H16
Calluna vulgaris-Arctostaphylos uva-ursi heath

Synonymy
Scottish *Calluna* heath Smith 1911*b p.p.*; *Calluna-Arctostaphylos* heath Muir & Fraser 1940, Gimingham 1964*a*, 1972; *Arctostaphyleto-Callunetum* McVean & Ratcliffe 1962, Ward 1971; *Vaccinio-Ericetum cinereae* (Birse & Robertson 1976) Birse 1980 *p.p.*; *Arctostaphylos* heath Urquhart 1986.

Constant species
Arctostaphylos uva-ursi, *Calluna vulgaris*, *Deschampsia flexuosa*, *Erica cinerea*, *Vaccinium vitis-idaea*, *Dicranum scoparium*, *Hylocomium splendens*, *Hypnum jutlandicum*, *Pleurozium schreberi*, *Cladonia impexa*.

Rare species
Arctostaphylos uva-ursi, *Lycopodium annotinum*, *Pyrola media*.

Physiognomy
Arctostaphylos uva-ursi can be found in a variety of heath types as an occasional, locally prominent associate but, in the heart of its range, it is most often found in this community which, though it has much in common with other sub-shrub vegetation of the region, frequently has a distinct boreal character. The *Calluna vulgaris-A. uva-ursi* heath, like its closest relative, the *Calluna-Vaccinium* heath, can have a variegated woody cover. *Calluna* is always present and overall it is the most frequent dominant, usually abundant and often overwhelmingly so, in a canopy that usually attains 2–4 dm in height and which can have a substantial total cover. Where, as is often the case, the vegetation is recovering from fairly recent burning, the heather can grow in dense building-phase stands from which many associates are all but excluded, and in such cases the diagnosis of the community is clearly very difficult. Frequently, however, other sub-shrubs make at least a minor contribution to the canopy and are able in various ways to exploit temporal and spatial gaps in the *Calluna* cover, attaining some measure of local abundance early in the heather-regeneration cycle and sometimes again where the bushes have been allowed to proceed to the degenerate phase. But more precise studies of the effects of fire have been made here than on any other kind of heath (see below) and they show that the patterns of recovery are very varied and often quite persistent (e.g. Hobbs & Gimingham 1984*b*) so, within the general definition, even the proportions of the most frequent contributors to the vegetation can be diverse.

A. uva-ursi, though, is likewise a constant of the community and it can become modestly abundant in gaps within the heather cover but, even there, it typically has a prostrate habit, the branches of the creeping stems forming low mats, often only 5 cm or so thick. Having foliage that is not very shade-tolerant, these patches are readily overwhelmed by the expanding heather cover, but the long monopodial shoots can extend far among the litter and then branch profusely where conditions of better illumination are met (Gimingham 1972). The low growth of the stems and the fact that they are often part-buried among the litter also afford the plant some protection against the effects of burning, and regeneration readily occurs from clusters of dormant buds on older parts of the stems: these may actually increase in numbers with repeated damage although, as in other ericoids, there is a general decline in the vigour of vegetative regeneration in *A. uva-ursi* with age (Mallik & Gimingham 1985).

Erica cinerea is also very common in the community, but it is generally of low cover: it can regrow from sprouting stools or from seed after burning but it rarely gains any ascendancy over *Calluna* in the rather harsh climatic conditions here, even where this vegetation extends on to locally warmer south-facing slopes. In many stands, too, there is some *Vaccinium vitis-idaea* and *V. myrtillus*. These are both rhizomatous so, even after quite severe fires, they have strong regenerative potential right from the start and one or both of them often spreads rapidly in the community in the immediate post-burn phase. They are also shade-tolerant, particu-

larly *V. vitis-idaea*, so they can persist as a patchy second tier beneath the heather as it thickens up. Where they are prominent, and especially where there is also some *Empetrum nigrum* ssp. *nigrum*, not universally well represented here but characteristic of one sub-community, it can become hard to separate this vegetation from the *Calluna-Vaccinium* heath. Then, it may be a matter of whether *A. uva-ursi* is present or not, such that the local extinction of this plant from the canopy can effectively result in a fine mosaic of the two communities.

Quite often, however, there are some other floristic features which help give the *Calluna-A. uva-ursi* heath a distinctive stamp. Quite commonly throughout the community there are small amounts of *Genista anglica*, a rather diffuse and somewhat frail-looking sub-shrub compared with the others frequent here, but actually rather resistant even to quite high fire temperatures, perhaps because of its relatively thick bark (Mallik & Gimingham 1985), and readily able to resprout from the burned stumps. It is a plant with a somewhat odd distribution through Europe, essentially Oceanic West European, but perhaps better described as sub-Atlantic, having a strong centre of its British range located in this heath in eastern Scotland and with some striking outliers towards central Europe (Matthews 1955). Then, more expectedly perhaps, there are some Northern Montane preferentials, such as *Listera cordata*, *Trientalis europaea* and *Antennaria dioica*, and Continental Northern plants, like the nationally rare *Pyrola media*, but these are not very frequent overall and indeed are often distinctly clustered in their occurrence in one particular kind of *Calluna-A. uva-ursi* heath. In fact, except in that sub-community, herbaceous associates are rather few and far between in this vegetation. *Luzula multiflora* and *L. pilosa* are rather more common than in the *Calluna-Vaccinium* heath and *Carex pilulifera* is not so restricted in its occurrence, but otherwise, this element of the flora can be very impoverished.

The bryophyte component is similarly somewhat variable in its composition, and also in its abundance since, as in some other heaths, the bulkier mosses are often strongly associated with particular stages in the heather-regeneration cycle, sometimes spreading among pioneer *Calluna* but frequently making their most prominent contribution among older bushes that are opening up somewhat; and there are also differences with the character of the soil exposed after burning. But *Hypnum jutlandicum*, *Pleurozium schreberi* and *Dicranum scoparium* are very common overall with *Hylocomium splendens* also a constant through much of the community, and *Rhytidiadelphus loreus*, *R. squarrosus* and *Ptilidium ciliare* occasional.

Lichens differ in their representation, too, with only *Cladonia impexa* constant and, in many stands, of but low cover. Fruticose species, such as *C. arbuscula* and *C. rangiferina*, tend to follow the larger pleurocarps in developing among the shadier and more humid conditions of older heather canopies and, there too, *Hypogymnia physodes* and, less commonly, *Cetraria glauca* can be seen on decaying woody stems. *Cladonia uncialis* also becomes frequent in such vegetation but it is rather more typical of the *Cladonia* sub-community where the lichen contribution tends to be the most extensive and varied found in the *Calluna-A. uva-ursi* heath, with peat-encrusting species especially numerous and abundant.

Sub-communities

***Pyrola media-Lathyrus montanus* sub-community:** *Arctostaphyleto-Callunetum* McVean & Ratcliffe 1962; *Arctostaphyleto-Callunetum*, herb-rich type Ward 1971; *Vaccinio-Ericetum cinereae*, *Viola riviniana* subassociation Birse 1980 *p.p.*; *Arctostaphylos* heath Urquhart 1986. It is here that *A. uva-ursi* tends to make its most prominent contribution to this community, frequently occupying more than 25% of the ground and occasionally rivalling *Calluna* in abundance and forming a variegated patchwork with it. *Erica cinerea* can have fairly high cover, too, though it is usually present as small, scattered bushes, and the two *Vaccinia* are likewise common but generally sparse. *Genista anglica* is fairly frequent, again at low cover, and very occasionally there can be a little *Juniperus communis* ssp. *communis*. *E. nigrum* ssp. *nigrum* is noticeably sparse.

The most striking feature of this kind of heath, though, is the associated herb flora and it is among this element that the community differs particularly from the *Calluna-Vaccinium* heath. First, grasses are noticeably more common than elsewhere in the *Calluna-A. uva-ursi* heath, with *Festuca ovina* frequently joining *Deschampsia flexuosa* and occasional records for *Anthoxanthum odoratum*, *Agrostis capillaris* and, at some sites, *A. canina* ssp. *montana*. With their clustered tillers protected by insulating old leaf-sheaths, each of these can escape severe damage in fires to attain some degree of abundance in the early years of recovery though they later become sparse. Then, there are some widespread calcifuge plants which can be very frequent in this sub-community, notably *Potentilla erecta* and *Galium saxatile* with, more indicative of the transitional soil base status that seems characteristic here, *Lathyrus montanus*, *Hypericum pulchrum* and, less commonly, *Succisa pratensis*. Third, some distinctly mesophytic species can be found, with *Viola riviniana* and *Lotus corniculatus* occurring frequently, *Campanula rotundifolia* rather less often. Most striking of all, perhaps, is the fairly consistent occurrence of *Pyrola media* and the less common, but still preferential, presence of *Trientalis*, which add a strong boreal feel. *Anemone nemorosa*, too, which is fairly frequent in this sub-community, can be seen as reflecting climatic conditions in its occurrences here

outside of woodland and, among the bryophytes, there is a noticeable increase in *Rhytidiadelphus triquetrus*, a feature of a number of different vegetation types in this part of the country. Again, many of the herbs are well adapted vegetatively to survive the effects of burning, having growing points clustered among leaf-bases in rosettes (*Pyrola*, *Succisa*, *Viola*) or underground perennating organs which can rapidly produce new shoots (*Potentilla*. *Lathyrus*, *Lotus*, *Campanula*, *Anemone*, *Trientalis*) so, in newly-burned tracts, there can sometimes be seen abundant new growth of these plants (Mallik & Gimingham 1985). With age, however, all but the more shade-tolerant, among which *Pyrola* is rather noteworthy, can become very much more thinly distributed and rather patchy from stand to stand (e.g. Hobbs *et al.* 1984).

Overall, with the high total cover of the sub-shrubs and herbs, bryophytes and lichens tend to be less well represented in this sub-community than in other kinds of *Calluna-A. uva-ursi* heath. The community mosses are all very common but neither they, nor the preferential *R. triquetrus*, are very abundant as a rule and, among the lichens, only *Cladonia impexa* occurs frequently and then with low cover.

***Vaccinium myrtillus-Vaccinium vitis-idaea* sub-community.** *A. uva-ursi* remains constant in this sub-community but *Calluna* is usually a fairly uncompromising dominant among the sub-shrub cover with, as a patchy mosaic or a rather sparse understorey, *V. myrtillus* and, usually a little more abundant, *V. vitis-idaea*. *Erica cinerea* and *Genista anglica* are somewhat less common than in the *Pyrola-Lathyrus* sub-community but *E. nigrum* ssp. *nigrum* is much more frequent, occasionally with locally high cover, though generally with fairly sparse shoots intermingled among the other sub-shrubs. More obvious, however, is the scarcity of herbs here because, though *Festuca ovina*, *Carex pilulifera*, *Potentilla erecta*, *Luzula multiflora*, *L. pilosa* and *Listera cordata* are occasionally recorded, there is nothing like the richness and variety among this element characteristic of the *Pyrola-Lathyrus* type. Conversely, the cryptogams tend to be a little more diverse and considerably more extensive, with the bulky pleurocarpus mosses *Hypnum jutlandicum*, *Pleurozium schreberi* and *Hylocomium splendens* often abundant beneath the canopy and particularly where the branches are more open. Larger lichens are also more apparent, with *Cladonia arbuscula*, *C. uncialis* and *C. rangiferina* frequently accompanying *C. impexa*, and *Cetraria glauca* and *Hypogymnia physodes* occasional over older stools.

***Cladonia* spp. sub-community:** *Arctostaphyleto-Callunetum*, herb-poor type Ward 1971. Although *A. uva-ursi* is sometimes quite abundant here, *Calluna* is more often overwhelmingly dominant. Both *Erica cinerea* and *Genista anglica* occur frequently, but *V. myrtillus* is absent and *V. vitis-idaea* and *E. nigrum* ssp. *nigrum* very scarce. The herbs of the *Pyrola-Lathyrus* sub-community are hardly ever found but *Carex pilulifera* and *Scirpus cespitosus* are preferentially common and there is occasionally a little *Carex panicea*. More peculiar, however, is the cryptogam element because, in this sub-community, some of the characteristic mosses of the *Calluna-A. uva-ursi* heath, notably *Hylocomium splendens* and *Pleurozium schreberi*, become very patchy in their occurrence. *Hypnum jutlandicum* and *Dicranum scoparium* remain frequent and there is often a little *Pohlia nutans* but it is lichens, especially peat-encrusting species, that are more noticeable. None is ever really abundant but, along with *Cladonia impexa* and *C. uncialis*, there is frequent *C. floerkeana*, *C. coccifera* and *C. squamosa* and occasional *C. crispata*, *C. deformis* and *C. cornuta* occurring as scattered patches over the areas of open ground among the bushes.

Habitat

The *Calluna-A. uva-ursi* heath is characteristic of base-poor to circumneutral soils at moderate altitudes in the cold continental climate of the east-central Highlands of Scotland. Edaphic differences play some part in determining floristic variation in the community but their effects are often overlain and modified by the influence of burning which ultimately maintains this vegetation as a plagioclimax.

A. uva-ursi has a wide geographical and altitudinal distribution through the extreme north of Britain where the summers are at their coolest in this country: virtually all its Scottish localities (and those in Eire) fall within the 24 °C mean annual maximum isotherm (Conolly & Dahl 1970). In this community, however, it makes an important contribution to sub-shrub vegetation which is rather strictly confined to those parts of this range with a more continental climate. Thus, while summer maxima experienced by this heath are generally between 21 and 23 °C (Conolly & Dahl 1970) – temperatures which, in eastern Scotland, can prevail at moderately high altitudes – the winter climate is harsh, with low February minima and frequent late frosts (*Climatological Atlas* 1952, Page 1982). Compared with the conditions felt by heaths at identical altitudes to the west, therefore, the annual temperature range is greater. Furthermore, in contrast to the more oceanic zone in Scotland, the rainfall is very much lower. Annual precipitation here is, indeed, often less than 1000 mm and rarely over 1200 mm (*Climatological Atlas* 1952) with only 140–180 wet days yr^{-1} (Ratcliffe 1968). In the winter months, then, snowfall totals are only modest though, with the low spring temperatures, there is usually morning snow-lie on 40 days or more yr^{-1} (Page 1982).

Such conditions as these prevail throughout the foothills of the east-central Highlands where the com-

munity can be found, generally between 250 and 600 m, centred around Speyside, but extending eastwards to the Muir of Dinnet and other sites near Morven, west beyond Strathdearn and south, in more fragmentary fashion, through the Forest of Atholl (McVean & Ratcliffe 1962, Ward 1971*a*, Urquhart 1986). And the distinctive climate of this region is reflected in the vegetation in two ways. First, there is the generally montane character of the sub-shrub canopy with its frequent records for *V. myrtillus* and *E. nigrum* ssp. *nigrum*, and the more strictly Arctic-Alpine *V. vitis-idaea* and *A. uva-ursi*. Winter conditions here are not so blisteringly severe as to exclude *E. cinerea*, a plant which preserves some measure of physiological activity through the coldest months (Bannister 1965) though it tends to be less prominent than in those oceanic heaths, where *A. uva-ursi* can also occasionally figure, along the western seaboard of Scotland. On the other hand, *E. nigrum* ssp. *hermaphroditum* and *Loiseleuria* are very scarce in this vegetation: these species are largely confined to areas within the 22 °C mean annual maximum isotherm (Conolly & Dahl 1970) and tend to take over from *E. nigrum* ssp. *nigrum* and *A. uva-ursi* with the shift to more exposed conditions in eastern Scotland, at altitudes over 600 m and particularly on wind-blasted spurs and summits, where the dwarfed *Calluna-Cladonia* heath replaces the *Calluna-A. uva-ursi* heath and the other sub-shrub community which can be found there at lower altitudes, the *Calluna-Vaccinium* heath.

The second, and more particular, influence of climate is the occurrence of the boreal element in the flora of the *Calluna-A. uva-ursi* heath, though this is only really well seen in the *Pyrola-Lathyrus* sub-community. There the community occasionals *Listera cordata* and *Antennaria dioica* are often joined by *Pyrola media* and *Trientalis europaea* and other less specifically Continental Northern or Northern Montane plants, such as *Anemone nemorosa* and *Rhytidiadelphus triquetrus*, which in other communities in the east-central Highlands, like the *Juniperus-Oxalis* scrub and certain types of *Pinus-Hylocomium* woodland, add a distinctive climatically-related component. These are some of the plants which ultimately help separate the *Calluna-A. uva-ursi* heath from the *Calluna-Vaccinium* heath, which is common (indeed preponderant) through the foothills of this part of Scotland. And, when these species are, for one reason or another, sparse here, as in the *Vaccinium* and *Cladonia* sub-communities, it is that much harder to distinguish these communities along what then becomes a virtual continuum of floristic variation (McVean & Ratcliffe 1962, Ward 1970, 1971*a*, *b*).

But there are other peculiarities of the *Pyrola-Lathyrus* sub-community which are related to edaphic variation. By and large, the *Calluna-A. uva-ursi* heath is a vegetation type of more acidic soils developed from lime-poor parent materials, of which there is an abundance through the region, both bedrocks like the granites of the Cairngorms and Monadhliath hills, and superficials which, through Speyside, underlie the terraced haughlands above the limits of cultivation over which this community is particularly well represented. However, the range of profile types which has developed from the pervious rocks and coarse free-draining moraine material is quite broad, including brown earths, brown podzolic soils and humo-ferric podzols. And, among these, there is a clear association between the brown soils and the *Pyrola-Lathyrus* sub-community, many of the preferentials of which reflect more mesophytic edaphic conditions and a base-status transitional between acidic and neutral: superficial pH under this kind of *Calluna-A. uva-ursi* heath is usually from 4.5 to 5.5 and there is a tendency for the formation of moder humus rather than mor, with perhaps a fairly active nutrient turnover (McVean & Ratcliffe 1962, Ward 1971*a*, Birse 1980). Beneath the more herb-poor sub-communities, on the other hand, podzolic soils tend to predominate.

It is very clear, though, that the full expression of the climatically-related peculiarities of the *Calluna-A. uva-ursi* heath and the development of edaphic trends are strongly influenced by burning: as with the *Calluna-Vaccinium* heath, though not on so extensive a scale, the community forms an important part of grouse-moors in the east-central Highlands, having been burned fairly regularly, if not always judiciously, over at least a century and sometimes nearly two (Gimingham 1972). Indeed, it is in this kind of vegetation that some of the most precise observations on the effects of fire on heaths have been made, notably by Gimingham and his co-workers on the Muir of Dinnet, a site towards the eastern, drier and warmer lowland fringe of the range of the community, but having a fairly typical mix of *Calluna-A. uva-ursi* and *Calluna-Vaccinium* heaths over fluvio-glacial gravels (Ward 1970, Legg 1978, Marren 1979, Hobbs & Gimingham 1984*a*).

Such studies have shown that most of the associated herbs of the *Calluna-A. uva-ursi* heath reappear in abundance only in those stands which had heather in the pioneer or building phase when burned, but that the variety of such plants afterwards is only partly related to their pre-burn numbers. With pioneer heather stands, virtually all the species appearing after the burn were present before; in building stands, many new species appeared; where older tracts than this were burned, fewer species returned than were originally found (Hobbs & Gimingham 1984*b*). Such trends reflect differences in the potential for regrowth from either vegetative organs or dormant seed, both of which are influenced by the age of the *Calluna* canopy. In general, the variety and numbers of associated herbs seen in the

Calluna-A. uva-ursi heath decline with the progression from open pioneer to closed building and mature phases, then increase again as the bushes collapse in late maturity and degeneration, so the potential for regrowth from surface rosettes or tillers follows the same trend. The greater diversity of the post-burn herb flora when building stands are fired must therefore originate more from persistent underground organs or stored seed.

Most of the herbs of the community can store seed in the soil (Mallik & Gimingham 1983) and little non-vegetative regeneration in burned stands seems to originate from dispersal from outside (Hobbs *et al.* 1984). But stand-age has a marked effect on local input to the seed-bank because of the demise of fruiting parents with the closure of the heather canopy, and the declining performance of any ageing survivors (Legg 1978, Mallik *et al.* 1984). Furthermore, apart from *Carex pilulifera* (and *Calluna* itself: Hill & Stephens 1981), the soil stores themselves become depleted by the time the mature phase is reached, with some slight increase as the canopy opens again at degeneration (Mallik *et al.* 1984), so re-establishment in stands past their middle years of heather growth is unlikely. Even where soil stores remain appreciable, and well protected from the effects of fire by a mat of pleurocarpous mosses (Hobbs & Gimingham 1984*a*), conditions for post-burn germination may be poor, perhaps hindered by the same thick bryophyte mats or layers of litter (Miles 1974, Hobbs 1981, Mallik *et al.* 1984).

Thus, although it is generally true that the most important ecological character of the community associates is the ability to regenerate sexually or, even more so, vegetatively in the specialised post-burn environment (Mallik & Gimingham 1985), this may depend on the rather precise coincidence of critical life-history events among both these associates and the dominant sub-shrubs in relation to the burning cycle (Hobbs *et al.* 1984). And, where there is any perturbation to the usual pattern of firing and regrowth, evidence shows that peculiarities of composition can persist long into the post-burn period perpetuating the disturbance (and, incidentally, making it dangerous to devise time-sequences from spatial variation among stands of differing age: Hobbs & Gimingham 1984*b*).

The survival of the characteristically rich and diverse herb flora of the *Pyrola-Lathyrus* sub-community from one cycle to the next may thus be a rather precarious affair, these plants being ultimately dependent on burning treatments for their renewal, but readily succumbing to local extinction, not only in the short term with canopy closure, but over longer periods with perhaps only slight variation in the fire regime. Few of the species are constant even in the *Pyrola-Lathyrus* sub-community itself, and some appear particularly patchy in their occurrence: *Hypericum pulchrum*, for example, can readily resprout from remnant shoots and seems to have seed whose germination is actually fire-enhanced (Mallik & Gimingham 1985) and it was very characteristic of the more herb-rich stands described by Ward (1970, 1971*a*), whereas in the samples of very similar vegetation in McVean & Ratcliffe (1962) and Urquhart (1986), it is noticeably sparse.

In the *Vaccinium* and *Cladonia* sub-communities, however, the absence of very nearly all these plants is a much more consistent feature and it is likely that at least some of the stands included here are of vegetation which has lost the *Pyrola-Lathyrus* herbs but which could regain the flora with the re-establishment of a pioneer heather canopy. This is perhaps especially true of the *Vaccinium* sub-community which, with its sprinkling of herbs, abundance of pleurocarps and fruticose lichens and scattered shoots of woody associates among the heather, has much of the character of the late building-phase *Calluna-A. uva-ursi* heath described by Hobbs *et al.* (1984). It does include more stands from higher altitudes than the *Pyrola-Lathyrus* sub-community, with some looking almost transitional to *Calluna-Cladonia* heath, but climatic differences are not such in themselves as to exclude the herbs.

It is difficult to be so precise about interactions between burning and edaphic conditions in the *Calluna-A. uva-ursi* heath but it seems possible that continued exclusion of the *Pyrola-Lathyrus* herbs could sometimes indicate not simply an inimical burning regime but also the kind of soil impoverishment consequent upon long-unrelieved dominance of *Calluna*, such that a more irreversible degradation was initiated. The effects of initially poorer profiles and injudicious management could thus mutually confirm one another and this may have played an important part in the contrast seen today between 'richer' and 'poorer' grouse-moors (Miller *et al.* 1966, Jenkins *et al.* 1967, Moss 1969). On the former, developed over less base-poor substrates and with careful burning to maintain the higher bird numbers, the more species-rich *Calluna-A. uva-ursi* heath and the *Galium-Festuca* sub-community of the *Calluna-Vaccinium* heath predominate; over the latter, which are concentrated on less productive soils, the trend towards the more species-poor kinds of *Calluna-Vaccinium* heath is very marked.

In the *Calluna-A. uva-ursi* heath itself, the floristic impoverishment among the vascular element is most obvious in the *Cladonia* sub-community which, in Ward's (1970, 1971*a*) studies, was the kind of vegetation associated with podzols with a distinctly humic top-soil. On such substrates, recolonisation after burning was slow such that even after 10–15 years encrusting *Cladonia* spp. were still in occupation of ground that with a good mineral soil would have been long covered by sub-

shrubs and herbs. *Carex pilulifera*, the fruits of which are longer lived than most of those of the herbs and which is thus well able to exploit late-developing niches, is best represented here and the high frequency of *Scirpus cespitosus* and occasional occurrence of *Carex panicea* perhaps reflect the surface moisture of such soils where a peaty crust holds rain for an appreciable time. It would seem unlikely that this kind of *Calluna-A. uva-ursi* heath could readily regain the floristic richness of the *Pyrola-Lathyrus* type.

In the more species-poor vegetation included here, it can sometimes be simply the regularity with which *A. uva-ursi* is encountered that helps distinguish this heath from other heather-dominated communities, notably the *Calluna-Vaccinium* heath. The species is certainly a persistent element of regularly-burned sub-shrub vegetation in the region and, though new plants do not attain reproductive maturity until the building phase of the *Calluna* among which they have established, the seeds of *A. uva-ursi* are present in the soil at all stages and vegetative regrowth can also occur immediately after fire. These features, together with the distinctive growth habit of mature plants that enables the far-spreading stems to branch vigorously into local gaps, give the plant advantages which outreach those of its peculiar associates in the species-rich kind of *Calluna-A. uva-ursi* heath.

Stretches of moorland including stands of the community are often open to stock but there is very little information on the impact of their grazing on this vegetation. *A. uva-ursi* figures little in the diet of grouse, but may perhaps provide some bite for sheep among the valuable winter-green elements of the vegetation on these grazings. Urquhart (1986) reported that one of the sites identified by McVean & Ratcliffe (1962) as having this community had become herb-rich sheep pasture and certainly there can be some floristic overlap between the *Pyrola-Lathyrus* sub-community and certain kinds of *Festuca-Agrostis-Galium* and *Nardus-Galium* grasslands. It is fairly easy to see how heavy grazing might lead to an expansion of the grassy element in the richer *Calluna-A. uva-ursi* sward with a reduction in the cover of the sub-shrubs and avoiding such treatment after burning is probably vital for the well-being of the community.

Zonation and succession

With woodland, scrub, other sub-shrub communities and grasslands, the *Calluna-A. uva-ursi* heath comprises a distinctive suite of vegetation types in the sub-montane zone of the east-central Highlands. These are the variously-modified derivatives of the original forest cover, produced by clearance, burning and grazing and, in the case of this community, dependent upon management as grouse-moor or rough pasture to prevent regression to secondary woodland. The *Calluna-A. uva-ursi* heath can be seen in large-scale altitudinal sequences, giving way above to dwarfed heaths and fell-field communities, which are climatic climax vegetation, and there are zonations to wet heath and mire with changes in topography and soils.

Long and quite intensive histories of land use in this part of Scotland (e.g. Birks 1970, O'Sullivan 1977, Carlisle 1977) mean that substantial tracts of more natural vegetation are rare. There is little doubt that, in the east-central Highlands, the climax forest type is similar to the vegetation seen today in the *Pinus-Hylocomium* woodland, but many surviving stands of this have been treated for timber production, sometimes involving planting, and the natural regeneration of the community is often somewhat problematical (Steven & Carlisle 1959, McVean & Ratcliffe 1962, Ratcliffe 1977). Then, although birch and juniper clearly figured in the original forest patchwork, and sometimes remain today in close association with native pine, many tracts of the *Juniperus-Oxalis* scrub behave as remnant understoreys, being perpetuated distant from the kind of woodland one might imagine could succeed them and rarely showing any natural progression. Indeed here, too, there is sometimes only sporadic regeneration of the scrub cover itself (Carlisle & Brown 1968, Carlisle 1977, Miles & Kinnaird 1979). The *Calluna-A. uva-ursi* heath can probably be seen as a further stage in this disruptive reversal of vegetation development, a plagioclimax community that has much in common floristically with the field layers of both these communities, which is sometimes seen among and around them, but which perhaps reverts only with difficulty to its more natural forebears, even when the constraints of regular burning are released.

So, although all three communities are very characteristic of the region and form integral elements in the large-scale landscape of what is understood as 'Caledonian pine forest' (Steven & Carlisle 1959, McVean & Ratcliffe 1962), it is only in a relatively few places that they can be seen in a more intimate juxtaposition and, even then, their relationship is rarely in any sense a dynamic one. The stretch of country between Rothiemurchus and Abernethy, in the middle reaches of the Spey, is one of the best areas where the similarities between the vegetation types can be appreciated. On a general level, there can be frequent records in all three for *Calluna*, *V. myrtillus*, *V. vitis-idaea*, *Deschampsia flexuosa*, *Hypnum jutlandicum*, *Dicranum scoparium*, *Pleurozium schreberi*, *Hylocomium splendens*, such that it often appears as if the heath runs virtually unaltered under the more open stretches of shrubs and trees. More strikingly, although *A. uva-ursi* itself rarely figures in the scrub or woodland, being intolerant of extensive areas

of deeper shade from which it cannot extend out, there is quite often some continuity between the different communities in the kind of associated herb flora so distinctive of the *Pyrola-Lathyrus* sub-community of the *Calluna-A. uva-ursi* heath. Where the *Pinus-Hylocomium* woodland and *Juniperus-Oxalis* scrub extend on to the less oligotrophic brown soils, for example, more mesophytic grasses and also herbs such as *Luzula pilosa*, *Viola riviniana* and *Campanula rotundifolia* can be found throughout. Moreover, there are also records in each for certain of the Continental Northern and Northern Montane species which give some stands of the *Calluna-A. uva-ursi* heath a particular phytogeographic stamp: *Listera cordata*, *Trientalis europaea* and *Pyrola media*, for example, provide a common element which confirms the boreal character of these peculiar eastern Scottish vegetation types.

Establishment of juniper and pine in stands of *Calluna-A. uva-ursi* heath seems to be rare: although both can exploit the post-burn habitat (indeed, perhaps depend on it to a great extent), any regeneration is curtailed by repeated burning or overgrowth of heather. Seed-parents are often distant, too, so, if there is any progression to woodland with cessation of treatment, it is birch that generally predominates among the invaders. On the Muir of Dinnet, for example, Urquhart (1986) indicates a very substantial reduction of the area of the community since 1946 as a result of the spread of birch. The likely development over the less-impoverished brown soils would be the *Quercus-Betula-Oxalis* woodland, a common secondary forest type in this region and having there a distinctive *Anemone* sub-community, with, again, such species as *A. nemorosa*, *Trientalis*, *Luzula pilosa*, *Lathyrus montanus* and *Rhytidiadelphus triquetrus* providing strong floristic continuity with the heath.

Where the *Calluna-A. uva-ursi* heath extends on to more base-poor and oligotrophic podzolised profiles, it is increasingly likely to be subordinate in its extent to the *Calluna-Vaccinium* heath and, in fact, through the east-central Highlands as a whole, this latter community is strongly predominant through the sub-montane zone, the former occurring as what are relatively small islands scattered through it (Urquhart 1986). As indicated earlier, treatment for grouse-rearing may have accentuated the partly edaphic contrast between 'rich' and 'poor' moors, and it seems likely that injudicious burning, leading to an overwhelming dominance of *Calluna*, with consequent enhancement of podzolisation, could shift the pattern from an abundance of the richer kind of *Calluna-A. uva-ursi* heath to the poorer *Calluna-Vaccinium* types. Certainly, with a move towards the latter, the peculiar boreal character of eastern Scottish sub-shrub vegetation is lost and, although seral progression to woodland can occur from such heath, where it is abandoned, the secondary birch-dominated *Quercus-Betula-Dicranum* woodland that develops is likewise much less floristically distinctive than its more mesophytic counterpart.

Mosaics of the two heath communities, with more fragmentary representation of juniper and pine vegetation, are a very characteristic feature of the Grampian foothills throughout Speyside and north of the Dee, and over the lower slopes of the Monadhliath and Cairngorm mountains (Ratcliffe 1977, Urquhart 1986). With the shift to higher altitudes through this region, above the forest zone where they now often comprise the bulk of the cover on more free-draining soils, there is a move to other kinds of sub-shrub vegetation. Over very exposed ridges and spurs, it is the dwarfed *Calluna-Cladonia* heath that is characteristic, replacing the *Calluna-A. uva-ursi* heath at around 670 m in the Cairngorms (McVean & Ratcliffe 1962): *A. uva-ursi* itself can run on in some abundance into the wind-pruned mat of the lichen heath, and more stunted stands of the *Vaccinium* sub-community of the *Calluna-A. uva-ursi* heath can form a transition zone between the two. Beyond, there is then a gradation to *Juncus-Racomitrium* heath. More sheltered situations at intermediate altitudes in such sequences, particularly where a northerly or easterly aspect ensures longer snow-lie, can have stands of the *Vaccinium-Rubus* heath.

Throughout these altitudinal and topographic zonations, a switch to soils with impeded drainage can see transitions to wet heaths and mires. At lower altitudes, as over the Cairngorm slopes, mosaics of *Calluna-A. uva-ursi* and *Calluna-Vaccinium* heaths can pass over gleyed peaty podzols to the *Ericetum tetralicis* in which mixtures of *Calluna* and *Scirpus* can predominate and where *Cladonia impexa*, *C. uncialis* and peat-encrusting lichens can provide additional continuity with the *Cladonia* sub-community of the *Calluna-A. uva-ursi* heath characteristic of surface-damp humic soils. Over higher ground, blanket peats on plateaus can have a cover of the *Calluna-Eriophorum* mire above the sub-montane heaths: a particularly striking sequence of this kind can be seen above the Findhorn River in the northern Grampians, where the *Calluna-A. uva-ursi* heath, including some good *Pyrola-Lathyrus* type, occupies the steeper slopes, passing over the gently-domed summit of Carn Nan Tri-Tighearnan to spectacular lichen-rich blanket bog.

Distribution

All the sub-communities of the *Calluna-A. uva-ursi* heath occur widely but fairly locally through the east-central Highlands, with especially good representation in Speyside. Urquhart (1986) identified a cluster of sites

around Craiggowrie, Tulloch Moor, Boat of Garten and Rothiemurchus as having particularly striking examples of the richer *Pyrola-Lathyrus* type with further fine stands between Crathie and Dinnet along the northern side of the Dee.

Affinities

Early descriptive studies regarded *A. uva-ursi* as an occasional, locally prominent plant within a compendious sub-montane *Callunetum* (Smith 1911*b*, Tansley 1939), and, though separate *Calluna-Arctostaphylos* vegetation was later recognised (Muir & Fraser 1940, McVean & Ratcliffe 1962, Gimingham 1964*a*, 1972), the difficulty of distinguishing more species-poor stands from other heaths largely lacking *A. uva-ursi* was acknowledged. The problem is particularly well seen in the investigations of Ward (1970, 1971*a*, *b*) where an *Arctostaphyleto-Callunetum*, as he termed it, following McVean & Ratcliffe (1962), formed part of a floristic continuum among sub-shrub vegetation in the east-central Highlands and, in the scheme of Birse (1980), there is a return to a single *Vaccinio-Ericetum* including virtually all the sub-montane heaths of this region.

Ward (1971b), however, considered it worthwhile to recognise a separate community, though his definition of the *Arctostaphyleto-Callunetum* was somewhat narrower than that of McVean & Ratcliffe (1962), concentrating even more on the richer stands included here in the *Pyrola-Lathyrus* sub-community. Although the preferentials of this sub-community agree very closely with the revised list of character species which Ward (1971*a*, *b*) proposed for his association, it has been thought better here to return to a somewhat broader diagnostic base for the community, not as all-inclusive as that of Birse (1980), but roughly similar to that of McVean & Ratcliffe (1962). Here, though, the recognition of distinct sub-communities helps clarify transitions to the *Calluna-Vaccinium* heath.

It was Gimingham (1949, 1964*a*) who pointed out the rather unexpected dissimilarity between the kind of vegetation included in the *Calluna-A. uva-ursi* heath and Scandinavian communities with *A. uva-ursi*. In western Norway, for example, the species is found in the kind of oceanic *Calluna-Erica cinerea* heath which, along the northern seaboard of Scotland, can also occasionally have this plant. In south-west Sweden, on the other hand, there is a much more obvious Continental influence with *Genista pilosa* and *Arnica montana* well represented in *A. uva-ursi* heath. Some Danish stands have *A. uva-ursi* with *Empetrum nigrum* ssp. *nigrum* and *Genista anglica*, but the other preferentials of the *Pyrola-Lathyrus* sub-community are generally sparse. Despite these peculiarities among European sub-shrub communities, the *Calluna-A. uva-ursi* heath, together with juniper, pine and birch woods of the same region, form a distinctive boreal component among British vegetation types.

Floristic table H16

	a	b	c	16
Calluna vulgaris	V (5–10)	V (4–10)	V (5–10)	V (4–10)
Arctostaphylos uva-ursi	V (4–8)	V (1–5)	V (1–8)	V (1–8)
Hypnum jutlandicum	IV (1–5)	V (1–10)	V (1–10)	V (1–10)
Cladonia impexa	IV (1–3)	IV (1–6)	V (1–4)	IV (1–6)
Pleurozium schreberi	IV (1–6)	V (1–8)	III (1–3)	IV (1–8)
Erica cinerea	IV (1–6)	III (1–4)	V (1–4)	IV (1–6)
Dicranum scoparium	IV (1–4)	III (1–4)	IV (1–4)	IV (1–4)
Vaccinium vitis-idaea	V (1–4)	IV (1–4)	II (1–6)	IV (1–6)
Deschampsia flexuosa	V (1–4)	IV (1–4)	II (1–4)	IV (1–4)
Hylocomium splendens	IV (1–6)	IV (1–6)	II (1–3)	IV (1–6)
Potentilla erecta	IV (1–4)	II (1–3)	I (1–3)	III (1–4)
Pyrola media	IV (1–3)	I (1–4)		II (1–4)
Lathyrus montanus	IV (1–3)			II (1–3)
Viola riviniana	IV (1–3)			II (1–3)
Festuca ovina	III (1–5)	II (1–3)	I (1–3)	II (1–5)
Rhytidiadelphus triquetrus	III (1–4)	II (1–3)		II (1–4)
Lotus corniculatus	III (1–3)	I (1–3)		II (1–3)
Galium saxatile	III (1–4)			I (1–4)

https://doi.org/10.1017/9780521391658.060 Published online by Cambridge University Press

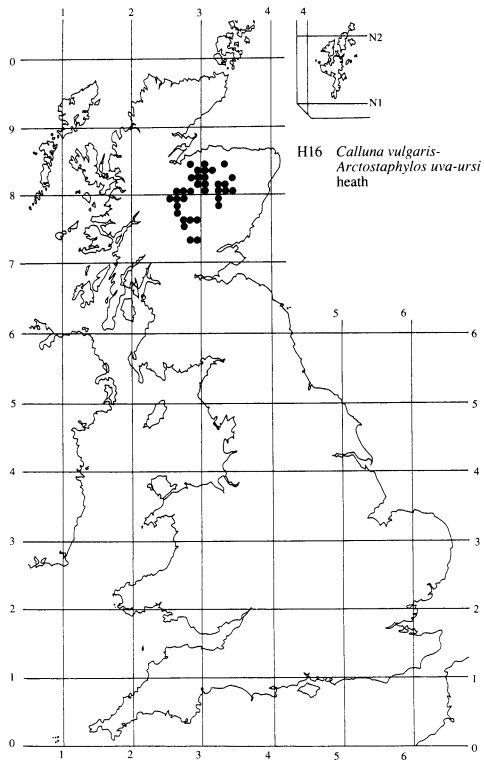
Hypericum pulchrum	III (1–3)			I (1–3)
Anemone nemorosa	III (1–4)			I (1–4)
Trientalis europaea	II (1–4)	I (1–3)		I (1–4)
Anthoxanthum odoratum	II (1–4)	I (1)		I (1–4)
Agrostis capillaris	II (1–3)	I (1–3)		I (1–3)
Pseudoscleropodium purum	II (1–4)			I (1–4)
Polygala serpyllifolia	II (1–3)			I (1–3)
Campanula rotundifolia	II (1–3)			I (1–3)
Succisa pratensis	II (1–3)			I (1–3)
Luzula campestris	I (1–3)			I (1–3)
Vaccinium myrtillus	III (1–4)	V (1–5)		III (1–5)
Empetrum nigrum nigrum	I (5)	III (1–6)	I (1)	II (1–6)
Cladonia arbuscula		III (1–5)	I (4)	II (1–5)
Cladonia rangiferina		II (1–4)	I (1–4)	I (1–4)
Polytrichum commune	I (1)	II (1–3)		I (1–3)
Cetraria glauca		II (1–4)		I (1–4)
Juncus squarrosus		I (1–4)		I (1–4)
Carex pilulifera	II (1–3)	II (1–3)	IV (1–3)	II (1–3)
Scirpus cespitosus	I (1–3)	I (1–4)	IV (1–5)	II (1–5)
Cladonia uncialis		III (1–3)	IV (1–3)	II (1–3)
Cladonia floerkeana	II (1–3)		III (1–3)	II (1–3)
Carex panicea	I (1)	I (1–3)	III (1–3)	I (1–3)
Pohlia nutans	I (1)	I (1)	III (1–4)	I (1–4)
Cladonia coccifera	I (1)		III (1–3)	I (1–3)
Cladonia squamosa		I (1–3)	III (1–3)	I (1–3)
Cornicularia aculeata		I (1–3)	II (1–3)	I (1–3)
Cladonia crispata			II (1–4)	I (1–4)
Cladonia deformis			II (1–3)	I (1–3)
Cladonia cornuta			II (1–3)	I (1–3)
Genista anglica	III (1–3)	II (1–4)	III (1–3)	III (1–4)
Hypogymnia physodes	II (1–4)	III (1–6)	III (1–4)	II (1–6)
Luzula multiflora	II (1–3)	II (1–3)	I (1)	II (1–3)
Listera cordata	II (1–3)	II (1–3)		II (1–3)
Rhytidiadelphus loreus	II (1–4)	II (1–3)		II (1–4)
Luzula pilosa	II (1–3)	II (1–3)		II (1–3)
Cladonia pyxidata	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Ptilidium ciliare	I (1–4)	I (1–3)	I (1)	I (1–4)
Antennaria dioica	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Rhytidiadelphus squarrosus	I (1–4)	I (1–3)	I (1–3)	I (1–4)
Polytrichum juniperinum	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Erica tetralix	I (1–3)	I (1–4)		I (1–4)
Betula pubescens seedling	I (1–3)	I (1–3)		I (1–3)
Plagiothecium undulatum	I (1–3)	I (1–3)		I (1–3)
Euphrasia officinalis	I (1–3)	I (1)		I (1–3)
Empetrum nigrum hermaphroditum	I (1–3)	I (1–6)		I (1–6)
Danthonia decumbens	I (1–4)		I (1–3)	I (1–4)
Polytrichum piliferum	I (1–3)		1 (1)	I (1–3)
Carex bigelowii		I (5)	I (1–3)	I (1–5)
Huperzia selago		I (1–3)	I (1–3)	I (1–3)

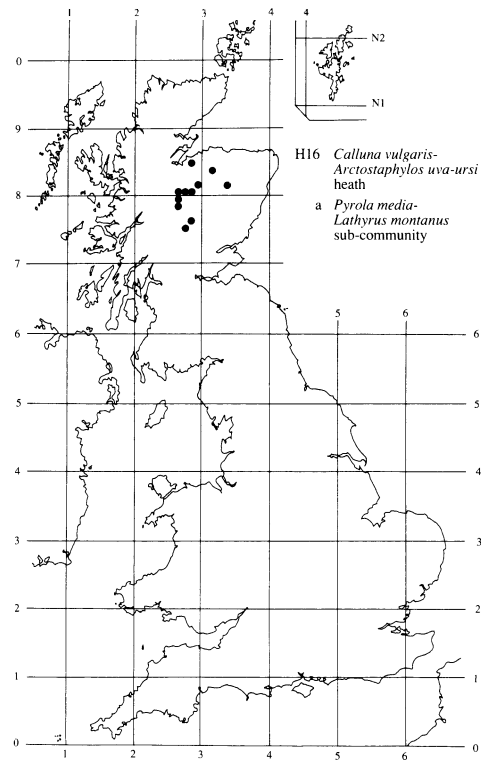
https://doi.org/10.1017/9780521391658.060 Published online by Cambridge University Press

Floristic table H16 *(cont.)*

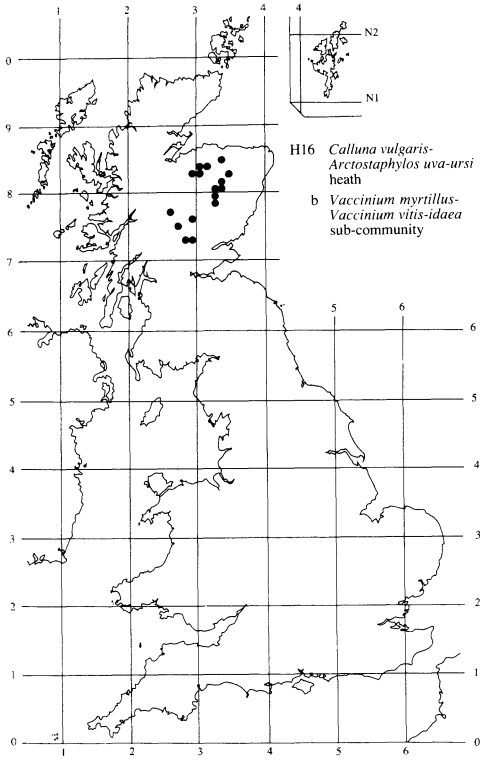
	a	b	c	16
Cladonia furcata		I (1–3)	I (1–3)	I (1–3)
Number of samples	18	25	13	56
Number of species/sample	24 (15–31)	17 (10–27)	17 (8–24)	19 (8–31)
Shrub height (cm)	28 (15–55)	20 (6–40)	24 (8–40)	20 (6–55)
Ground layer height (mm)	35 (30–40)	32 (10–80)	20	31 (10–80)
Shrub/herb cover (%)	96 (70–100)	87 (75–100)	88 (70–100)	90 (70–100)
Ground layer cover (%)	23 (0–80)	66 (40–95)	48 (5–90)	48 (0–95)
Altitude (m)	339 (92–472)	472 (238–750)	398 (251–700)	405 (92–750)
Slope (°)	15 (2–25)	9 (0–38)	15 (0–40)	12 (0–40)

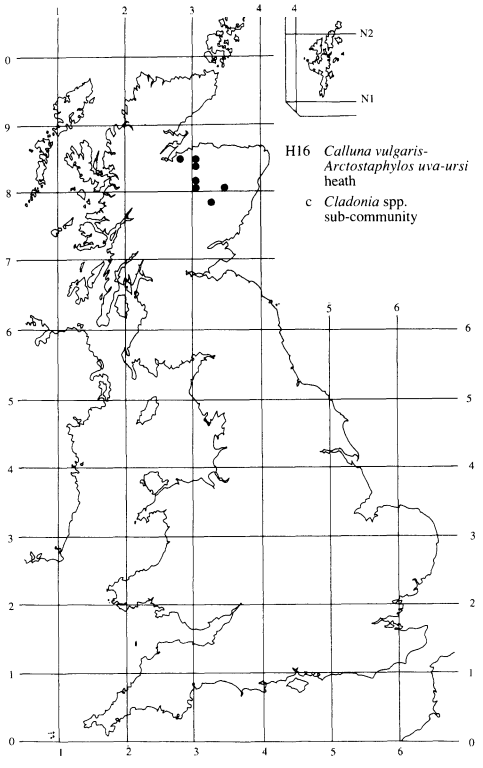
a *Pyrola media-Lathyrus montanus* sub-community
b *Vaccinium myrtillus-Vaccinium vitis-idaea* sub-community
c *Cladonia* spp. sub-community
16 *Calluna vulgaris-Arctostaphylos uva-ursi* heath (total)





https://doi.org/10.1017/9780521391658.060 Published online by Cambridge University Press





https://doi.org/10.1017/9780521391658.060 Published online by Cambridge University Press