearberry, though able in a similar fashion to extend beneath the heather mat and colonise sheltered bare ground beyond, forming quite large cushions.

The other common sub-shrubs of the *Calluna-Cladonia* heath are *Vaccinium myrtillus* and *V. vitis-idaea* and, in the early descriptions of Poore and McVean (1957), lichen-rich heaths in which bilberry was the dominant ericoid in the absence of *Calluna* were included together with those with abundant heather. In this scheme, following McVean & Ratcliffe (1962), a major separation is made between the *Calluna-Cladonia* heath and a *Vaccinium-Cladonia* heath, in which a dwarfed sub-shrub mat with an abundance of lichens remain general structural features, but where *Calluna* is very sparse and where many stands have a distinctly chionophilous character. Here, by contrast, the two Vaccinia, though very frequent, are almost always subordinate in cover: *V. vitis-idaea* sometimes plays an important role in stabilising loose mineral material on exposed ground but it is not usually abundant and *V. myrtillus* is generally found as separate shoots growing through the heather mat.

Other vascular associates are few in number and likewise characteristically sparse. The most frequent overall are *Deschampsia flexuosa* and *Carex bigelowii*, both generally occurring as scattered tufts or individual shoots, with some other species such as *Scirpus cespitosus*, *Agrostis canina* and *Molinia caerulea* appearing at lower altitudes, and *Juncus trifidus* becoming occasional towards higher levels. *Huperzia selago* is also frequent in higher-altitude stands with *Diphasium alpinum* sometimes recorded too. Dicotyledonous herbs are very scarce with just occasional records for *Potentilla erecta*, *Galium saxatile* and *Antennaria dioica*.

Much more important structurally than any of these are the lichens which form a variegated and sometimes quite species-rich mat among the sub-shrubs, frequently in discrete patches but often of equal or greater total cover and, with some species particularly, probably of considerable competitive power. Especially common and, in somewhat more sheltered situations, becoming very abundant is *Cladonia arbuscula* with, generally less extensive, though locally co-dominant with it, the similar-looking *C. rangiferina*. *C. uncialis* is also constant at low covers and *C. gracilis* and *C. crispata* become frequent in particular kinds of *Calluna-Cladonia* heath, with smaller species such as *C. squamosa* and *C. coccifera* occasional, though not of any structural significance. *C. impexa*, on the other hand, is rather scarce, which provides a further contrast with many stands of the *Calluna-A. uva-ursi* heath.

Also very common throughout the community is *Cetraria islandica*, the brown thalli of which are especially tolerant of the light snow cover that more sheltered stands can carry. The pale yellow *C. nivalis* can be found, too, though this is very much a plant of the opposite extremes, occurring most often on very exposed brows and summits at higher altitudes (Nordhagen 1943, Poore & McVean 1957). *C. glauca* also occurs but it is very occasional and much more typical of lichen-rich stands of the *Calluna-A. uva-ursi* heath.

Then, there is almost always some *Cornicularia aculeata*, whose little cushions of tangled reddish fronds seem particularly abundant where the large *Cladonia* spp. have become moribund (Metcalfe 1950). Finally, among the constants, is the filamentous *Alectoria nigricans*. *A. ochroleuca* can also sometimes be found, typically in similar exposed situations to *Cetraria nivalis*, but it never attains the luxuriance here that it has among similar Scandinavian heaths (Poore & McVean 1957). Birse (1980) recorded the rare Alpine lichen *A. vexillifera* (= *A. sarmentosa* var. *cincinnata*) in this vegetation.

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Other lichens occasionally encountered are the densely-cushioned *Sphaerophorus globosus* and, less commonly, *S. fragilis*, *Thamnolia vermicularis* with its distinctive creeping whitish worm-like thalli and the lumpy grey encrustations of *Ochrolechia frigida*.

Among this mat, bryophytes are generally very few and rarely of any abundance. *Racomitrium lanuginosum* is the commonest and it can form locally conspicuous patches, particularly among the older bare branches of the wind-flattened bushes. But it never has the dominant role among the ground carpet that is typical of the *Calluna-Racomitrium* heath. Occasional associates include *Hypnum jutlandicum*, *Dicranum scoparium* and *Ptilidium ciliare*, with scarce records for *Pleurozium schreberi*, *Dicranum fuscescens*, *Diplophyllum albicans* and *Pohlia nutans*.

**Sub-communities**

***Cladonia arbuscula-Cladonia rangiferina* sub-community:** Mountain *Callunetum*, *Calluna-Arctostaphylos* facies Metcalfe 1950; *Cladineto-Callunetum sylvaticosum* McVean & Ratcliffe 1962, Prentice & Prentice 1975; *Calluna* heath, dwarf lichen-rich facies Edgell 1969; *Alectoria-Callunetum*, *Agrostis canina* ssp. *montana* subassociation Birse 1980. In this sub-community, larger *Cladonia* spp., particularly *C. arbuscula*, but also on occasion *C. rangiferina*, are especially abundant, often exceeding the sub-shrubs in total cover. *C. impexa* can sometimes be found among the lichen carpet, too, though *C. gracilis* and *C. crispata* are scarce. *Calluna* is usually the most abundant sub-shrub, but *Empetrum nigrum* occurs very commonly, with ssp. *nigrum* often rivalling ssp. *hermaphroditum* in frequency, and each can have quite high cover. *Arctostaphylos uva-ursi* is found in some stands and it can be locally prominent. *Vaccinia* are only occasional and present as sparse shoots but there is sometimes a little *Erica cinerea* and rarely some *E. tetralix*.

Other low-frequency preferentials include *Scirpus cespitosus*, *Molinia*, *Nardus* and *Agrostis canina* (mostly ssp. *montana*), though all these, together with the occasional *Deschampsia flexuosa*, are usually found just as scattered tufts. *Potentilla erecta* and *Huperzia selago* can sometimes be seen but *Carex bigelowii* is rare.

***Empetrum nigrum* ssp. *hermaphroditum-Cetraria nivalis* sub-community:** *Calluna*-lichen heath Poore & McVean 1957; *Cladineto-Callunetum typicum* McVean & Ratcliffe 1962; *Empetrum hermaphroditum-Cetraria nivalis* nodum Huntley & Birks 1979; *Alectorio-Callunetum*, Typical subassociation Birse 1980 *p.p.* Although lichens as a group remain very abundant here, the balance of dominance generally lies with *Calluna* or occasionally *E. nigrum* ssp. *hermaphroditum*, which is very common and far outweighs ssp. *nigrum* in frequency. Both *V. myrtillus* and *V. vitis-idaea* occur more often here than in the last sub-community, but they usually remain of low cover. Again, some stands have a local abundance of *A. uva-ursi* but here, too, *Loiseleuria* can occasionally be found, though generally in small amounts.

In the lichen mat, *Cladonia arbuscula* is still the most abundant species but, along with *C. rangiferina* and *C. uncialis*, it is frequently joined by *C. gracilis* and more occasionally by *C. crispata* and *C. bellidiflora*. More striking is the common occurrence of *Cetraria nivalis*, sometimes of moderate cover, with scattered records for *Alectoria ochroleuca*.

Mosses make a generally very minor contribution to the ground cover and vascular associates are also usually present as scattered individuals. But *Deschampsia flexuosa* and *Carex bigelowii* are both very common, and preferential at low frequencies are *Diphasium alpinum* and *Juncus trifidus*.

***Cladonia crispata-Loiseleuria procumbens* sub-community:** Mountain *Callunetum*, *Calluna-Loiseleuria* facies Metcalfe 1950; *Alectorio-Callunetum*, Typical subassociation Birse 1980 *p.p. Calluna* is again the usual dominant in this sub-community but one or both of the subspecies of *Empetrum nigrum* are commonly present and they can be quite abundant. There is also often some *Loiseleuria*, though *A. uva-ursi* is very rare. The Vaccinia reach the peak of their frequency, but are still usually present just as sparse shoots.

Among the sub-shrub mat, which is often flattened against the ground even more markedly than usual, all the characteristic lichens of the community remain frequent, usually making up a carpet in which no single species is dominant. But there are some clear preferentials to this kind of heath, with *Cladonia crispata* being particularly common, *C. furcata*, *C. coccifera* and *C. squamosa* more occasional, *Ochrolechia frigida* and *Thamnolia vermicularis* frequent. Scattered shoots of *Carex bigelowii*, *Huperzia selago* and *Deschampsia flexuosa* often make up the sparse herbaceous element.

**Habitat**

The *Calluna-Cladonia* heath is the characteristic sub-shrub vegetation of base-poor soils over exposed ridges and summits of mountains in those parts of Britain with a cold continental climate. Burning and grazing may have curtailed its range in suitable localities in our more southerly uplands but, through its heartland in the eastern Highlands of Scotland, the vegetation seems little affected by treatments and the community can be considered a climax.

It certainly experiences some of the harshest weather conditions of any throughout the country, being typical

of what Poore & McVean (1957) called the low-alpine zone, generally between 600 and 900 m, in areas with a mean annual maximum temperature of less than 23 °C (Conolly & Dahl 1970) and where the February minimum falls well below freezing (*Climatological Atlas* 1952). It is thus especially characteristic of the east-central Highlands, with extensions westwards into the central Grampians and up the eastern fringes of the north-west Highlands, and far-flung fragmentary stands in certain parts of the Southern Uplands, the Lake District and north Wales (McVean & Ratcliffe 1962, Edgell 1969), where conditions are locally suitable. Through this region, the kinds of soils favoured by the community, rankers and often shallow podzols, frequently humic above and with a superficial pH between 4 and 5, are very widespread over shedding slopes cut into pervious acidic bedrocks and superficials. In the centre of its range, the *Calluna-Cladonia* heath is especially widespread on such soils over the rounded summits and spurs of the Cairngorms and Lochnagar and the higher slopes above the Spey and the Don, where massive granite intrusions form the basis of many of the mountains, with drift mantling the lower slopes. Other siliceous Dalradian rocks are locally important as parent materials in the Grampians with Moine schists underlying stands on Monadhliath, around Drumochter and on Ben Wyvis and other Moinian metasediments on Beinn Dearg.

In such sites, the *Calluna-Cladonia* heath thus provides an important locus for calcifuges adapted to a climate approaching the Arctic-Alpine in character, for example, *Empetrum nigrum* ssp. *hermaphroditum*, *Vaccinium vitis-idaea*, *Loiseleuria*, *Carex bigelowii* and, to a lesser extent, *Arctostaphylos uva-ursi*. Vascular plants typical of heaths developed in more equable climatic conditions, on the other hand, such as *Erica cinerea* and *Molinia*, tend to be confined to sites with some measure of local shelter or which are at lower altitudes than usual. Such species are best represented here in the *Cladonia* sub-community, together with ssp. *nigrum* as the predominant crowberry taxon, and this vegetation takes the *Calluna-Cladonia* heath to its lowest levels, notably on Orkney where, at well below 600 m, this vegetation is clearly transitional to lichen-rich oceanic *Calluna-Erica* heath (Prentice & Prentice 1975). *Scirpus cespitosus*, though it is a plant of some high-altitude mires, follows the same trend as *E. cinerea* here (Metcalfe 1950, Prentice & Prentice 1975).

Towards higher ground, and perhaps on soils which are more peaty above, offering a congenial surface for its distinctive suite of lichens, the *Cladonia-Ochrolechia* sub-community is characteristic, occurring on some of the bleaker Cairngorm spurs, where *Loiseleuria* is sometimes a prominent associate, but also common over the lower summits through the northern Grampians. Then, largely confined to the highest situations, with a mean altitude over 150 m more than that of the *Cladonia* sub-community and a mean annual maximum temperature of less than 21 °C (Conolly & Dahl 1970), there is the *Empetrum-Cetraria* sub-community. In the Cairngorms, this kind of vegetation takes heather-dominance to its upper limit, close on 1000 m and though, beyond this zone, dwarf-shrub heaths can run on, it is *E. nigrum* ssp. *hermaphroditum* and *V. myrtillus* that are the predominant woody plants. *V. myrtillus* is always subordinate to *Calluna* here, though the balance between these two species among dwarf-shrub heaths at lower altitudes is also strongly dependent on snow cover.

For the composition and physiognomy of this vegetation, then, it is not just the general character of the climate that is important. Through the low-alpine zone of our more continental mountains, this is inhospitable enough but harsh winds and frosts lend a particular severity to situations that are more exposed. Above all, the *Calluna-Cladonia* heath is a vegetation type of unsheltered slopes in these regions, usually fairly gentle and rounded, on summits and ridges where there is an almost constant blast of strong winds. And this means, too, that the ground is usually blown clear of any substantial accumulations of snow. In fact, though precipitation across this part of Britain is not very high, often below 1600 mm $yr^{-1}$ (*Climatological Atlas* 1952), in the winter months much of this falls as snow, such that there are generally through this region 60–100 or more days annually with snow lying. But it does not settle appreciably on the more wind-lashed slopes, which not only effectively reduces the amount of precipitation locally received by this community but which also exposes the vegetation, and the underlying soils, to the effects of frequent and severe frosts and their subsequent thaw.

Most of the structural features of this kind of heath are attributable to interactions between wind and frost and the different growth responses of the various sub-shrubs to them. There is the generally dwarfed character of the mat and the striking wind-waved physiognomy that sometimes develops, very noticeable in certain of the Cairngorm stands, with the different woody species able to exploit the modicum of shelter provided by the repeated belts of flattened vegetation. Such patterns may show some measure of cyclical alternation of dominance among the sub-shrubs (Watt 1947) but, with freeze-thaw often adding to the erosive effects of the wind on the soil mantle, it is doubtful how far such changes can go undisturbed and the constant check which these processes exert on the vegetation is sufficient to maintain it as a climax and, in extremes, to reduce it to a very sparse cover of plants at their limits of survival.

Provided the ground among the bushes remains

stable, with little or no frost-heaving or wind-blow, the exposure of bare patches of soil and more open areas of decaying sub-shrubs offers an opportunity in the cold continental climate for the local dominance by lichens so characteristic of this vegetation. In fact, in the opinion of Poore & McVean (1957) the maintenance of this typical abundance of lichens is a quite finely balanced matter in the relatively oceanic climate of the British Isles as compared with parts of Scandinavia. The provision of some shelter favours more luxuriant growth of the lichen mat and the preferential prominence of species such as *Cladonia arbuscula*, *C. rangiferina* and *Cetraria islandica* in the *Cladonia* sub-community is frequently related to a locally less exposed physiography than is usual, as where slight hollows perhaps accumulate a little snow, that thus protects the cover from the worst effects of frosts and the biting winds of winter. In such more humid situations, though, there is often a tendency for *Racomitrium lanuginosum* to expand its cover at the expense of the lichens and convert the vegetation to the kind of moss-heath so familiar in the west. At the opposite extreme, in the *Empetrum-Cetraria* sub-community, we can see the best representation of the chionophobous lichens *Cetraria nivalis* and, less commonly, *Alectoria ochroleuca*, over sites which are locally very bleak. But here *Juncus trifidus* begins to exert itself and it is this species which assumes dominance over lichens as altitude and local exposure combine to produce some of the most arctic conditions over the very high Cairngorm summits.

Outside the Scottish Highlands, this kind of heath is rare: vegetation approaching it can be seen on parts of Dollar Law and White Coomb in the Southern Uplands and fragments occur on Skiddaw in Cumbria (McVean & Ratcliffe 1962, Ratcliffe 1977); and some of the more lichen-rich heaths of Cader Idris (Edgell 1969) could perhaps be included in the community. However, even in sites where the topoclimate provides suitable conditions for the local development of this type of vegetation, the virtually ubiquitous treatments of burning and grazing may well have destroyed it. Through most of its present range, however, these seem to be of little importance to the appearance and composition of the community. Muirburns sometimes spread up into the zone in which it is found from the *Calluna-Vaccinium* and *Calluna-A. uva-ursi* heaths but damage does not seem to be widespread. Grazing by sheep and deer is probably high, although ptarmigan, very characteristic and locally numerous birds of these high slopes (Watson 1964, 1966) can take large amounts of heather when it is available, with *E. nigrum* and *V. myrtillus* also figuring in their diet (Gimingham 1972).

**Zonation and succession**

The *Calluna-Cladonia* heath is typically found with other sub-shrub communities, montane grass- and moss-heaths and snow-bed vegetation in zonations and mosaics which reflect altitudinal and local topographically-determined variations in climate, especially the general temperature trend in moving on to higher ground and exposure. Geological heterogeneity can introduce edaphically-related complications into these patterns and, towards lower altitudes, treatments have often modified the transitions. With the geographical shift to the west, the elements of the vegetation sequence are increasingly replaced by their oceanic counterparts and, in between the climatic extremes, complex intermediate patterns of communities can be seen.

The essential features of the altitudinal zonation characteristic of base-poor soils in our more continental mountains are best seen in the Cairngorms, where there is a strong measure of geological uniformity and a massive scale to the scenery, with the broad granite summits and watersheds and relatively gentle transitions in many areas to the lower slopes (Watt & Jones 1948, Poore & McVean 1957). Moreover, the prevailing infertility of the soils has meant that sheep-pasturing has figured little in the history of land-use there, such that sub-shrub heaths remain extensive throughout their climatic zones (Ratcliffe 1977). Not that there has been no modification to the natural vegetation pattern however: at lower altitudes, the *Pinus-Hylocomium* woodland is probably the climax community and, although stretches of this native pine forest remain, much of the ground below the *Calluna-Cladonia* heath now carries *Calluna-Vaccinium* heath which spread with clearance and which is now often maintained by burning for grouse-rearing. Many of the soils at these levels, though, are derived from superficials, so there is quite frequently some modest variation in soil fertility, with stands of the *Calluna-A. uva-ursi* heath marking out less oligotrophic brown earths, and in drainage impedence, the *Ericetum tetralicis* occupying strongly-gleyed podzols.

In some places, too, the *Juniperus-Oxalis* scrub occurs among mosaics of these heaths, essentially now behaving as a perpetually-renewed seral vegetation. Only on Creag Fhiaclach, at around 640 m on a north-western spur of the Cairngorm range, does this community form a convincing climatically-controlled fringe above the forest zone, grading up to the low-alpine belt, where the *Calluna-Cladonia* heath is typically found (Poore & McVean 1957). Generally, then, the upward transition to the *Calluna-Cladonia* heath is from one or other of the sub-shrub communities mentioned above, such that a predominance of heather is maintained, albeit in a dwarfed form at higher altitudes, right up to about 1000 m in these mountains. The shift from one vegetation type to the other is often gradual and the actual altitude at which the change decisively occurs varies with the degree of local exposure because of the strong dependence, in our prevailingly oceanic climate, on topography to maintain the required element of harshness of

climate characteristic of the whole low-alpine zone in more continental parts of northern Europe (Poore & McVean 1957). The stunting and wind-flattening of the sub-shrub mat and the abundance of lichens which are the chief general features of the transition thus appear at lower altitudes and more sharply where there is an early and abrupt move from sheltered slopes on to more open, wind-lashed ground. But there can be a strong continuity in the qualitative composition of the canopy even then and stands of the *Calluna-Vaccinium* and *Calluna-A. uva-ursi* heaths which are not in the dense pioneer or building phase of regeneration from burning sometimes develop lichen floras which approach those of the *Calluna-Cladonia* heath in variety, though not generally in abundance.

To such sub-montane heaths, the *Cladonia* sub-community can be seen as transitional and this characteristically occupies the lower and more sheltered situations that develop a cover of *Calluna-Cladonia* heath, with the *Empetrum-Cetraria* or *Cladonia-Ochrolechia* sub-community ranged above it on the more exposed ridges and summits. Where the zonation continues upwards, on to ground that is too inhospitable for the survival of *Calluna* and where the winds are so strong that even lichens cannot get a hold in any abundance, the *Calluna-Cladonia* heath typically peters out into a zone of the *Juncus-Racomitrium* heath. Again, there can be a measure of floristic continuity among the vegetation types: *J. trifidus* itself makes an occasional appearance in the *Calluna-Cladonia* heath and a number of species remain frequent over the higher ground, such as *Carex bigelowii*, *Deschampsia flexuosa*, *Vaccinium myrtillus* and, with much reduced covers, various of the lichens. But the overall character of the vegetation is very different and, on the extensive tracts of ground above 1000 m through the Cairngorms, the shift to this rush-dominated community, developed as an open network over the loose erosion surfaces of the high plateaus, is very striking (Poore & McVean 1957, Ingram 1958, McVean & Ratcliffe 1962).

The major complications to the higher zones of this kind of transition are related to a decrease in exposure (Poore & McVean 1957). In the low-alpine belt, the sub-communities of the *Calluna-Cladonia* heath themselves can be arranged, not in altitudinal bands, but in patches disposed according to the local variations in the amount of shelter provided by topography. The *Empetrum-Cetraria* and *Cladonia-Ochrolechia* sub-communities, for example, can be found at relatively low altitudes where the exposure is locally extreme, while the *Cladonia* sub-community can attain relatively high levels in hollows and on lee slopes. In this kind of situation, the latter type of *Calluna-Cladonia* heath is essentially transitional to the *Vaccinium-Cladonia* heath, which usually seems to experience longer snow-lie and which in some stands has a marked chionophilous character. Sometimes, the two sorts of lichen heath form mosaics over gently-undulating slopes, where the hollows catch a little snow and the convexities are largely blown clear, transitions from one community to the other being sometimes a matter of a shift in dominance from heather to bilberry. In other cases, the *Vaccinium-Cladonia* heath marks a clear intermediate zone between the *Calluna-Cladonia* heath and a snow-bed proper with *Nardus-Carex* grass-heath. At lower altitudes, where a shady aspect becomes progressively necessary to maintain long snow-lie, similar zonations to these can be found but with the *Calluna-Cladonia* heath giving way over the wind-blasted lip of the snow-bed, not to the *Vaccinium-Cladonia* heath, but to the *Vaccinium-Rubus* heath. At higher altitudes where, with some shelter, snow cover settles more uniformly, the *Vaccinium-Cladonia* heath may largely replace the *Calluna-Cladonia* heath, maintaining sub-shrub dominance for a further 100 m or so above the heather limit.

Quite often, however, the major variation in zonation at the upper limit of the *Calluna-Cladonia* zone is attributable not so much to increased snow-lie as to the greater constancy of humidity across the cloudy summits away from extreme exposure. Then, there is a progressive tendency for the *Calluna-Cladonia* heath to give way above, not to the *Juncus-Racomitrium* heath, but to the *Carex-Racomitrium* heath, in which dominance typically lies with *R. lanuginosum*. And, in fact, this is essentially the shift from continental to oceanic conditions for, though no other mountain massif in Britain has so much of the *J. trifidus* fell-field vegetation as the Cairngorms, even a slight shift away from the more easterly summits reinforces what is there a local trend. Above Glen Feshie, for example, where there are some particularly fine stands of *Calluna-Cladonia* heath on the south-west facing spurs, the *Carex-Racomitrium* heath predominates above and with the shift to the Moine schist hills around Drumochter and Ben Alder, a little to the west, the *Juncus-Racomitrium* heath can be distinctly patchy above the *Calluna-Cladonia* heath. On Ben Wyvis, a massive bulk of Moine pelitic gneiss some 90 km to the north across the Great Glen, are the biggest tracts of the *Carex-Racomitrium* heath that we have in Britain, disposed over the broad summits and spurs and having some intricate marginal mosaics with the *Calluna-Cladonia* heath, fragments of each community being included within a ground of the other in the boundary zone (McVean & Ratcliffe 1962). Then, moving just 25 km to the west, to Beinn Dearg in Ross-shire, there is a decisive shift to a much more oceanic pattern. This massif is unusual among the mountains of the north-west Highlands in that its Moine granulites and schists have been worn down to the kind of broad domed structure so typical of the Cairngorms but here, on the more exposed spurs and summits, *R. lanuginosum* has a strong edge over the lichens even among the dwarf-

shrub heaths. Below the *Carex-Racomitrium* zone, then, the *Calluna-Cladonia* heath is still to be found but it is increasingly replaced through the low-alpine zone in this part of Scotland by the *Calluna-Racomitrium* heath in which it is mosses that are co-dominant among the dwarfed sub-shrub mat. And, with the move downslope into the forest zone, the *Calluna-Vaccinium* heath typical of the eastern part of the country is often replaced by the *Calluna-Vaccinium-Sphagnum* heath or, closer to the coastal fringe, the *Calluna-Erica* heath. As in the more continental sequence, bearberry heath can figure where the soils have moder humus rather than mor, but here it is *Arctostaphylos alpinus* rather than *A. uva-ursi* which is characteristic of the higher-altitude complexes of dwarfed sub-shrub heaths. On Beinn Dearg in Ross and Ben Wyvis, the *Calluna-Cladonia* and *Calluna-Racomitrium* heaths can both be found in patchworks with the *Calluna-A. alpinus* heath, their distributions governed by what are probably quite subtle differences in microclimate and soils.

In the hills fringing the heart of its range, through Speyside and over some of the central Grampians, the characteristic zonations have been more drastically affected below with the sub-montane heath zone often largely occupied by grasslands derived by long-continued pasturing, and the impact of this sometimes penetrates on to the higher exposed ground where the *Calluna-Cladonia* heath is typical. Burns, too, can stray upwards though the diminutive canopy of the community does not readily take fire. For the most part, though, such treatments have little effect and this kind of heath can be considered a climax where progression to scrub and woodland is prevented by locally-severe exposure.

**Distribution**

The community is most widespread and abundant through the east-central Highlands of Scotland, thinning out westwards into the central Grampians and north-west Highlands where it is progressively replaced by its oceanic counterpart, the *Calluna-Racomitrium* heath, and having but very few fragmentary localities further south into northern England and Wales. The *Cladonia* sub-community extends the distribution to lower altitudes, the *Empetrum-Cetraria* to the higher.

**Affinities**

Although Smith (1911*a*, *b*) and Crampton (1911) both hinted at the distinctive character of high-altitude heather vegetation in Scotland, it was not until the account of Metcalfe (1950) that the structure and floristics of the *Calluna-Cladonia* heath received detailed attention, continuing upwards the Cairngorm zonation first described by Watt & Jones (1948) and then subsequently modified in the light of further investigations over higher ground still (Burges 1951, Ingram 1958) by Poore & McVean (1957). The diagnoses of both Metcalfe's (1950) Mountain *Callunetum* and, less so, Poore & McVean's (1957) lichen heaths were broader than the *Calluna-Cladonia* heath as defined here, which is essentially an expanded version of McVean & Ratcliffe's (1962) *Cladineto-Callunetum*, distinguished from both the *Calluna-Vaccinium* heaths that extend on to higher ground and from the *Vaccinium-Cladonia* heath, by the balance between the different sub-shrubs and in the representation of lichens. The recent work of Birse (1980; see also Birse & Robertson 1976) has been especially helpful in extending our knowledge of what is here called the *Cladonia-Ochrolechia* sub-community, though Birse's (1980) *Alectoria-Callunetum* takes in a little of what would in this scheme be separated off into the *Calluna-A. alpinus* heath. The distinctions between these various dwarfed lichen-rich heaths of the low-alpine zone are, in fact, sometimes difficult to discern and have to be based on the proportions of the different components in critical cases. But, as a group, they are worthy of separation from the sub-montane and largely anthropogenic heaths of the Calluno-Ulicetalia and represent the British equivalent of the Scandinavian communities placed in the Loisleurieto-Arctostaphylion (Nordhagen 1928, Kalliola 1939) or Arctostaphyleto-Cetrarion (Dahl 1956), alliances of chionophobous dwarf-shrub heaths and grass-heaths usually gathered into the Caricetea curvulae (Braun-Blanquet 1948), though separated off into a Loiseleurio-Vaccinetea by some (see, for example, Birse 1980, 1984). *Cladonia alpestris*, a species perhaps extinct in Britain (Dahl 1968), is very characteristic of the more Continental lichen-rich heaths of this kind in Norway (Dahl 1956), while in the Sylene district, a more oceanic part of Scandinavia, Nordhagen (1928) reported a *Cladonia silvatica-rangiferina*-reiche *Calluna* Assoziation similar to some stands of the *Calluna-Cladonia* heath (McVean & Ratcliffe 1962).

## Floristic table H13

| | a | b | c | 13 |
|---|---|---|---|---|
| *Calluna vulgaris* | V (4–10) | V (1–10) | V (6–10) | V (1–10) |
| *Cladonia arbuscula* | V (1–4) | V (1–4) | V (1–8) | V (1–8) |
| *Cetraria islandica* | V (1–4) | V (1–4) | V (1–4) | V (1–4) |
| *Cladonia uncialis* | V (1–4) | V (1–4) | V (1–4) | V (1–4) |
| *Cornicularia aculeata* | V (1–4) | V (1–6) | IV (1–6) | V (1–6) |
| *Racomitrium lanuginosum* | V (1–4) | IV (1–4) | V (1–4) | V (1–4) |
| *Cladonia rangiferina* | V (1–4) | V (1–4) | IV (1–4) | V (1–4) |
| *Empetrum nigrum hermaphroditum* | III (1–8) | V (1–6) | IV (1–6) | IV (1–8) |
| *Alectoria nigricans* | IV (1–4) | III (1–6) | IV (1–6) | IV (1–6) |
| *Scirpus cespitosus* | II (1–3) | I (1–3) | | I (1–3) |
| *Cladonia impexa* | II (1–4) | I (1–4) | | I (1–4) |
| *Agrostis canina* | II (1–3) | I (1–4) | | I (1–4) |
| *Potentilla erecta* | II (1–2) | | | I (1–2) |
| *Erica cinerea* | II (1–3) | | | I (1–3) |
| *Molinia caerulea* | II (1–3) | | | I (1–3) |
| *Nardus stricta* | I (1–4) | | | I (1–4) |
| *Carex panicea* | I (1–4) | | | I (1–4) |
| *Festuca ovina* | I (1–3) | | | I (1–3) |
| *Campylopus paradoxus* | I (1–3) | | | I (1–3) |
| *Erica tetralix* | I (1–3) | | | I (1–3) |
| *Deschampsia flexuosa* | II (1–3) | IV (1–4) | II (1–3) | III (1–4) |
| *Cetraria nivalis* | I (1–4) | IV (1–4) | II (1–4) | II (1–4) |
| *Cladonia gracilis* | I (1–3) | III (1–3) | | II (1–3) |
| *Juncus trifidus* | | II (1–4) | I (1–3) | I (1–4) |
| *Diphasium alpinum* | I (1–3) | II (1–3) | | I (1–3) |
| *Cladonia bellidiflora* | I (1–3) | II (1–3) | | I (1–3) |
| *Alchemilla alpina* | | I (1–6) | | I (1–6) |
| *Vaccinium myrtillus* | II (1–4) | III (1–4) | IV (1–4) | III (1–4) |
| *Cladonia crispata* | I (1–3) | II (1–4) | V (1–4) | II (1–4) |
| *Ochrolechia frigida* | II (1–4) | II (1–4) | IV (1–6) | II (1–6) |
| *Loiseleuria procumbens* | I (1) | II (1–6) | III (1–4) | II (1–6) |
| *Cladonia coccifera* | I (1–3) | I (1–3) | III (1–3) | I (1–3) |
| *Thamnolia vermicularis* | I (1–3) | | III (1–3) | I (1–3) |
| *Cladonia squamosa* | I (1–3) | I (1–3) | II (1–4) | I (1–4) |
| *Cladonia furcata* | | | II (1–3) | I (1–3) |
| *Vaccinium vitis-idaea* | II (1–4) | III (1–4) | III (1–4) | III (1–4) |
| *Empetrum nigrum nigrum* | III (1–6) | I (3) | III (1–6) | III (1–6) |
| *Carex bigelowii* | I (1) | III (1–4) | III (1–3) | III (1–4) |
| *Huperzia selago* | II (1–3) | II (1–3) | III (1–4) | II (1–4) |
| *Hypnum jutlandicum* | II (1–4) | II (1–3) | II (1–4) | II (1–4) |
| *Dicranum scoparium* | II (1–3) | II (1–3) | II (1–3) | II (1–3) |
| *Arctostaphylos uva-ursi* | II (1–6) | II (1–6) | I (4) | II (1–6) |
| *Sphaerophorus globosus* | II (1–3) | II (1–4) | I (1–3) | II (1–4) |
| *Cetraria glauca* | II (1–4) | I (1–4) | II (1–4) | II (1–4) |

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**Floristic table H13** *(cont.)*

| | a | b | c | 13 |
|---|---|---|---|---|
| *Ptilidium ciliare* | I (1–3) | II (1–3) | II (1–3) | II (1–3) |
| *Alectoria ochroleuca* | I (1–3) | I (1–3) | I (1) | I (1–3) |
| *Pleurozium schreberi* | I (1–6) | I (1–4) | I (1) | I (1–6) |
| *Dicranum fuscescens* | I (1–3) | I (1–3) | I (1–3) | I (1–3) |
| *Diplophyllum albicans* | I (1) | I (1–3) | I (1) | I (1–3) |
| *Pohlia nutans* | I (1) | I (1) | I (1–3) | I (1–3) |
| *Hylocomium splendens* | I (4) | I (1–3) | | I (1–4) |
| *Rhytidiadelphus loreus* | I (1) | I (1–3) | | I (1–3) |
| *Galium saxatile* | I (1–3) | I (1–3) | | I (1–3) |
| *Antennaria dioica* | I (1) | I (1) | | I (1) |
| *Sphaerophorus fragilis* | I (1–3) | | I (1–3) | I (1–3) |
| *Polytrichum commune* | I (1–3) | | I (1–4) | I (1–4) |
| *Hypogymnia physodes* | I (1–3) | | I (1–4) | I (1–4) |
| *Carex pilulifera* | I (1–3) | | I (1–3) | I (1–3) |
| *Alectoria sarmentosa* | | I (1) | I (1–3) | I (1–3) |
| *Nardia scalaris* | | I (1–3) | I (1) | I (1–3) |
| *Polytrichum alpinum* | | I (1–3) | I (1) | I (1–3) |
| *Salix herbacea* | | I (1–3) | I (1–4) | I (1–4) |
| Number of samples | 35 | 52 | 36 | 123 |
| Number of species/sample | 17 (9–30) | 18 (10–28) | 17 (12–22) | 17 (9–30) |
| Vegetation height (cm) | 5 (2–12) | 5 (2–15) | 3 (2–12) | 4 (2–15) |
| Shrub/herb layer cover (%) | 73 (20–90) | 69 (50–90) | 71 (60–90) | 70 (20–90) |
| Ground layer cover (%) | 64 (40–85) | 71 (50–98) | 57 (20–85) | 63 (20–98) |
| Altitude (m) | 544 (105–885) | 805 (640–950) | 737 (625–922) | 683 (105–950) |
| Slope (°) | 5 (0–18) | 9 (0–25) | 5 (0–25) | 7 (0–25) |

a *Cladonia arbuscula-Cladonia rangiferina* sub-community
b *Empetrum nigrum hermaphroditum-Cetraria nivalis* sub-community
c *Cladonia crispata-Loiseleuria procumbens* sub-community
13 *Calluna vulgaris-Cladonia arbuscula* heath (total)

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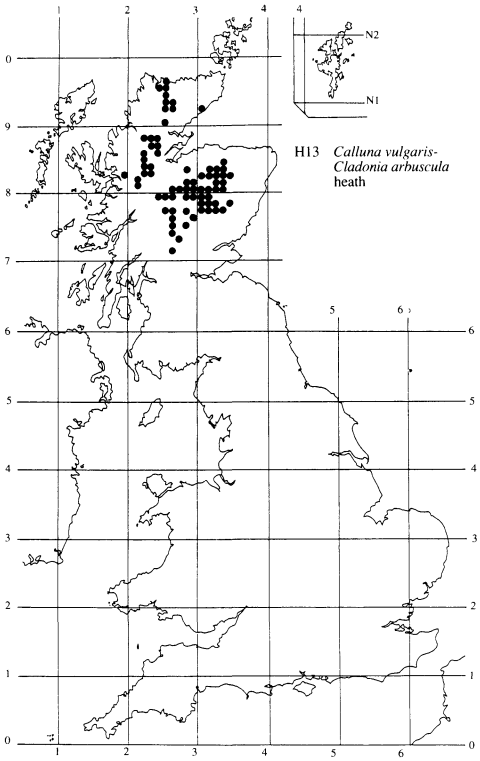


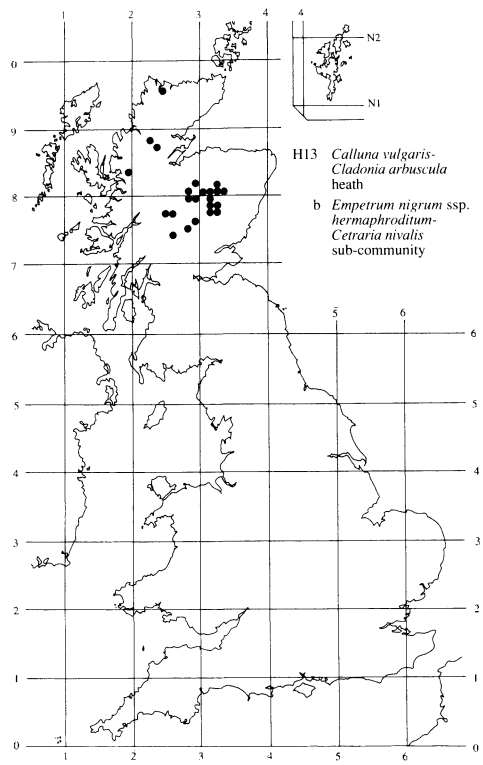


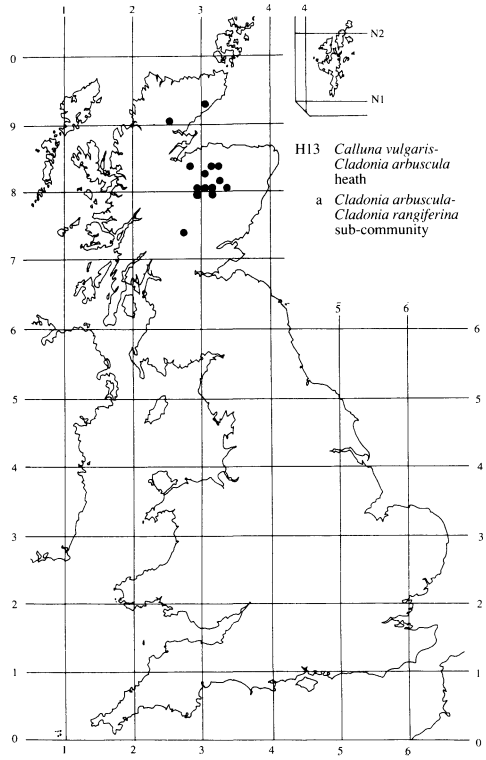


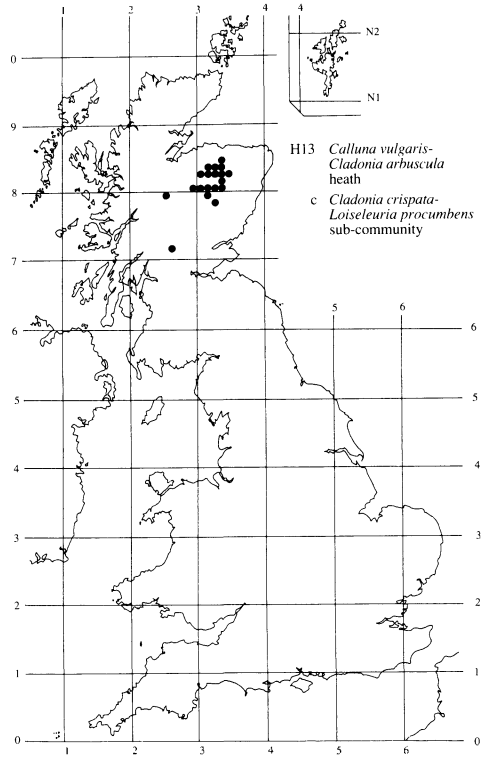


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