H18
Vaccinium myrtillus-Deschampsia flexuosa heath

Synonymy
Vaccinietum myrtilli Smith 1900, Lewis & Moss 1911, Tansley 1939, Fidler *et al.* 1971; *Vaccinium*-ridge & *Vaccinium*-summit Smith & Moss 1903, Smith & Rankin 1903; *Gramino-Vaccinetum* Smith 1911*b*; *Vaccinium*-edge Moss 1913; *Empetreto-Vaccinetum* Burges 1951 *p.p.*; Lichen-rich *Vaccinium-Festuca* association Poore 1955*b*; *Vaccinium-Chamaepericlymenum* nodum Poore & McVean 1957 *p.p.*; *Vaccineto-Empetretum* McVean & Ratcliffe 1962; *Festuceto-Vaccinetum* McVean & Ratcliffe 1962, Evans *et al.* 1977, Ferreira 1978; *Festuca ovina/Deschampsia flexuosa* grassland King 1962 *p.p.*; *Vaccinium myrtillus*-heath moss sociation Edgell 1969; Mountain *Vaccinium* heaths Gimingham 1972 *p.p.*; *Phyllodoce caerulea* sites Coker & Coker 1973 *p.p.*; *Huperzio-Vaccinetum* Hill & Evans 1978; *Rhytidiadelphus loreus-Vaccinium myrtillus* community Birse 1980.

Constant species
Deschampsia flexuosa, *Galium saxatile*, *Vaccinium myrtillus*, *Dicranum scoparium*, *Pleurozium schreberi*.

Rare species
Loiseleuria procumbens, *Minuartia sedoides*, *Phyllodoce caerulea*, *Salix lapponum*, *Barbilophozia lycopodiodes*, *Scapania ornithopodiodes*.

Physiognomy
The *Vaccinium myrtillus-Deschampsia flexuosa* heath includes a variety of moss-rich and grassy sub-shrub vegetation in which *Vaccinium myrtillus* is the most frequent and generally the most abundant ericoid, with *Calluna vulgaris* typically having a rather inconspicuous role: heather is usually only occasional here and present as scattered plants that are often noticeably lacking in vigour. *V. myrtillus* is not always truly dominant, however, and other sub-shrubs sometimes make a sizeable contribution to the canopy, which is generally 1–2 dm tall, occasionally rather open and, even where extensive, is without that uniform density of growth found in heaths with much young *Calluna*. Most frequent among the associated sub-shrubs is *Empetrum nigrum*, usually ssp. *hermaphroditum* where it has been possible to distinguish the taxa, though sometimes clearly ssp. *nigrum*, and occasionally both plants growing together. Typically, the procumbent stems of the crowberry penetrate quite far among the bilberry, branching out into patches which can be locally abundant. Some of the vegetation subsumed here has co-dominant *E. nigrum* as in the various kinds of *Vaccinio-Empetretum* described by Burges (1951) and McVean & Ratcliffe (1962), and, of course, being evergreen, the crowberry catches the eye more than the deciduous bilberry in stands without a covering of winter snow.

V. vitis-idaea is about as common as *E. nigrum*, though typically much less abundant. *V. uliginosum*, on the other hand, is rather scarce and preferential for one sub-community but it can have locally high cover there, even attaining co-dominance in some stands (Poore & McVean 1957, McVean & Ratcliffe 1962). Also strongly diagnostic of one particular kind of *Vaccinium-Deschampsia* heath, and occurring occasionally elsewhere, is *Alchemilla alpina*, strictly speaking a woody herb, but able to make quite bushy growth among the ericoids and to contribute substantially to the canopy in certain cases.

The rare *Loiseleuria procumbens*, more a plant of wind-blasted lichen-rich heaths, occurs very occasionally and inaccessible patches of this community sometimes shelter bushes of *Salix lapponum*. The *Vaccinium-Deschampsia* heath is also the locus in this country for the very restricted *Phyllodoce caerulea*, a sub-Arctic ericoid of low, bushy growth, known in Britain only from the Sow of Atholl in Perthshire and the Ben Alder range in Inverness (McBeath 1967, Coker & Coker 1973, Perring & Farrell 1977). Here, its survival looks very precarious and the longest-known colony at the former site has certainly suffered from the predations of collectors and growers, but its close vegetative resemblance to

Empetrum and its rather shy flowering habit afford the plant some protection.

The vascular associates of the sub-shrubs vary considerably in their number and prominence. Constant throughout are *Deschampsia flexuosa* and *Galium saxatile* with *Nardus stricta*, *Agrostis canina* ssp. *montana* and *Potentilla erecta* all very frequent, and in some stands these provide virtually all the herbaceous element and a rather sparse cover among the bushes. *Carex bigelowii* occurs occasionally but its relative infrequency and generally low cover help distinguish the community from the *Vaccinium-Cladonia* heath with which it is sometimes closely associated (e.g. Burges 1951). Then, there is occasionally some *Dryopteris dilatata* and *Cryptogramma crispa* with *Blechnum spicant* becoming very common in one sub-community.

As a group, though, it is grasses which often make the most notable contribution to the herbaceous element of the vegetation, with *Festuca ovina* (much less commonly *F. vivipara* and *F. rubra*), *Agrostis capillaris* and *Anthoxanthum odoratum* occurring at least occasionally and, in some sub-communities, increasing considerably in frequency and abundance, so as to become with *D. flexuosa*, *Nardus* and *A. canina*, a sometimes co-dominant component of the cover, as in the various kinds of grassy-heath subsumed here (Smith 1911*b*, Poore 1955*b*, McVean & Ratcliffe 1962). In such stands, too, small monocotyledons such as *Luzula campestris*, *Carex pilulifera* and *C. binervis* tend to have their best representation in the community.

The other element of the vegetation which is frequently prominent comprises bulky mosses. *Dicranum scoparium*, *Pleurozium schreberi* and *Hypnum cupressiforme s.l.* (often *H. jutlandicum*) are very common throughout, *Hylocomium splendens* is also conspicuous in many stands and, in various kinds of *Vaccinium-Deschampsia* heath, there can be frequent *Rhytidiadelphus loreus*, *R. squarrosus*, *Plagiothecium undulatum*, *Dicranum majus* and *Racomitrium lanuginosum*. *Ptilidium ciliare* and *Polytrichum commune* are also found occasionally throughout and a variety of other species are scarce associates: *Rhytidiadelphus triquetrus*, *Thuidium tamariscinum*, *Polytrichum alpestre*, *P. alpinum* and *Pohlia nutans*.

Some lichens also occur frequently and in all types of *Vaccinium-Deschampsia* heath there can be found stands in which these are rather more varied than usual, but it is in only one of the sub-communites that they become even moderately abundant and there is really never attained here the kind of rich and extensive lichen carpet typical of the *Vaccinium-Cladonia* heath. Among the commonest species are *Cladonia arbuscula*, *C. impexa* and *C. uncialis*, with *C. pyxidata*, *C. rangiferina*, *C. gracilis* and *Cetraria islandica* occurring much less frequently.

Sub-communities

***Hylocomium splendens-Rhytidiadelphus loreus* sub-community:** *Vaccinetum myrtilli* Smith 1900, Lewis & Moss 1911, Tansley 1939; *Vaccinium*-ridge & *Vaccinium*-summit Smith & Moss 1903, Smith & Rankin 1903; *Vaccinium*-edge Moss 1913; *Empetreto-Vaccinetum* mossy facies Burges 1951; *Vaccinium-Chamaepericlymenum* nodum Poore & McVean 1957 *p.p.*; *Vaccineto-Empetretum* McVean & Ratcliffe 1962; *Vaccinium myrtillus*-heath moss sociation Edgell 1969; *Phyllodoce caerulea* sites Coker & Coker 1973 *p.p.*; *Rhytidiadelphus loreus-Vaccinium myrtillus* community Birse 1980. Sub-shrubs are generally clearly dominant here, but with mosses forming an extensive ground carpet. In many stands, *V. myrtillus* is overwhelmingly abundant, but *E. nigrum* is occasionally co-dominant and, in some stands, *V. vitis-idaea* or *V. uliginosum*, this last preferential here, though still not common. *Calluna* is rather more frequent than usual in the community, though still of characteristically low cover and, although *Alchemilla alpina* occurs occasionally this, too, is rarely abundant. The small colonies of *Phyllodoce* on Sgur Iuthurn and Meall an-t-Slugain appear to be in this kind of *Vaccinium-Deschampsia* heath and other stands have been found with bushes of *Salix lapponum*.

Deschampsia flexuosa is very common and sometimes quite abundant and there is occasionally also some *Nardus*, *Agrostis canina* ssp. *montana*, *A. capillaris* and *Anthoxanthum* but, as a rule, grasses are nothing like so consistent in their frequency and total abundance here as in the *Alchemilla-Carex* sub-community. The sedges that are typically found there are also very scarce in this vegetation, though *Carex bigelowii* occurs occasionally and *Luzula sylvatica* is a preferential occasional, sometimes with moderately high cover. A fairly high frequency of *Blechnum spicant* is also a good diagnostic feature and there is occasionally some *Melampyrum pratense*, *Oxalis acetosella* and *Cornus suecica* but, along with *Galium saxatile* and *Potentilla erecta*, more typical of the community as a whole, these are often the only herbs represented.

The bryophyte element, on the other hand, attains its most diverse and extensive cover in this kind of *Vaccinium-Deschampsia* heath, often forming a quite luxuriant carpet among the sub-shrub branches and over their decumbent shoots. *Hylocomium splendens* and *Rhytidiadelphus loreus* join *Dicranum scoparium* and *Pleurozium schreberi* as constants and there are occasional records for *Plagiothecium undulatum*, *Dicranum majus*, *Hylocomium umbratum*, *Sphagnum quinquefarium* and *S. capillifolium*, for *Barbilophozia floerkii*, *Anastrepta orcadensis* and very occasionally for such rare hepatics as

Scapania ornithopodioides and *Barbilophozia lycopodiodes*. The community associates *Hypnum cupressiforme s.l.*, *Polytrichum commune* and *Ptilidium ciliare* also remain occasional to frequent.

Lichens are generally much less obvious, although *Cladonia arbuscula* occurs often and *C. uncialis*, *C. gracilis* and *Cetraria islandica* can occasionally be found and when these occur together and with a little *Carex bigelowii*, the vegetation approaches the *Racomitrium-Cladonia* sub-community in its composition.

***Alchemilla alpina-Carex pilulifera* sub-community:** *Gramino-Vaccinetum* Smith 1911*b*; Lichen-rich *Vaccinium-Festuca* association Poore 1955*b*; *Festuceto-Vaccinetum* McVean & Ratcliffe 1962, Evans *et al.* 1977, Ferreira 1978; *Festuca ovina/Deschampsia flexuosa* grassland King 1962; *Phyllodoce caerulea* sites Coker & Coker 1973 *p.p. V. myrtillus* can still be quite abundant here but *E. nigrum* is much scarcer than in the first sub-community and *V. vitis-idaea* and *Calluna*, though quite frequent, make little contribution to the cover. Indeed, the ericoids as a whole are often co-dominant with *Alchemilla alpina*, which is strongly preferential here, and/or with grasses which also have their best representation as a group in this sub-community. Along with *D. flexuosa*, *Festuca ovina* is especially frequent and abundant but *Agrostis capillaris* and *Anthoxanthum* are also common and can have moderately high cover and there is occasionally some *Danthonia decumbens*, *Deschampsia cespitosa*, *Festuca rubra*, *F. vivipara*, *Nardus stricta* and *Agrostis canina* ssp. *montana*. *Luzula campestris* and *Carex pilulifera* are also strongly diagnostic, though not usually abundant, and there is occasionally some *C. binervis* and *C. panicea*. It is amongst this kind of vegetation that *Phyllodoce* occurs on the Sow of Atholl (Coker & Coker 1973).

There is also quite often a variety of dicotyledonous herbs. Along with *Galium saxatile*, *Potentilla erecta* attains its highest frequency here and there is occasionally some *Campanula rotundifolia*, *Viola riviniana*, *Ranunculus acris*, *Polygala serpyllifolia*, *Anemone nemorosa* and *Veronica officinalis*. Sometimes, bulkier plants such as *Alchemilla glabra* and *Rumex acetosa* can figure and, when *Luzula sylvatica* is also present, the vegetation can approach tall-herb ledge communities in its appearance. More often, however, the herbage is rather short and quite commonly cropped into a heathy sward. Where plants like *Thymus praecox* and *Carex pulicaris* make an occasional appearance in such stands, the *Vaccinium-Deschampsia* heath comes closest to the *Festuca-Agrostis-Alchemilla* grass-heath.

As in the *Hylocomium-Rhytidiadelphus* sub-community, bulkier mosses can be quite frequent here, though they do not have the same variety and abundance: *Dicranum scoparium*, *Pleurozium schreberi*, *Hylocomium splendens* and *Hypnum cupressiforme s.l.* all remain very common and preferentially there is often some *Rhytidiadelphus squarrosus*, but these usually occur as scattered shoots among the turf. In the fairly dense grassy herbage, lichens are sparse with typically just a little *Cladonia arbuscula* and scarce *C. impexa*, *C. uncialis* and *C. gracilis*.

***Racomitrium lanuginosum-Cladonia* spp. sub-community:** *Vaccinetum myrtilli* Fidler *et al.* 1971; *Huperzio-Vaccinetum* Hill & Evans 1978. *V. myrtillus* or mixtures of this with *E. nigrum* usually dominate in this sub-community, with rather infrequent sparse plants of *Calluna* and *V. vitis-idaea*. *D. flexuosa* and *F. ovina* are both very frequent and each can be abundant but other grasses tend to be rather poorly represented with just occasional plants of *Nardus*, *A. capillaris*, *A. canina* ssp. *montana* and *Anthoxanthum*. *Carex pilulifera* can sometimes be found but other preferentials of the *Alchemilla-Carex* sub-community are rare. *Carex bigelowii* is infrequent but locally abundant.

Apart from *Galium saxatile*, herbaceous dicotyledons in general are rather uncommon with just occasional *Potentilla erecta* and the only vascular preferentials are *Diphasium alpinum* and *Huperzia selago*, with even these occurring at low frequency. Except for *Pleurozium schreberi* and *Hypnum cupressiforme s.l.*, the pleurocarps common elsewhere are rather inconspicuous here, although *Racomitrium lanuginosum* is more frequent than usual and, along with scattered tufts of *Dicranum scoparium*, there is occasionally a little *Campylopus paradoxus*. Lichens, however, tend to have their best representation here, with *Cladonia arbuscula* showing locally high cover and *C. uncialis* and *C. impexa* preferential at low frequency.

Habitat

The *Vaccinium-Deschampsia* heath is typical of moist but free-draining, base-poor to circumneutral soils over steeper slopes at moderate to high altitudes through the uplands of northern Britain. The generally cold and damp character of the climate is often locally enhanced by a sunless aspect and snow-lie in sheltered situations can play some part in determining the floristics and distribution of the community. At higher levels, this kind of vegetation is probably natural but, towards the sub-montane zone, it may have been derived by burning and grazing and, in some places, treatments have precipitated its spread on to blanket peats.

In broad terms, this community represents an extension to higher altitudes of the kind of mixed sub-shrub vegetation seen in less assiduously managed stands of the *Calluna-Vaccinium* heath (or, through the southern Pennines, its polluted equivalent, the *Calluna-Deschampsia* heath). The *Vaccinium-Deschampsia* heath has

a roughly similar overall geographical range to these two, but they are essentially sub-montane in their distribution, being found mostly between 200 and 600 m and extending into areas where the climate is relatively mild. The *Vaccinium-Deschampsia* heath, by contrast, is largely confined to altitudes above 400 m and it often extends up to 800 m, with a mean height in available samples of around 600 m, and although it can be found over higher ground in Wales, through the Pennines, the Lake District and the Southern Uplands, it is strongly concentrated in northern Scotland, and particularly in the central and eastern Highlands where the climate is distinctly harsh. At these generally higher altitudes the summers are cool, with mean annual maximum temperatures for the most part below 22 °C (Conolly & Dahl 1970) and winters, particularly in the heartlands of its range, are bitter. Such conditions are reflected in the composition of the vegetation in the disappearance of *Erica cinerea*, a rather oceanic plant already at some disadvantage in the *Calluna-Vaccinium* heath, but which here just cannot tolerate the even lower winter temperatures (Bannister 1965); and in the increased frequency of the Arctic-Alpines *V. vitis-idaea* (Ritchie 1955*a*) and *E. nigrum* ssp. *hermaphroditum* as against the more broadly montane ssp. *nigrum* (Bell & Tallis 1973). The fairly common occurrence of *Carex bigelowii*, a third species whose national distribution pattern roughly matches that of the community, also marks this move into the montane zone, though it is by no means as frequent here as in the more exposed bilberry heaths of these altitudes or of the moss-heaths and fell-field vegetation above.

The second climatic effect relates to precipitation. In fact, this is not especially high through much of the range of the community: conditions are very wet towards the north-west Highlands, where annual precipitation can far exceed 1600 mm with over 200 wet days yr^{-1} but, in many areas, the levels are between 1200 and 1600 mm, with 180–200 wet days yr^{-1} (*Climatological Atlas* 1952, Ratcliffe 1968). This is sufficient, however, to maintain a generally humid atmosphere throughout the year, and to keep the soils moist, particularly where the community extends on to shaded and sheltered northern and eastern slopes, a common occurrence. In such situations, too, the winter snow, which can be frequent and heavy through the range of the community but especially so in the central and eastern Highlands (Manley 1940), is able to persist long. Quite often, then, this is a distinctly chionophilous vegetation type, marking out early snow-beds or the fringes of more long-lasting accumulations or just more sheltered sites over generally wind-lashed slopes. Even where snow-lie is not appreciable, however, the prevailingly damp conditions strongly favour the vigorous growth of *V. myrtillus* (Ritchie 1956) and contribute to the poor performance here of *Calluna*. Most stands of the *Vaccinium-Deschampsia* heath do, in fact, occur below the altitudinal limit of *Calluna* but, at these heights, heather tends to be better represented over more exposed slopes where, though often reduced to a tight mat of flattened bushes, it can withstand the bitterly cold, but drier, conditions (Watt & Jones 1948). The difference in exposure and humidity between the two kinds of habitat is also seen in the contrasting cryptogam element in the vegetation cover: whereas it is lichens that predominate among the dwarfed sub-shrubs of the *Calluna-Cladonia* heath and the *Vaccinium-Cladonia* heath that replaces it at higher altitudes, mosses are typically much more abundant beneath the taller but often rather open (and in part deciduous) canopy of the *Vaccinium-Deschampsia* heath. *Dicranum scoparium* and pleurocarps such as *Pleurozium schreberi*, *Hypnum cupressiforme*, *Hylocomium splendens* and *Rhytidiadelphus loreus*, which provide the most consistent contribution, are well able to subsist over the fairly loose damp litter that accumulates beneath the sub-shrubs and among the culms in grassier stands.

The combination of cold with some shelter associated with long snow-lie is probably also of prime importance for the survival of *Phyllodoce* in this kind of vegetation. This is a chionophilous plant throughout its range (Polunin 1948, Dahl 1956) and all its Scottish localities have a northerly or easterly aspect with 100 or more days of persistent snow, lasting sometimes into April. Under normal conditions, fresh growth begins under the protective mantle with the shoots expanding fully after the melt in May or early June and, where frosts occur outside the period of snow-lie, damage to growing points can be permanent (Coker & Coker 1973).

Although rainfall and snow-melt help maintain the soil surface beneath the *Vaccinium-Deschampsia* heath in a generally moist state, this is characteristically a community of moderate to steep slopes cut into pervious, drift-free bedrocks, so drainage is free. The tendency to leaching is also strong, such that the community sometimes extends even on to calcareous rocks like the limestones and more lime-rich schists of the Dalradian assemblage in the central Highlands. There, the soils are of a primitive brown podzolic type, micaceous or rich in silt and sand below, and with a superficial pH of as high as 5.5 (McVean & Ratcliffe 1962). Similar profiles can be found beneath the community over less acidic lavas among the Cheviot rocks (King 1962) and the Silurian shales of the Southern Uplands and Wales (Evans *et al.* 1977). Often, though, the soils are more base-poor than this, having developed from quartzites, sandstones or other siliceous rocks that occur widely through the range of the community. Surface pH can then fall as low as 3.5, though the structure of the profiles can vary from very fragmentary rankers over block scree, a very character-

istic feature of the '*Vaccinium* edges' of the Pennine grits (Moss 1913), to quite shallow but fully-developed podzols. Typically, however, the soils are strongly organic above, the litter and mor humus providing a very congenial medium among which the bilberry rhizomes can grow.

The floristic differences among the sub-communities can be understood partly in relation to variations in these climatic and edaphic variables. The *Hylocomium-Rhytidiadelphus* type of heath, with its quite luxuriant sub-shrub canopy and well-developed suite of lush bryophytes and preferential records for *Vaccinium uliginosum*, *Blechnum* and *Cornus suecica*, is generally associated with higher altitudes, sunless aspects and sheltered situations over siliceous rocks and, where such conditions coincide, the vegetation has a strongly calcifuge and chionophilous character and provides an occasional niche, even in regions of bitter winter climate, for more oceanic plants which benefit from the locally enhanced humidity and freedom from exposure. This kind of *Vaccinium-Deschampsia* heath is thus typical of large shallow snow-beds and the surrounds of deeper nivation hollows throughout the central and eastern Highlands, where it largely corresponds to McVean & Ratcliffe's (1962) *Vaccinio-Empetretum*. There it comes close floristically to the *Vaccinium-Rubus* heath, a community of similar situations in the sub- and low-alpine zones, where the preferentials noted above become more consistent and are often accompanied by *Rubus chamaemorus*, a plant not generally found here. The *Hylocomium-Rhytidiadelphus* sub-community also extends into the north-west Highlands, where it descends to somewhat lower altitudes and is less tied to sheltered aspects, sometimes having more of the oceanic hepatics associated with the *Vaccinium-Calluna-Sphagnum* heath. It can be found, too, over cold, humid slopes in the Southern Uplands, the Lake District, Wales and down the Pennines, though often with a reduced list of associates, particularly in the last region, where even the higher-altitude heaths have been strongly affected by pollution.

The duration of snow-lie over the *Hylocomium-Rhytidiadelphus* sub-community can be considerable, but it is probably not so long as over the *Nardus-Carex bigelowii* snow-bed vegetation; and there, too, the slopes are generally not so steep, so any melt-water drains away less readily. The contrast in habitats between the two kinds of vegetation is well seen in the terrace profiles described from the Cairngorms by Burges (1951) and in the sketches of snow-beds included in McVean & Ratcliffe (1962) and floristically the change from the one to the other involves a shift in dominance from *V. myrtillus* and pleurocarpous mosses to *Nardus*, *C. bigelowii* and *R. lanuginosum*, with lichens sometimes prominent and *Diphasium alpinum* becoming frequent. The *Racomitrium-Cladonia* sub-community includes some stands which can be considered transitional to such vegetation, although even there plants like *Juncus squarrosus* and *Scirpus cespitosus* remain very uncommon. This kind of *Vaccinium-Deschampsia* heath has also been described from wet, humic rankers in the Southern Uplands (Hill & Evans 1978) and it can develop, too, where peaty soils have been burned, either around snow-beds (as in some of the anthropogenic *Vaccinium* heath noted in McVean & Ratcliffe 1962) or on degraded blanket peats at higher altitudes. In the latter kind of situation, *V. myrtillus* and *E. nigrum* are often the sub-shrubs which spread most rapidly over the mire fringes and the *Racomitrium-Cladonia* sub-community sometimes takes in the heathy developments of the kind of retrogressive *Eriophoretum* described from the Pennines (Lewis & Moss 1911, Moss 1913, Fidler *et al.* 1970).

The *Alchemilla-Carex* sub-community represents a different trend of development away from the *Hylocomium-Rhytidiadelphus* type of heath, tending to replace it at somewhat lower altitudes within the overall range of the community and to favour sunnier aspects with less humic and sometimes less base-poor soils. Such slopes are not so cold and humid as those favoured by the *Hylocomium-Rhytidiadelphus* sub-community and they do not accumulate snow for so long, if indeed at all, a shift which encourages the move away from pronounced bilberry dominance towards an abundance of grasses and sedges, with a less luxuriant contribution from the bulkier pleurocarps and even the occasional occurrence of the Oceanic West European *Carex binervis*. Although the bulk of the plants represented are calcifuge to varying degrees, there is often quite a mesophytic character to this kind of *Vaccinium-Deschampsia* heath and the soils, though sometimes fragmentary, often have but a thin layer of mor, with a lithomorphic or brown podzolic structure below. In some cases, too, plants like *Luzula campestris*, *Campanula rotundifolia*, *Viola riviniana*, *Anemone nemorosa* and *Cerastium fontanum*, indicative of more mesotrophic conditions, are joined by *Thymus praecox* and *Carex pulicaris*, a feature particularly well seen over the Dalradian limestones (McVean & Ratcliffe 1962). But the substrates are not always calcareous and, indeed, beneath stands of this sub-community in the Southern Uplands, markedly base-poor soils can occur (King 1962).

In this part of the range of the *Vaccinium-Deschampsia* heath, too, it is very clear that grazing can probably play a major role in favouring the development of the *Alchemilla-Carex* sub-community towards lower altitudes, both by helping tip the balance of dominance away from the palatable *V. myrtillus* towards grasses and by bringing some modest enrichment to the sward through the dunging. Towards the sub-montane zone, therefore, it is possible that the sometimes quite exten-

sive tracts of this vegetation have been biotically derived as a result of woodland clearance and pasturing and, in fact, there is a virtual floristic continuity between the *Alchemilla-Carex* sub-community and, on the one hand, the grazed field layers of our north-western Quercion woods and, on the other, the Nardo-Galion swards of the *Festuca-Agrostis-Alchemilla* grassland. In such situations, then, the *Vaccinium-Deschampsia* heath represents a continuation northwards of the anthropogenic vegetation with bilberry seen in the *Ulex gallii-Agrostis* and *Calluna-U. gallii* heaths. At higher altitudes, the community can probably be seen as a natural climax community, although McVean & Ratcliffe (1962) suggested that marked trampling and fouling might have an effect on montane bilberry vegetation: patches of calcifuge grassland in nivation hollows, for example, appeared to develop where sheep had survived beneath the cover of winter snow.

Zonation and succession

The *Vaccinium-Deschampsia* heath can be seen as a part of altitudinal sequences from sub-montane woodlands, grasslands and sub-shrub vegetation through to high-level moss-heaths and fell-field where transitions reflect increasing harshness of climate above and biotic influences below, with additional zonations to mire communities with edaphic shifts. Within the low-alpine zone, the *Vaccinium-Deschampsia* heath occurs as a climax vegetation type among dwarfed sub-shrub communities and snow-beds, patterns being determined largely by gradients of exposure and snow-lie.

Through much of its range, fragmentation of the forest cover towards the upper limit of the sub-montane zone is such that it is often difficult to see the *Vaccinium-Deschampsia* heath as the high-altitude replacement of woodland or sub-alpine scrub. But the floristic continuity between the different vegetation types is very striking and many of the heath plants form an integral part of the field layers of the Quercion and Dicrano-Pinion woodlands found over more base-poor soils on siliceous bedrocks and drift at lower levels. Towards the west of Scotland and down through northern England and Wales, the *Hylocomium-Rhytidiadelphus* sub-community reaches down to the upper altitudinal limits of the *Quercus-Betula-Dicranum* woodland and, where fragments of this remain in ravines or on screes, they sometimes give way above to a fringe of the bilberry heath (Lewis & Moss 1911, Ferreira 1978). Similar patterns occur in eastern Scotland, too, though here it is the *Pinus-Hylocomium* woodland that probably represents the sub-montane climax vegetation and, around the Cairngorms, the *Hylocomium-Rhytidiadelphus* sub-community replaces it on more sheltered sites above. Here, also, the *Juniperus-Oxalis* scrub can be seen as a convincing intermediate in the sequence, occurring at the natural upper limit of tree growth in some places, though hardly ever in zonations which run right through from the montane heath above to the woodland below. In other places, it is tall-herb vegetation, generally of the *Luzula-Vaccinium* type, or the *Thelypteris limbosperma* community, that provides floristic continuity between the extremes of the sequence, ferns, tall herbs, shrubs and trees thus representing the structural elements appearing towards lower altitudes.

Analogous patterns to these can be seen where less base-poor profiles developed from calcareous substrates are disposed over slopes of increasing altitude. Here, the *Vaccinium-Deschampsia* heath can maintain its representation on the higher ground, but it occurs generally as the *Alchemilla-Carex* sub-community, a replacement well seen in comparing the zonations of the Cairngorms with those of the Breadalbane-Clova area, or in moving across the boundary of siliceous and calcareous rocks on the summit ridge of Carn a'Chlarsaich near The Cairnwell (McVean & Ratcliffe 1962). And, in the sub-montane, the climax forest is the *Quercus-Betula-Oxalis* woodland or the less markedly calcifuge types of *Pinus-Hylocomium* woodland. Again, floristic similarity is obvious, spatial continuity rare because of forest destruction.

The widespread occurrence of woodland clearance and the prevalence of burning and grazing through the sub-montane zone thus often mean that the *Vaccinium-Deschampsia* heath gives way below to anthropogenic sub-shrub communities maintained for sheep or grouse-rearing. Through much of its range, its replacement at lower altitudes is the *Calluna-Vaccinium* heath, with the *Calluna-A. uva-ursi* heath figuring on less infertile soils in eastern Scotland, and the *Calluna-Deschampsia* heath prevailing in the polluted southern Pennines. Heather tends to be an overwhelming dominant in each of these vegetation types and, even where other sub-shrubs play a part, as in the early stages of regeneration after burning, the Arctic-Alpines are generally less prominent than in the bilberry heath, but the floristic similarities are considerable, both among the vascular plants and the cryptogam element. In some situations, as over the crags and screes of the Pennine grits, which rise to higher ground separated by intervening tracts of blanket mire on the dips, the contrast between the sub-montane *Calluna-Deschampsia* heath and the high-altitude *Vaccinium-Deschampsia* heath can be quite striking (Lewis & Moss 1911, Tansley 1939). In other places, the shift to higher ground is also marked by an increase in slope and, on northern exposures, of shade which favour the *Vaccinium-Deschampsia* heath on cool steep talus and cliffs, well seen in Edgell's (1969) map of Cader Idris. But, often, the transition between the vegetation types is a gradual one, and it can be particularly complicated where shelter below favours bilberry, while the extension of treatments on to higher ground favours heather.

Towards its lower altitudinal limits, and particularly

over warmer south-facing slopes, it seems likely that some stretches of the *Alchemilla-Carex* sub-community have been biotically derived and are now maintained as plagioclimax intermediates between the forest types noted above and Nardo-Galion grasslands. In parts of the Southern Uplands, for example, in the Cheviot (King 1962), Breadalbane (McVean & Ratcliffe 1962) and Caenlochan (Huntley 1979), this kind of *Vaccinium-Deschampsia* heath is commonly found among *Festuca-Agrostis-Thymus* and *Festuca-Agrostis-Alchemilla* grasslands, the disposition of the different elements of the mosaics being a rather complex function of treatments, topoclimate and edaphic factors (King 1962, Huntley 1979). Zonations to the *Festuca-Agrostis-Alchemilla* grassland can be especially gradual, but the difference between the communities is partly one of the proportions of sub-shrubs to grasses and *A. alpina* and partly to do with the more frequent occurrence of mesophytes and mildly calcicolous plants in the grassland.

With increasing altitude, however, and a decisive shift into the low-alpine zone of the higher mountains within the range of the *Vaccinium-Deschampsia* heath, it is natural factors, particularly exposure and snow-lie, which determine the major trends in the vegetation patterns. Thus, wherever there is a move on to slopes which feel the force of strong winds and which are thus blown clear of snow, the community tends to be replaced by dwarfed sub-shrub vegetation in which *V. myrtillus* plays but a small role and where stunted heather is generally abundant. In the central and eastern Highlands, such vegetation is usually of the *Calluna-Cladonia* heath, where the lichens which are generally of small cover in the *Vaccinium-Deschampsia* heath assume a sometimes co-dominant role and where distinctly chionophobous species can be found. In the opposite direction, with an increase in the duration of snow-lie, the *Vaccinium-Deschampsia* heath is replaced by *Nardus-Carex* vegetation, with its shift to abundance of *Nardus* and *C. bigelowii* and preferentially frequent *Scirpus cespitosus* and *Juncus squarrosus*. Zonations between these communities can be found disposed over slopes of differing aspect, around nivation hollows (McVean & Ratcliffe 1962) and over the treads and risers of terraced slopes (Burges 1951), where sometimes quite subtle variations in inclination and shelter are sufficient to influence the balance between the species. A further complication in some sites is the occurrence among these sequences of the *Vaccinium-Rubus* heath, a vegetation type that seems equally chionophilous to the *Vaccinium-Deschampsia* heath, but where *Calluna* can maintain a better representation, with *Rubus chamaemorus* preferentially frequent.

Sometimes, too, the *Vaccinium-Cladonia* heath can be found at similar altitudes to the *Vaccinium-Deschampsia* heath. Like the *Calluna-Cladonia* heath, this is very lichen-rich vegetation in which sub-shrubs are often reduced to a co-dominant role, but it is not a chionophobous community: indeed, it probably experiences similar duration of snow-lie to the *Vaccinium-Deschampsia* heath. *V. myrtillus* maintains its frequency there and both *E. nigrum* ssp. *hermaphroditum* and *V. vitis-idaea* are common, the former often in abundance. But *Cladonia* spp. are much more plentiful along with *Carex bigelowii* and this is a vegetation type which can extend to higher levels than the *Vaccinium-Deschampsia* heath, representing a transition to the *Juncus-Racomitrium* or *Carex-Racomitrium* heath on summit fell-fields. The *Racomitrium-Cladonia* sub-community can sometimes be found as a transition to these low-alpine communities.

With the geographical shift towards the north-west Highlands the elements in these zonations tend to move to somewhat lower altitudes and, in some cases, to be replaced by more oceanic equivalents. The *Vaccinium-Deschampsia* heath can still be found in this part of Scotland, although in this scheme, some of the vegetation which McVean & Ratcliffe (1962) grouped within their *Festuceto-Vaccinetum rhacomitrosum* is transferred to the *Vaccinium-Racomitrium* heath. With its typically western abundance of *R. lanuginosum*, this community, together with the local stands of *Vaccinium-Deschampsia* heath, occupies part of the low-alpine zone, being replaced below by the *Calluna-Vaccinium-Sphagnum* heath, where oceanic hepatics can play a prominent role, and passing at higher altitudes to *Carex-Racomitrium* heath. Sub-shrub vegetation dependent on a humid climate, is, in this part of Britain, less strictly confined to shaded aspects but transitions to *Nardus-Carex* vegetation can be seen where snow persists and the community is also found among stretches of the chionophilous *Deschampsia-Galium* grassland. Over exposed spurs in this part of Scotland, the *Vaccinium-Deschampsia* heath is replaced by the *Calluna-Racomitrium* or *Calluna-A. alpinus* heaths.

Distribution

The community is widespread through the uplands of Britain, but is particularly common in northern Scotland, where the heart of its range occurs in the central and eastern Highlands with more sporadic occurrences to the north-west. All the sub-communities can be found throughout the distribution, but the *Alchemilla-Carex* type is especially characteristic of the Breadalbane-Clova region.

Affinities

Early accounts of this kind of vegetation (Smith 1900, Smith & Moss 1903, Smith & Rankin 1903, Lewis & Moss 1911, Moss 1913, Tansley 1939) tended to concentrate on the dominance of bilberry as opposed to heather as its major distinguishing feature, and indeed there is

ecological meaning in the recognition of a *Vaccinetum* alongside a *Callunetum*. Variations within these broad categories were, however, recognised from the start in vegetation types like the *Gramino-Vaccinetum* of Smith (1911*b*), the kind of heath transitional to Nardo-Galion grasslands included in McVean & Ratcliffe's (1962) *Festuceto-Vaccinetum* (see also Poore 1955*b*, King 1962, Evans *et al.* 1977, Ferreira 1978). In this scheme, however, this vegetation, subsumed in the *Alchemilla-Carex* sub-community, is united in the *Vaccinium-Deschampsia* heath with the less grassy bilberry-crowberry stands first described in detail by Burges (1951) and included in the *Vaccineto-Empetretum* of McVean & Ratcliffe (1962: see also Poore & McVean 1957, Birse 1980). This *Hylocomium-Rhytidiadelphus* sub-community represents the core of the revised vegetation type locating it among the mildly chionophilous communities of Nordhagen's (1943) Phyllodoco-Vaccinion myrtilli alliance. Included here would be such Scandinavian relatives of the *Vaccinium-Deschampsia* heath as the *Phyllodoco-Vaccinetum*, an extensive association of the Rondane (Dahl 1956), and the oceanic *Vaccinetum* with *Cornus suecica* from western Norway (Nordhagen 1943). More lichen-rich stands among the *Alchemilla-Carex* and particularly the *Racomitrium-Cladonia* sub-community could then be seen as a link with the fell-field vegetation of the Loiseleurieto-Arctostaphylion.

Floristic table H18

	a	b	c	18
Vaccinium myrtillus	V (1–10)	V (4–8)	V (1–10)	V (1–10)
Deschampsia flexuosa	V (1–6)	V (1–8)	V (1–8)	V (1–8)
Galium saxatile	V (1–4)	V (1–8)	V (1–6)	V (1–8)
Dicranum scoparium	IV (1–3)	IV (1–2)	IV (1–4)	IV (1–4)
Pleurozium schreberi	V (1–8)	V (1–8)	III (1–6)	IV (1–8)
Hylocomium splendens	V (1–10)	IV (1–8)	I (1–4)	III (1–10)
Rhytidiadelphus loreus	IV (1–6)	II (1–4)	II (1–6)	III (1–6)
Blechnum spicant	III (1–4)	II (1–3)		II (1–4)
Plagiothecium undulatum	II (1–4)	I (1–3)	I (1–4)	I (1–4)
Dicranum majus	II (1–9)	I (1–4)	I (1–2)	I (1–9)
Melampyrum pratense	II (1–4)	I (1–3)	I (1–3)	I (1–4)
Barbilophozia floerkii	II (1–3)	I (1–3)	I (1–3)	I (1–3)
Sphagnum capillifolium	II (1–8)	I (1–3)	I (1–4)	I (1–8)
Luzula sylvatica	II (1–6)	I (1–4)	I (1–3)	I (1–6)
Oxalis acetosella	II (1–4)	I (1–3)		I (1–4)
Vaccinium uliginosum	II (1–6)			I (1–6)
Cornus suecica	II (1–4)			I (1–4)
Hylocomium umbratum	I (1–4)			I (1–4)
Sphagnum quinquefarium	I (1–4)			I (1–4)
Ptilium crista-castrensis	I (1–4)			I (1–4)
Anastrepta orcadensis	I (1–4)			I (1–4)
Festuca ovina	II (1–4)	IV (1–8)	IV (1–10)	III (1–10)
Potentilla erecta	III (1–3)	IV (1–4)	II (1–4)	III (1–4)
Agrostis capillaris	II (1–8)	IV (1–6)	II (1–4)	III (1–8)
Anthoxanthum odoratum	II (1–4)	IV (1–6)	II (1–4)	III (1–6)
Rhytidiadelphus squarrosus	II (1–4)	IV (1–8)	II (1–4)	III (1–8)
Alchemilla alpina	II (1–4)	IV (1–6)	I (1–6)	III (1–6)
Carex pilulifera	I (1–3)	IV (1–4)	II (1–3)	II (1–4)
Luzula campestris		IV (1–4)	I (1–3)	II (1–4)
Campanula rotundifolia	I (1–3)	III (1–3)	I (1–3)	II (1–3)
Carex binervis	I (1–3)	II (1–4)	I (1–3)	I (1–4)

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Polygala serpyllifolia	I (1–3)	II (1–3)	I (1–3)	I (1–3)
Viola riviniana	I (1–3)	II (1–4)		I (1–4)
Ranunculus acris	I (1–3)	II (1–3)		I (1–3)
Rumex acetosa	I (1–3)	II (1–3)		I (1–3)
Deschampsia cespitosa	I (1–4)	II (1–4)		I (1–4)
Danthonia decumbens		II (1–3)	I (4)	I (1–4)
Anemone nemorosa		II (1–4)	I (1–3)	I (1–4)
Cerastium fontanum		II (1–3)	I (1–3)	I (1–3)
Veronica officinalis		II (1–4)		I (1–4)
Thymus praecox		I (1–4)		I (1–4)
Alchemilla glabra		I (1–4)		I (1–4)
Polygonum viviparum		I (1–3)		I (1–3)
Racomitrium lanuginosum	I (1–6)	II (1–4)	III (1–4)	II (1–6)
Diphasium alpinum	I (1–3)	I (1–3)	II (1–4)	I (1–4)
Cladonia impexa	I (1–3)	I (1–3)	II (1–6)	I (1–6)
Campylopus paradoxus	I (1–3)	I (1–3)	II (1–4)	I (1–4)
Huperzia selago	I (1–3)	I (1–3)	II (1–3)	I (1–3)
Cladonia uncialis	I (1–3)	I (1–3)	II (1–3)	I (1–3)
Hypnum cupressiforme s.l.	III (1–6)	III (1–6)	III (1–8)	III (1–8)
Nardus stricta	III (1–6)	III (1–4)	III (1–4)	III (1–6)
Empetrum nigrum	III (1–10)	II (1–4)	III (1–6)	III (1–10)
Vaccinium vitis-idaea	III (1–6)	III (1–4)	II (1–4)	III (1–6)
Cladonia arbuscula	III (1–6)	II (1–6)	III (1–4)	III (1–6)
Calluna vulgaris	III (1–8)	II (1–6)	II (1–4)	III (1–8)
Polytrichum commune	II (1–6)	II (1–4)	II (1–4)	II (1–6)
Agrostis canina montana	II (1–4)	II (1–6)	II (1–6)	II (1–6)
Carex bigelowii	II (1–4)	II (1–4)	II (1–6)	II (1–6)
Ptilidium ciliare	II (1–4)	II (1–4)	II (1–3)	II (1–4)
Dryopteris dilatata	I (1–4)	I (1–3)	I (1–3)	I (1–4)
Thuidium tamariscinum	I (1–4)	I (1–3)	I (1–3)	I (1–4)
Rhytidiadelphus triquetrus	I (8)	I (1–5)	I (1–3)	I (1–8)
Festuca rubra	I (1–6)	I (1–4)	I (1–4)	I (1–6)
Cryptogramma crispa	I (1–3)	I (1–3)	I (1–4)	I (1–4)
Juncus squarrosus	I (1–3)	I (1–4)	I (1–6)	I (1–6)
Festuca vivipara	I (1–4)	I (1–8)	I (1–6)	I (1–8)
Polytrichum alpestre	I (1–6)	I (1–4)	I (1–3)	I (1–6)
Polytrichum alpinum	I (1–4)	I (1–4)	I (1–4)	I (1–4)
Carex panicea	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Diplophyllum albicans	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Pohlia nutans	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Cladonia pyxidata	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Cetraria islandica	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Cladonia rangiferina	I (1–6)	I (1–4)	I (1–3)	I (1–6)
Cladonia gracilis	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Luzula multiflora	I (1–3)	I (1–3)	I (1–3)	I (1–3)
Solidago virgaurea	I (1–3)	I (1–3)		I (1–3)
Euphrasia officinalis agg.	I (1–3)	I (1–3)		I (1–3)
Number of samples	73	39	58	170
Number of species/sample	20 (9–41)	28 (11–44)	18 (5–33)	21 (5–44)

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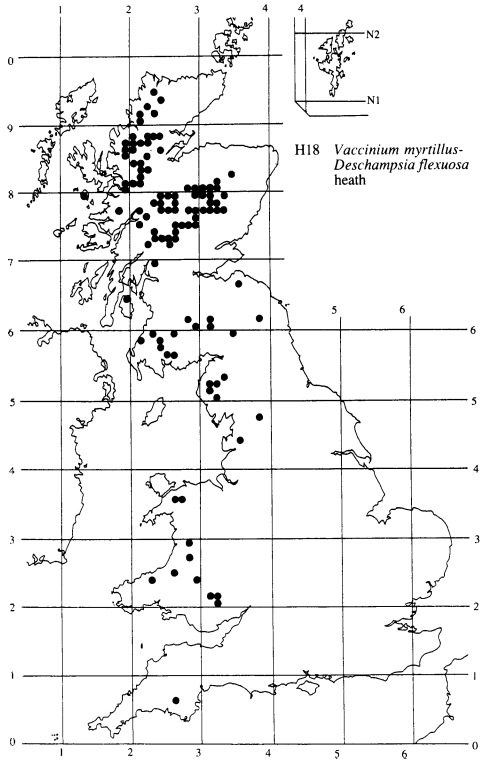
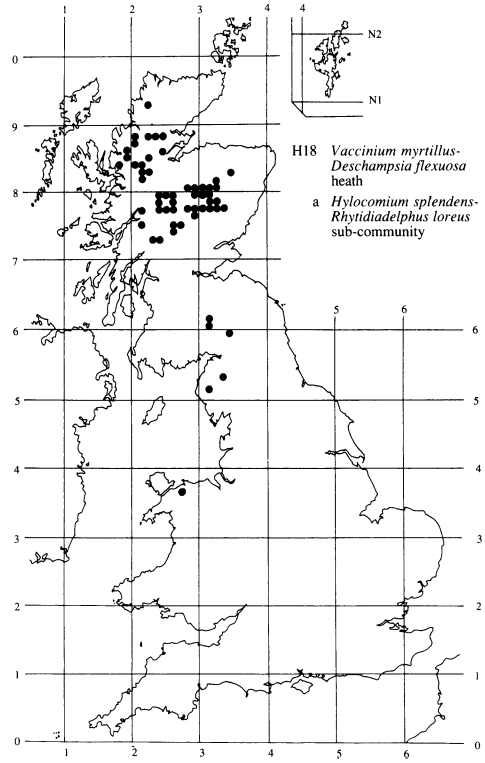
Floristic table H18 *(cont.)*

	a	b	c	18
Vegetation height (cm)	16 (6–38)	11 (1–40)	12 (2–35)	13 (1–40)
Vegetation cover (%)	96 (10–100)	91 (65–100)	85 (50–100)	92 (10–100)
Altitude (m)	650 (30–910)	558 (198–914)	623 (210–950)	598 (30–950)
Slope (°)	28 (3–70)	29 (2–80)	20 (0–75)	26 (0–80)

a *Hylocomium splendens-Rhytidiadelphus loreus* sub-community
b *Alchemilla alpina-Carex pilulifera* sub-community
c *Racomitrium lanuginosum-Cladonia* spp. sub-community
18 *Vaccinium myrtillus-Deschampsia flexuosa* heath (total)





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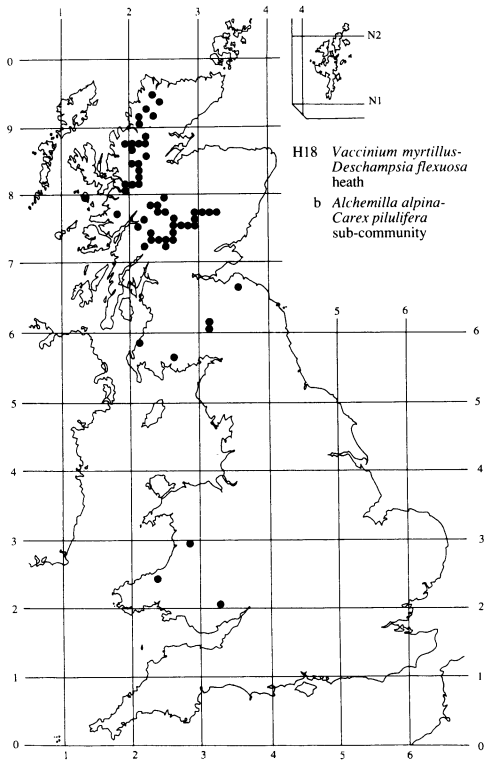

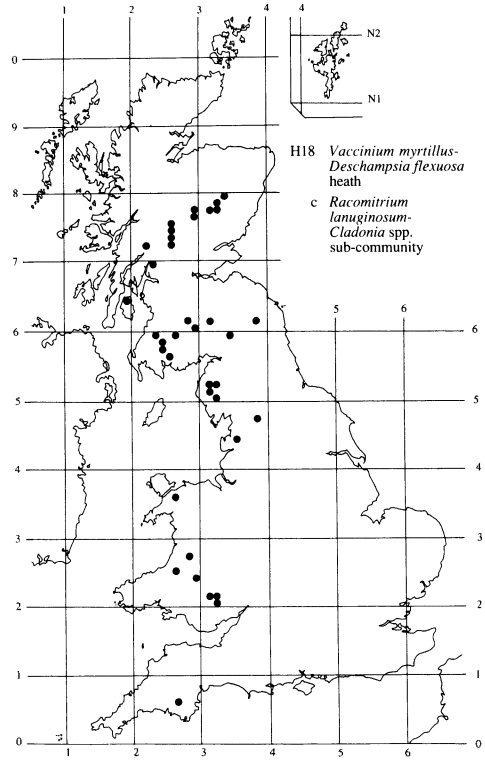

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