H7

Calluna vulgaris-Scilla verna heath

Synonymy

Festuca ovina-Calluna 'Rock Heath' Coombe & Frost 1956a p.p.; Erica vagans-Ulex europaeus 'Mixed Heath', Genista pilosa variant Coombe & Frost 1956a; Calluno-Scilletum vernae Malloch 1971 p.p.; Maritime heath Urquhart & Gimingham 1979 p.p.; Genisto maritimae-Ericetum cinereae Bridgewater 1970; Anthyllio corbierei-Ericetum cinereae Bridgewater 1970; Festuca ovina-Calluna vulgaris heath Hopkins 1983; Erica vagans-Ulex europaeus heath, Genista pilosa variant Hopkins 1983.

Constant species

Calluna vulgaris, Erica cinerea, Festuca ovina, Holcus lanatus, Hypochoeris radicata, Lotus corniculatus, Plantago lanceolata, P. maritima, Potentilla erecta, Scilla verna, Thymus praecox.

Rare species

Allium schoenoprasum, Astragalus danicus, Erica vagans, Euphorbia portlandica, Genista pilosa, Herniaria ciliolata, Isoetes histrix, Minuartia verna, Primula scotica, Scilla autumnalis, S. verna, Spiranthes spiralis, Trifolium bocconei, T. occidentale.

Physiognomy

In the Calluna vulgaris-Scilla verna heath, sub-shrubs are a consistent feature of the vegetation, though they are not always very obvious at first sight. For one thing, the canopy is typically of very short stature, rarely over 20 cm and usually less than 10 cm, with the bushes often wind-shaped over the unconformities of the ground. Then, the cover of the woody plants is rarely continuous and quite often rather open, particularly in unsheltered or rocky situations where it can be reduced to scattered bushes with stretches of grassy sward or exposures between. Even where the sub-shrubs are more extensive, their branches are commonly inter-penetrated by the herbs and, in grazed sites, which occur throughout the range of the community but which are especially preva-

lent to the north, the whole vegetation can be trimmed to a neat, tight mat, just 2 or 3 cm high.

Of the sub-shrubs, Calluna vulgaris is the most frequent throughout and the commonest dominant though, on drier soils, it is characteristically accompanied by Erica cinerea and this, too, can be abundant. Where the community extends on to wetter ground, as it often does in the rainier north of the country, the latter is much reduced in frequency and E. tetralix and/or Empetrum nigrum ssp. nigrum (generally one or the other) are the more usual associates of Calluna and sometimes codominant with it.

No other woody species occurs frequently throughout. Ulex gallii can occasionally be found but it is generally excluded by the salt-spray characteristic here and the vegetation which Malloch (1971) included in a U. gallii sub-association of his Calluno-Scilletum is in this scheme transferred to the essentially non-maritime Calluna-U. gallii heath. U. europaeus is even more sensitive to salt-spray and it occurs only occasionally and then on deeper and better-drained soils. On the Lizard, in Cornwall, however, the nationally rare E. vagans can extend a little way into the zone occupied by this community, in vegetation which Coombe & Frost (1956a) and Hopkins (1983) included within their E. vagans-Ulex heaths. At this site, too, and at various other places around the south-west coast of Britain, the Calluna-Scilla heath provides one locus for prostrate ecotypes of Cytisus scoparius, Genista tinctoria and the rare G. pilosa. Juniperus communis (probably ssp. communis, though often of diminutive habit) also survives very locally in the community in this part of the country and at a few sites in south-west Scotland. On wetter ground, Salix repens can be locally prominent.

Among the herbaceous associates growing among and between the sub-shrubs, grasses often bulk fairly large, though the species involved are few and the plants are usually found as small tussocks or as rather indistinguishable components of a closely-nibbled sward. Festuca ovina (including some records for F. vivipara in

Scotland) is by far the most frequent grass, though F. rubra also occurs quite commonly and the two may be difficult to separate in short turf. Very common, too, though not generally of high cover, is Holcus lanatus, often accompanied by Dactylis glomerata on drier soils, or by Danthonia decumbens on moister ground. In the wetter, northern heaths of this community, too, Agrostis capillaris and Anthoxanthum odoratum become very common and they can be quite abundant. Molinia caerulea, however, is rather infrequent, even where the vegetation makes its closest approach to Ericion tetralicis heath in the *Erica* sub-community, and, in southwest Britain, that common companion of Molinia in damper heaths, Agrostis curtisii, typically stops short of the zone occupied by this community. Scattered patches of bare soil can provide an occasional niche for the annual grasses Aira praecox and A. caryophyllea.

In this grassy ground is found a variety of other herbs which help make this community one of our most consistently rich lowland heaths. Most distinctive among the constants are Plantago maritima and Scilla verna: these two species also occur fairly often in more maritime stands of the Calluna-U. gallii heath and S. verna extends through much of the E. vagans-Ulex heath on the Lizard, but nowhere else among British subshrub communities are they both so frequent overall. Scilla verna is typically present as scattered individuals, striking in spring with its violet-blue flowers, but in leaf only in the wetter months of the year and, even then, easily missed amongst the grasses. S. autumnalis, which can also be found here at a few localities in south-west England, shows a similar pattern of foliar development, though its bractless and more purple flowers appear from July to September. Plantago maritima, on the other hand, is often very conspicuous, its rosettes being especially numerous in heavily-grazed swards, and other hemicryptophytes occur frequently too, P. lanceolata being common throughout, Hypochoeris radicata tending to favour drier soils. Potentilla erecta is common on all but the most parched and maritime soils, but usually more abundant are mats of Lotus corniculatus and the chamaephyte Thymus praecox which add prominent splashes of colour to the vegetation in summer. Also noticeable in this respect, though more strongly confined than these species to drier soils, is Anthyllis vulneraria, banks of which can be locally dominant over broken ground and very striking. Finally, among this group, are the Euphrasia spp., of which E. tetraquetra is the most common, these finding a place in small patches of open ground.

Then, there are species which, though occurring occasionally throughout, are rather unevenly represented in the different sub-communities, being to some degree or other preferential for particular environmental conditions. Certain sedges belong among this group, *Carex*

flacca and C. caryophyllea favouring the more freedraining and base-rich profiles, C. panicea and C. nigra extending on to wetter and more acidic soils. Viola riviniana and Succisa pratensis are also more frequent on moister ground with, less commonly, Trifolium repens, Cerastium fontanum, Luzula campestris and Leontodon autumnalis. In drier situations, Daucus carota ssp. gummifer, Polygala vulgaris and Leontodon taraxacoides are occasionally found and, on the most parched and exposed ground on cliff tops, some more maritime species and therophytes.

Such trends as these, among both the woody and herbaceous plants, help define the different sub-communities of this quite variable kind of heath. Locally, stands can gain further individuality by the occurrence of rare species which, in this widespread community, show a diversity of phytogeographical affinities. On the Lizard, for example, the community can provide a locus not only for E. vagans, but also for Herniaria ciliolata, Isoetes histrix, Trifolium occidentale and T. bocconei and for the peculiarly far-flung Minuartia verna; extending somewhat further around the Cornish coast is Scilla autumnalis and, spreading much further northwards, Euphorbia portlandica and Spiranthes spiralis. Then, on the north Scottish coast, Primula scotica can be found here and, particularly on the coast of north-east Scotland, Astragalus danicus.

The general richness of the vascular flora is not matched by the cryptogams, which are very few in number and never of high cover. Among the mosses, only *Hypnum cupressiforme* attains moderate frequency, though rockier stands can have some *Trichostomum brachydontium* and, on base-rich substrates, *Homalothecium sericeum* (as in Hopkins' (1983) samples). *Frullania tamarisci* is the commonest hepatic and, even then occurs fairly infrequently. *Cladonia rangiformis*, *C. chlorophaea*, *C. impexa* and *C. subrangiformis* can occasionally be found, usually in small amounts.

Sub-communities

Armeria maritima sub-community: Festuca ovina-Calluna 'Rock Heath' Coombe & Frost 1956a p.p.; Calluno-Scilletum vernae, Armeria maritima subassociation Malloch 1971; Festuca ovina-Calluna vulgaris heath Hopkins 1983. The canopy of sub-shrubs here is generally less extensive than in other sub-communities, usually having a mosaic of more open areas or quite often being reduced to discrete patches of bushes, wind-pruned and almost prostrate, growing in pockets of soil among rock outcrops. Even Calluna cannot maintain high cover in this vegetation in very exposed situations and E. cinerea shows a general reduction in both frequency and abundance though, with a measure of shelter, it can attain co-dominance. The other common

woody species of the community, E. tetralix, Empetrum and the Ulex spp., are all either extremely scarce or absent though, at some sites, scattered bushes of Juniperus can be found, and, in south-west England, prostrate ecotypes of Cytisus, Genista tinctoria and G. pilosa.

Growing among and between the low bushes, Festuca ovina, sometimes with F. rubra, is the usual dominant in the herbaceous component, frequently with a little Holcus lanatus and, weakly preferential to this subcommunity, Dactylis glomerata. Compared with maritime heath in northern Britain, however, Agrostis capillaris and Anthoxanthum are rather infrequent and Danthonia, too, occurs only rarely. Sedges are also poorly represented. Apart from *Potentilla erecta*, which is unusually scarce, all the other community constants are well represented. Scilla verna (accompanied at some sites in the south-west by S. autumnalis) is very common at low cover and there are frequent plants of Hypochoeris radicata, Plantago lanceolata and P. maritima, with P. coronopus also figuring here occasionally, these rosette hemicryptophytes being particularly abundant where grazing is locally heavy. Often, however, it is the extensive patches of Lotus corniculatus and Thymus praecox that catch the eye, together with a variety of preferential herbs characteristic of maritime vegetation of rocky outcrops. Important among these are Armeria maritima and Sedum anglicum, both of which, growing as chamaephytes, can form prominent mats or cushions. Anthyllis vulneraria, too, is rather more common here than elsewhere in the community and can be locally abundant and occasionally there are a few plants of Silene vulgaris ssp. maritima. Then, Jasione montana is very frequent and small patches of bare ground, especially common around the rock exposures where the thin mantle of soil becomes easily parched, often have some ephemerals, such as Aira caryophyllea, A. praecox, Centaurium erythraea, Cerastium diffusum ssp. diffusum, Bromus hordeacus ssp. ferronii and, on the Lizard, the rare annual clovers Trifolium bocconei and T. occidentale (Coombe & Frost 1956a, Coombe 1961, Hopkins 1983).

Other species occurring occasionally here include Daucus carota ssp. gummifer, Rumex acetosa, Polygala vulgaris, Viola riviniana, Leontodon taraxacoides, Leucanthemum vulgare and Hypericum humifusum. On the Lizard, the sub-community also provides a locus for Herniaria ciliolata, Minuartia verna and Isoetes histrix. Somewhat more widely distributed is Allium schoenoprasum and, at some Scottish sites, Astragalus danicus can be found.

On shallow soils among rocks, mosses such as *Trichostomum brachydontium*, *Weissia* spp. and *Homalothecium sericeum* may be quite common here, together with a variety of *Cladonia* spp. (as in Hopkins's 1983 data).

Viola riviniana sub-community: Erica vagans-Ulex europaeus 'Mixed Heath', Genista pilosa variant Coombe & Frost 1956a; Calluno-Scilletum vernae, Viola riviniana subassociation Malloch 1971; Erica vagans-Ulex europaeus heath, Genista pilosa variant Hopkins 1983. The sub-shrub canopy in this sub-community is generally more extensive than in the last, though not usually any taller, and both Calluna and E. cinerea are very frequent, often co-dominating. E. tetralix and Empetrum are typically very scarce, even in stands in the wetter north of Britain, but both U. europaeus and U. gallii can occasionally be found and, on the Lizard, E. vagans can extend into this kind of heath in considerable abundance. There, too, Genista pilosa is quite common.

In general, however, it is in the herbaceous element that the most distinctive features of the vegetation are to be found. All the community constants are well represented and, among these and the preferential species, grasses and sedges are especially prominent. In addition to Festuca ovina, which is particularly frequent and plentiful, Holcus lanatus and Danthonia decumbens are common, and Agrostis stolonifera, A. capillaris and Anthoxanthum occasional. Koeleria macrantha can also sometimes be found. Then, Carex flacca and C. caryophyllea are strongly diagnostic of this kind of Calluna-Scilla heath, and the former can be quite abundant.

Among the dicotyledons, this sub-community shares with the last occasional records for *Polygala vulgaris*, *Anthyllis vulneraria*, *Leontodon taraxacoides* and *Daucus carota* ssp. *gummifer*. More strikingly preferential is *Viola riviniana* with, rather less frequent, *Galium verum*, *Achillea millefolium* and, often occurring together in the more southerly part of the range of this heath type, *Serratula tinctoria* and *Stachys betonica*, the latter often as a dwarf ecotype, 5–10 cm tall. *Succisa pratensis* also becomes common here, a floristic feature which continues into the damper heaths of the *Erica* and *Empetrum* sub-communities.

Erica tetralix sub-community. Two features in particular distinguish this kind of Calluna-Scilla heath. First, among the sub-shrubs, E. cinerea is much reduced and largely replaced as the usual companion to Calluna by E. tetralix, with Empetrum nigrum ssp. nigrum and Salix repens occasionally present too. The canopy is typically extensive, though again usually of very short stature with the ericoids often very obviously nibbled by herbivores into a tight, densely-branched cover. The impact of grazing is often evident, too, among the herbs and this, together with a shift towards plants of moister and more base-poor soils, constitutes the second diagnostic character. As in the Viola sub-community, grasses are prominent but here F. ovina is quite often replaced by F. rubra as the most abundant species and Agrostis capillaris, Anthoxanthum and Danthonia are also very common and, on occasion, co-dominant in a mixed sward. Sometimes, too, there is locally abundant *Molinia* and *Nardus stricta* can also be found. *Holcus lanatus*, by contrast, is much reduced and *Dactylis* is rare. Among the sedges, *C. flacca* is hardly ever found but *C. nigra* is frequent and *C. panicea* occasional. *Luzula campestris* becomes moderately common as scattered plants.

Among the other species, *Plantago maritima* is often particularly abundant here with *P. lanceolata* also common though not usually so prominent. *Hypochoeris radicata*, however, fares badly on these moist soils and *Thymus praecox* also shows some reduction in frequency and cover. *Viola riviniana* remains quite common but a better preferential among the dicotyledons is *Succisa pratensis*, though it is often nibbled down to a small basal rosette. *Cerastium fontanum, Leontodon autumnalis, Trifolium repens* and *Prunella vulgaris* can all occur occasionally and sometimes there can be a little *Selaginella selaginoides*.

On the moist soil surface, *Hypnum cupressiforme s.l.* and *Frullania tamarisci* are fairly frequent.

Empetrum nigrum ssp. nigrum sub-community. This kind of Calluna-Scilla heath shares a number of features with the last. E. cinerea, for example, is only very occasionally found, though here its usual replacement is Empetrum nigrum ssp. nigrum which is often co-dominant with Calluna in a low but generally extensive canopy. E. tetralix and Ulex spp. are rare. Then, among the bushes, F. ovina, F. rubra, A. capillaris and Anthoxanthum are all again frequent with Carex panicea also common, C. nigra more occasional. Danthonia decumbens, however, is much scarcer than in the Erica sub-community. Luzula multiflora joins L. campestris as an occasional.

Among the rosette dicotyledons, *Plantago maritima* and *P. lanceolata* are once more very frequent, the former especially being abundant where grazing is heavy, and *Hypochoeris radicata* is again very rare on the moist soils. *Thymus praecox* and *Lotus corniculatus*, though common, both tend to have low covers and *Succisa* is less frequent than in the *Erica* sub-community. *Trifolium repens* and *Rumex acetosa* occur fairly often and *Cerastium fontanum* and *Leontodon autumnalis* are occasional. Among rarer species, *Astragalus danicus* is found in eastern Scotland and, on the north Scottish coast, *Primula scotica* can be locally frequent.

Calluna vulgaris sub-community: Species-poor Calluno-Scilletum vernae Malloch 1971. In its general floristics, this type of Calluna-Scilla heath resembles impoverished versions of the Armeria and Viola sub-communities, though it generally has a somewhat taller canopy. Calluna is the usual dominant, often forming a windwaved cover of quite large bushes, though E. cinerea is

common and sometimes abundant. All other sub-shrubs are scarce.

F. ovina is the most frequent grass, with F. rubra less common and usually less abundant, and Agrostis capillaris and Anthoxanthum only occasional and generally of low cover. Hypochoeris radicata is quite frequent but rosette herbs as a whole are rather poorly represented in the fairly rank herbage with both Plantago maritima and P. lanceolata reduced in frequency and cover. Thymus and Lotus, though very common, are often not very abundant. Some stands have a little Armeria, Sedum anglicum, Dactylis, Daucus and Anthyllis with the vegetation disposed over steeper rocky ground; in others, Viola riviniana, Potentilla erecta and Luzula campestris are the commonest associates. But such enrichment is modest and not consistently maintained throughout.

Habitat

The Calluna-Scilla heath occurs over a wide variety of moderately base-poor soils on the less exposed parts of maritime cliffs around much of the coast of Britain. Floristic and structural variation within the community is influenced by climatic and edaphic differences through this considerable geographic range and over particular stretches of cliff. Grazing also affects the composition and appearance of the vegetation and probably contributes to maintaining it against successional change.

The single most distinctive difference between the habitat of this kind of heath and the habitats of other sub-shrub communities is the input of sea-salts from spray, generated by breaking waves and carried inland by the wind. The overall distribution of the community, concentrated in a narrow zone on cliffs around the west coast and then running along the northern and eastern seaboards of Scotland, reflects the general prevalence over the British Isles of south-westerly winds with their long Atlantic fetch and, in the far north-east, the local occurrence of north-westerlies blowing down from the Arctic (Shellard 1976). The Calluna-Scilla heath is absent from the more sheltered east coast of England and, where sub-shrub vegetation occurs there close to the sea, it is of an inland heath type. Along much of the south coast, east of Devon, exposure can be high, but many of the otherwise suitable sites for the development of the community are on calcareous rocks, the one kind of hard cliff substrate which cannot support this vegetation.

Of the various chemical constituents of sea-spray, sodium chloride is the most influential on vegetation and the striking effect of heavy deposition is sometimes to be seen here, particularly after strong gales in hot summer weather, in the scorching of the sub-shrubs on their windward side. Compared with almost all other vegetation of maritime cliffs, however, the amount of salt deposition here, measured in terms of soil sodium/loss

on ignition (Malloch 1972), is low: on average, about half that recorded in the Festuca-Holcus and Festuca-Plantago grasslands which characteristically replace the community to seaward. The deposition of spray falls off very rapidly with distance from the point of its production (Malloch 1970, 1972) and, in cliff zonations, the Calluna-Scilla heath is thus typically found towards the inner limit of the unenclosed vegetation over relatively gentle slopes. And its abundance, in relation to other more maritime communities, increases with the relative shelter that a local switch to an easterly aspect brings, or with the greater height of the cliffs or where they are bevelled, profiles which set back the upper levels far from the breaking waves.

Apart from observable damage, salt or chloride may influence the water balance of tissues or soils or affect cell metabolism, limiting the vigour of more sensitive species or excluding them altogether, and conferring an absolute or relative advantage on more tolerant ones. In fact, as one might expect from its general position in zonations, the number of strictly maritime species occurring in the community is small. Among the constants, only Scilla verna and Plantago maritima have general distributions which are largely confined to the coast and such species as Armeria maritima, Plantago coronopus and Silene vulgaris ssp. maritima are of limited occurrence. Nonetheless, this small assemblage provides a positive distinction between the Calluna-Scilla heath and all other sub-shrub communities. Some of these plants can be found sporadically towards the seaward limit of some other heaths, like the E. vagans-U. europaeus and Calluna-U. gallii heaths, and S. verna in particular can extend a long way inland in some areas, as on the Lizard in Cornwall, but they do not occur consistently throughout these communities or any of their sub-types. Moreover, the gorse spp. and E. vagans do not penetrate far into the Calluna-Scilla heath because of their sensitivity to salt. In general, therefore, the community occupies the intermediate zone between such inland heaths, or scrub (though these have often been reclaimed, of course) and the limit of final extinction of the most salt-tolerant of the sub-shrubs. And over this zone, the absence of bulkier woody species, and the frequently limited vigour of those which persist in the exposed environment, play an important part in encouraging the species-richness of this kind of heath.

The degree of maritime influence up and along seacliffs, interacting with local and regional variations in climate and soils, exerts a strong control on the floristics and distribution of the different kinds of *Calluna-Scilla* heath. In the *Armeria* sub-community, for instance, salt-spray deposition is high and *Calluna*, the most tolerant of the sub-shrubs occurring throughout the whole range of the community, is generally the leading woody plant, though its cover is often discontinuous, and the bushes

wind-waved or windcut and sometimes scorched; and *E. cinerea*, which is more sensitive, is reduced in vigour. Here, too, maritime herbs have their strongest representation.

At this limit of the heath zone on sea-cliffs, maritime influence tends to override smaller differences in substrates and soils, so the Armeria sub-community can be found over a wide range of bedrocks, from ultrabasic serpentine to acidic granites and quartzites, though not on limestones which weather to rendzinas inimical to the development of any kind of ericoid heath. In their physical characteristics, however, the profiles are rather uniform, being shallow and rock-dominated, often discontinuously distributed over the steep slopes characteristic here, with numerous rock outcrops whose exact disposition is strongly controlled by the bedding and jointing of the substrates. In summer, particularly towards the sunnier and drier south of Britain, where this kind of Calluna-Scilla heath is concentrated, such thin rankers are very susceptible to parching: annual precipitation is generally less than 1000 mm through this region with a clear winter peak (Climatological Atlas 1952), the mean annual maximum temperature is usually over 25 °C (Conolly & Dahl 1970) and spring and summer insolation totals are among the highest in the country (Collingbourne 1976). Such parching further checks the vigour of the sub-shrubs, keeping the vegetation open, and favours the abundance of ephemerals and those perennials, like Sedum anglicum, which thrive on patches of thin, dry soil. It is these, just as much as the more strictly maritime species, which characterise this sub-community. And, in the warm, oceanic climate of this part of Britain, this kind of Calluna-Scilla heath provides a locus for therophytes and more long-lived species with an Oceanic Southern (Daucus carota ssp. gummifer, Scilla autumnalis, Trifolium bocconei, T. subterraneum) or Oceanic West European distribution (Bromus hordeaceus ssp. ferronii, Herniaria ciliolata).

Both maritime and ephemeral elements extend a little way into the Calluna sub-community, together with the general tendency towards heather-dominance. This vegetation can likewise tolerate high levels of saltdeposition but it is characteristic of deeper soils on somewhat gentler slopes than those of the Armeria subcommunity, still dry, though typical of more uniformly acidic rocks. With a drop in maritime influence and moving on to still shallower slopes, where deeper soils are kept a little moister, and particularly over more baserich parent materials, the Viola sub-community is the usual kind of Calluna-Scilla heath. With the greater shelter here, both Calluna and E. cinerea grow with vigour, and the more sensitive gorse spp. and E. vagans can figure occasionally. And, among both constant and preferential species, more mesophytic and base-tolerant plants are well represented, such that the herbaceous element of the vegetation comes to resemble a Mesobromion sward.

In the *Erica* and *Empetrum* sub-communities, low but vigorous sub-shrub growth and a prominent herbaceous component remain characteristic, but there is a shift among both elements which can be related in part to climatic differences in moving to the north of Britain, to where these two types of Calluna-Scilla heath are largely confined. Cooler summer temperatures and higher rainfall both play a part in this change. Annual rainfall varies considerably around the northern coasts of Britain, but it is generally over 1000 mm (Climatological Atlas 1952), with more than 160 wet days yr⁻¹ (Ratcliffe 1968) and high humidity all the year round. In the west, the winters are mild, but mean annual maximum temperature is always less than 24°C (Conolly & Dahl 1970). Both these factors exert a strong control on the national distribution of Empetrum nigrum ssp. nigrum (Bell & Tallis 1973), a sub-shrub which is as salt-tolerant as Calluna and well able, with its mat-like growth habit, to subsist in very windy situations. This plant becomes very abundant in the Calluna-Scilla heath in northern Britain, where the community extends on to deep freedraining acidic soils, particularly on humic rankers over sandstones, which are common on the north and east coasts of Scotland, and on drier peats. The Empetrum sub-community is often the most maritime form of this heath in such situations, and can provide a locus for such Continental Northern plants as Primula scotica and Astragalus danicus.

Along the west Scottish coast, annual rainfall rises to over 2000 mm, with 200 or so wet days yr⁻¹ (Climatological Atlas 1952, Ratcliffe 1968), so even free-draining mineral soils can be kept very moist and quite deep peats accumulate on steeper slopes down to sea-level. Where such profiles are not subject to strong maritime influence, E. tetralix is able to play a prominent role in the Calluna-Scilla heath. In the drier south of Britain, this sub-shrub, like E. cinerea, can thrive in the more oceanic west but, though the two are roughly similar in their salt-tolerance, E. tetralix tends to occur close to cliff tops only where there is drainage impedence, so it is usually confined to very gentle slopes which, set further back from the cliff edge, carry non-maritime heath. In the north, the Erica sub-community comes quite close in its floristics to soligenous Scirpus-Erica wet heath yet retains many of the typical Calluna-Scilla heath features.

However, along with these changes in the sub-shrub canopy of the *Erica* and *Empetrum* sub-communities, and the complementary decline in both of *E. cinerea*, there are also differences in the herbaceous element of these northern kinds of *Calluna-Scilla* heath. The increase in frequency and abundance of *Festuca rubra*, *Agrostis capillaris* and *Anthoxanthum*, together with the

appearance of Carex nigra and/or C. panicea and weakly preferential occurrence of Luzula campestris, L. multi-flora, Cerastium fontanum, Leontodon autumnalis and Trifolium repens, are all of them fairly gentle shifts but, taken together, they give the grassy matrix of these vegetation types a rather different appearance to that of the Viola sub-community, more like a Nardo-Galion sward.

But there is a further environmental feature which plays a part in distinguishing these northern sub-communities, and that is grazing. Many coastal cliffs are open to stock and, except where enclosure has been so assiduous as to take in all the heath zone for improvement, sub-shrub vegetation often constitutes a large proportion of the herbage that is on the more readily accessible gentler slopes. In fact, over much of the southern cliffs of Britain, grazing is now light or nonexistent, and from the mid-1950s until recently, there have been few rabbits to compensate for the low stock numbers. Where farm animals do have access, they have generally been beef cattle rather than sheep, and their less close cropping has tended to leave a rougher and uneven sward. Although there are local attempts to reintroduce cliff-top grazing, sometimes using horses or Soay sheep, the general picture is thus one of ungrazed Calluna-Scilla heath giving way beyond an artificial boundary to improved pasture.

In the north of Britain, there are areas where grazing of cliff vegetation is light, as around much of the Caithness coast where the quality of the pasture inland is relatively good. Down much of the west coast of Scotland, however, the hinterland is mantled by blanket mire and the cliff tops provide an important source of herbage. Sheep are the usual stock and the effect of their close nibbling is well seen in many stretches of the Erica and Empetrum sub-communities, where the palatable subshrubs, particularly Calluna, can be kept down to a very low cover and the rosette hemicryptophytes, particularly Plantago maritima and P. lanceolata, increase in abundance greatly in relation to the grasses. In more sheltered places, such grazing may be important in maintaining the community as a plagioclimax.

Zonation and succession

The Calluna-Scilla heath is characteristically found in zonations developed over maritime cliffs in relation to gradients of salt-spray deposition and soil moisture, themselves complex functions of exposure and cliff physiography. Bedrock type also has an important influence on soil development, the disposition and character of the profiles, and these factors, together with regional variations in climate, affect the vegetation sequences. Grazing can alter zonations and, together with exposure, may prevent successional change. Agricultural improvement, particularly around our southern

coasts, has often abruptly truncated the zonations inland, sometimes totally obliterating the heath zone.

Except over limestones, from which the Calluna-Scilla heath is usually absent and where ericoid vegetation of any kind is typically limited to drift-contaminated slopes set back some way from the sea, the community forms the inner limit of maritime vegetation. Generally speaking, in the southern part of Britain, where grazing is light or absent, it is replaced to seaward by the Festuca-Holcus grassland, which can experience up to twice as much salt-spray deposition. Over basic bedrocks, as on the serpentine, gabbro and hornblende schists of the Lizard and on basalt or calcareous mudstones and shales in Dyfed, Gwynedd, Cumbria and Galloway & Dumfries, the Calluna-Scilla heath is typically represented by the Viola sub-community over soils which are reasonably deep and moist. To seaward, over more exposed and shallower profiles, this passes to the Dactylis sub-community of the Festuca-Holcus grassland or, where soil moisture is maintained, as over north-facing slopes for example, to the Primula subcommunity. The seaward limit of the heath is usually

Figure 27. Zonations on the less exposed tops of maritime cliffs on (a) more basic bedrock in the southwest of Britain, with enclosure for agriculture behind, (b) more acidic bedrock in southern Britain with light grazing, (c) more acidic bedrock in northern Scotland with heavier grazing.

H7a Calluna-Scilla heath, Armeria sub-community

H7b Calluna-Scilla heath, Viola sub-community

H7c Calluna-Scilla heath, Erica sub-community

H7d Calluna-Scilla heath, Empetrum sub-community

well marked by the edge of the sub-shrub canopy but, where the wind keeps this very low, the boundary may be scarcely visible from a distance except as a slight tonal difference. And, of course, there is considerable floristic continuity through species like Festuca rubra, Holcus lanatus, Plantago lanceolata, P. maritima, Lotus corniculatus, Scilla verna, Daucus carota ssp. gummifer, Hypochoeris radicata, and Viola riviniana.

Within the heath zone itself, there is often a mosaic over more base-rich soils between the *Viola* subcommunity and the *Armeria* type according to the distribution of deeper and shallower profiles (Figure 27). And where rock outcrops break the mantle, the zonation may continue to the *Armeria-Cerastium* community, where the sub-shrubs and mesophytic herbs disappear and therophytes and succulents become prominent. These vegetation types can also form a more ordered zonation running down cliffs where the soils become progressively discontinuous but, in complex topography, it may be very difficult to demarcate their limits.

In this southern part of Britain, the sequence of

H7e Calluna-Scilla heath, Calluna sub-community

H8d Calluna-Ulex gallii heath, Scilla

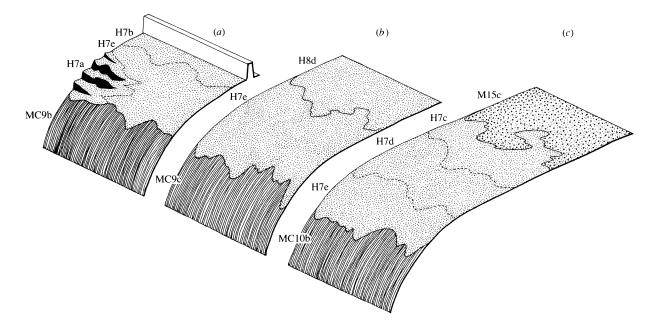
sub-community

M15c Scirpus-Erica wet heath, Cladonia sub-community

MC9b Festuca-Holcus grassland, Dactylis sub-community

MC9c Festuca-Holcus grassland, Achillea sub-community

MC10b Festuca-Plantago grassland, Carex sub-community



communities is often terminated landwards at the level of the Calluna-Scilla heath by the boundary of the improved cliff-top grassland but, in a few places, the zonation continues inland to non-maritime heaths. The most extensive patterns of this kind are to be seen on the Lizard, though they are of a rather unusual type because of the local importance there of E. vagans. This, together with occasional *U. europaeus*, can run into the *Viola* subcommunity a little way but, on the free-draining, baserich brown earths of the cliff-top slopes and around the cove valleys, these two sub-shrubs become co-dominant above the Calluna-Scilla zone in the E. vagans-Ulex heath. Over the Lizard hinterland, this then gives way to the E. vagans-Schoenus heath over base-rich gleys or the U. gallii-Agrostis heath on base-poor, free-draining soils over acidic superficials.

Essentially similar patterns of Festuca-Holcus grassland, Calluna-Scilla heath and inland heath can be seen over ungrazed cliffs cut into neutral or acid bedrocks which are of widespread occurrence up the west coast of Britain but particularly important on Land's End, where granite occurs, on the north Cornish and Dyfed coasts, where sandstones and shales crop out, and in Anglesey with its Pre-Cambrian rocks. Here, the Calluna sub-community is the usual Calluna-Scilla heath of deeper, free-draining soils, passing seawards into the Achillea or Plantago sub-communities of the Festuca-Holcus grassland, the sub-shrubs again fading at the transition but Festuca rubra, Holcus lanatus, Plantago spp., Scilla verna, Rumex acetosa and Potentilla erecta continuing throughout. Again, the Armeria subcommunity can occur patchily within the Calluna type on areas of shallower soil and mark a transition to the Armeria-Cerastium therophyte vegetation, or form a seaward transition to this or Festuca-Armeria grassland. Landward continuations are once more rare but, in some localities, the sequence passes into the Scilla subcommunity of the Calluna-U. gallii heath.

Where such southern zonations are subject to grazing, the basic pattern of heath and grassland remains, though heavy herbivore pressure may reduce the height of the sub-shrubs further, making the boundary even harder to see, or actually move it inland somewhat where palatable species, notably *Calluna*, are eaten out completely. Also, the *Festuca-Holcus* grassland is often represented just by the *Plantago* sub-community or is totally replaced by the *Festuca-Plantago* grassland, the abundance of *Plantago* spp. running into the heath.

In northern Britain, where grazing is more widespread, this kind of pattern is very common, the *Festuca-Plantago* grassland occupying the bulk of the more accessible cliff slopes with its *Armeria*, *Carex* and *Schoe-nus* sub-communities distributed according to decreasing maritime influence and increasing soil moisture. Any of these can grade into the *Calluna-Scilla* heath above, though in this region, of course, the sub-communities tend to be different: on drier, shallower soils the Calluna type is characteristic, the *Empetrum* on somewhat deeper mineral profiles and the Erica on wet mineral soils or peat. All these kinds of Calluna-Scilla heath persist on ungrazed cliffs in the north, though the Calluna sub-community seems particularly common there and, with relaxation of herbivore pressure, the Festuca-Plantago grassland tends to be replaced by the Festuca-Holcus grassland, often in this part of Britain by the Anthoxanthum sub-community, an abundance of Nardo-Galion herbs running throughout. Once more, on both grazed and ungrazed cliffs, the Armeria subcommunity of the Calluna-Scilla heath can mark shallower soils under strong maritime influence though it tends to be scarce in the wet climate. And the Viola subcommunity is likewise rather local, picking out areas of mull soils over more base-rich substrates.

Although, in some parts of Scotland the typical southern pattern of enclosure to the cliff edge is quite common, in the west, the Calluna-Scilla heath is often contiguous with inland semi-natural vegetation which, in the wet climate of this part of Britain, is usually Ericion tetralicis wet heath or Erico-Sphagnion blanket mire on peats which thicken up to a continuous deep mantle on inland slopes. Typically, the Erica or, on drier ground, the Empetrum, sub-community of the heath grades to the Scirpus-Erica wet heath or the Scirpus-Eriophorum bog, the various sub-shrubs maintaining their cover but the herbaceous component of the heath passing to a Molinia or Scirpus-dominated suite of associates. On steeper ground where, even in this humid climate, the peat mantle has not been able to accumulate, the Calluna sub-community of the heath usually passes to Festuca-Agrostis-Galium grassland devoid of sub-shrubs and maritime species.

In sheltered situations on the upper reaches of cliffs, particularly in the south, the Calluna-Scilla heath can give way laterally to bracken or scrub, often with a fringe of the Festuca-Hyacinthoides grassland or rank Arrhenatheretum, and such vegetation often runs inland through the heath zone up head-filled gullies. The main woody colonisers in such situations are U. europaeus on drier, more acidic soils and Prunus spinosa on moister mulls and, where exposure is not too severe, grazing may play some part in preventing these species gaining a hold in the Calluna-Scilla heath. In many cases, however, susceptibility to even small amounts of salt-spray hinders their invasion into the community, so over much of its range this vegetation can be considered a climatic climax.

Distribution

The Calluna-Scilla heath occurs all around the coast of the British mainland and offshore islands except to the

east and south between Durham and Dorset. The Armeria, Viola and Calluna sub-communities occur throughout the range, though the first two are better developed to the south of Galloway, with only local stations beyond this; the last is also rather rarer to the north, though it is well represented on Shetland. The Erica and Empetrum sub-communities are both predominantly northern: the former is especially common on the west coast, particularly in the Hebrides and Sutherland, with scattered occurrences down to Anglesey; the latter is commonest on the Caithness and Moray Firth cliffs with outlying stands in Orkney and Shetland and on the west coast. White & Doyle (1982) have recorded heath of this general kind along the eastern and northern coasts of Ireland.

Affinities

Apart from the description of 'Rock Heath' from the Lizard by Coombe & Frost (1956a), the extreme maritime fringe of British sub-shrub vegetation was almost totally neglected until Malloch (1970, 1972 and unpublished data) began his study of Cornish cliffs, later extended to cover the entire British coastline. When

variation in this kind of vegetation is seen in such a national context, the close relationship of the communities to inland heaths is very clear, but, apart from Malloch's (1972) *U. gallii* sub-community, which is here transferred to the *Calluna-U. gallii* heath, the vegetation types coinhere quite well with a unique and strong block of constants.

Similar communities, considered as true climax heaths, have since been described by Bridgewater (1970), Géhu & Géhu (1973) and Géhu (1975) from sea-cliffs in the Isle of Man, Wales, Cornwall, Brittany and southwestern France, and sometimes placed in a distinct Dactylo-Ulicion alliance, within which vegetation types are often distinguished on the basis of the representation of intra-specific taxa such as Dactylis glomerata forma marina, Ulex europaeus forma maritima, U. gallii forma humilis, Genista pilosa forma maritima and Anthyllis vulneraria ssp. corbierei. These communities are for the most part rare and little studied and these taxa not widespread in Britain and Malloch's (1971) suggestion that the Calluna-Scilla heath be placed in the Ericion cinereae seems, at the moment, much more sensible.

Floristic table H7

	a	b	С	d	e	7
Calluna vulgaris	V (2-9)	V (4–8)	V (4–9)	V (4–8)	V (4–10)	V (2–10)
Festuca ovina	V (2-8)	V (4-8)	IV (3–7)	IV (2-7)	V (2-8)	V (2–8)
Plantago maritima	IV (2-4)	IV (1–7)	V (3-7)	V (2-5)	III (1–8)	IV (1-8)
Scilla verna	IV (1-4)	IV (2-4)	III (1–4)	IV (1-3)	IV (1–4)	IV (1-4)
Lotus corniculatus	IV (1-5)	V (2-4)	IV (2-4)	IV (2-4)	IV (1-4)	IV (1-5)
Thymus praecox	V (2-5)	V (1-5)	III (2-5)	IV (2–4)	III (1–4)	IV (1-5)
Potentilla erecta	I (2-5)	IV (1-4)	V (2-4)	V (2-4)	III (2-4)	IV (1-5)
Holcus lanatus	V (1-5)	III (1–4)	II (2–4)	IV (2-4)	IV (1-5)	IV (1-5)
Plantago lanceolata	IV (1-4)	V (1-4)	III (1–4)	IV (1–4)	II (1–4)	IV (1-4)
Erica cinerea	IV (2–8)	V (1–8)	II (1–6)	II (4-7)	IV (3–8)	IV (1–8)
Hypochoeris radicata	IV (1-4)	IV (1-4)	II (1–3)	I (1–2)	IV (1–4)	IV (1-4)
Armeria maritima	V (1-4)	I (1-3)		I (3)	II (1-4)	II (1–4)
Sedum anglicum	V (1-4)	I (1–2)	I (2)	I (3)	I (1–4)	II (1-4)
Dactylis glomerata	III (2–7)	II (1-5)	I (2-3)	I (2)	II (1–5)	II (1–7)
Anthyllis vulneraria	III (1-7)	II (1–7)	I (2)	I (2–3)	II (1-6)	I (1–7)
Jasione montana	III (1–3)	I (1-3)		I (1)	I (1-3)	I (1-3)
Aira caryophyllea	II (1–3)	I (2)		I (2)	I (1-3)	I (1–3)
Plantago coronopus	II (1-5)	I (1-3)		I (2)	I (2)	I (1-5)
Centaurium erythraea	II (1–2)	I (1–3)			I (1)	I (1–3)
Silene vulgaris maritima	II (1–4)		I (2-4)	I (2)	I (2-4)	I (1-4)
Cerastium diffusum diffusum	I (1-2)					I (1–2)
Juniperus communis communis	I (3–4)		_			I (3–4)
Viola riviniana	II (2-3)	IV (1–3)	II (2-3)	II (2-3)	II (1-3)	III (1–3)
Carex flacca	I (2-4)	IV (1-4)	I (1)	I (4)	I (2)	II (1–4)
Polygala vulgaris	II (2–4)	III (1-3)		I (2)	I (1-2)	II (1 -4)
Carex caryophyllea	I (2–4)	III (1 -4)			I (1)	II (1–4)
Leontodon taraxacoides	II (2–4)	II (2-3)	I (2)			I (2-4)
Koeleria macrantha	I (2-4)	II (2–4)	I (2-4)	I (3)	I (3)	I (2-4)
Agrostis stolonifera		II (2-5)	I (3–5)	I (2-3)	I (2-5)	I (2-5)
Achillea millefolium		II (1 -4)		I (3)	I (1)	I (1-4)
Galium verum	I (1–3)	II (1–4)		I (3)	I (1)	I (1–4)

Floristic table H7 (cont.)

	a	b
Stachys betonica		II (1–4)
Ulex europaeus		II (3–5)
Serratula tinctoria		II (1 -4)
Erica vagans		II (5–8)
Leucanthemum vulgare		I (1–3)
Succisa pratensis	I (3-4)	III (1–4)
Danthonia decumbens	I (2-3)	III (1-5)
Erica tetralix		I (4)
Carex nigra		I (3-4)
Frullania tamarisci	I (4)	I (3)
Prunella vulgaris		I (1–4)
Selaginella selaginoides		
Molinia caerulea		I (3)
Salix repens		
Nardus stricta		
Carex serotina		
Dactylorhiza majalis purpurella		
Agrostis capillaris	II (2–4)	II (2–4)
Anthoxanthum odoratum	II (3-5)	II (2–6)
Empetrum nigrum nigrum	I (7)	I (4)
Trifolium repens	I (2-3)	II (1–3)
Carex panicea	I (3)	I (4)
Luzula multiflora		I (1)
Festuca rubra	II (1-3)	II (3-7)
Euphrasia spp.	I (2-3)	II (1–3)
Hypnum cupressiforme	I (1-3)	II (2-5)
Luzula campestris	I (2-4)	I (1-3)
Rumex acetosa	II (1-3)	I (2-3)
Daucus carota gummifer	II (1 -4)	II (1-3)
Cerastium fontanum	I (1-3)	I (1-2)
Leontodon autumnalis		I (2)

С	d	e	7
		I (2)	I (1-4)
	I (5)	I (4)	I (3-5)
		I (1)	I (1-4)
			I (5–8)
			I (1–3)
IV (1-5)	II (2–4)	I (2-6)	II (1–6)
V (2–5)	I (2–4)	I (2–7)	II (1–7)
V (48)	I (2–4)	I (2)	I (2–8)
III (2–4)	II (2–5)	I (1–4)	I (1–5)
II (3–4)	I (3–4)	I (2–6)	I (2–6)
II (1–4)		I (2–3)	I (1–4)
II (2-3)		I (2)	I (2–3)
II (2-5)		I (3)	I (2-5)
II (3–7)	I (2)	I (2)	I (2-7)
II (2–5)	I (3–5)	I (2-4)	I (2-5)
I (2–3)			I (2-3)
I (1-2)			I (1-2)
IV (2-4)	IV (3-4)	II (2-4)	II (2–4)
III (2–5)	IV (3–6)	II (1–7)	II (1–7)
II (2-7)	V (1–8)		II (1–8)
II (3–4)	III (2–3)	I (2-4)	II (1–4)
II (2–4)	III (2–4)	I (2-5)	I (2-5)
I (2-4)	II (1-3)		I (1–4)
III (3–5)	III (2–6)	III (3–8)	III (1–8)
III (1–3)	II (1–3)	II (2–3)	II (1–3)
II (3–5)	II (2-4)	II (1-5)	II (1-5)
II (1–2)	II (1-3)	II (1-3)	I (1–4)
I (2)	II (2-3)	II (1–4)	I (1–4)
I (1)		II (1–4)	I (1–4)
II (1–3)	II (1-2)	I (2)	I (1-3)
II (1–3)	II (2–4)	I (1-2)	I (1–4)

Aira praecox	II (1–4)	I (3)
Polygala serpyllifolia	I (1–3)	I (1)
Cladonia rangiformis	I (2-5)	I (3)
Cladonia chlorophaea	I (2-3)	I (2)
Carex pulicaris		I (2–4)
Filipendula vulgaris	I (2–4)	I (3–4)
Genista pilosa	I (3)	I (2–8)
Astragalus danicus	I (2–3)	
Number of samples	60	104
Number of species/sample	20 (10–30)	21 (13–31)
Vegetation height (cm)	9 (2–50)	9 (2–50)
Vegetation cover (%)	96 (70–100)	99 (80–100)
Altitude (m)	34 (4–80)	32 (3–70)
Slope (°)	19 (0-40)	14 (0-45)
Soil pH	4.9 (4.3–5.7)	5.3 (4.3–6.4)

a Armeria maritima sub-community

b Viola riviniana sub-community

c Erica tetralix sub-community

d Empetrum nigrum nigrum sub-community

e Calluna vulgaris sub-community

⁷ Calluna vulgaris-Scilla verna heath (total)

II (2-3)	I (2-3)	I (2-3)	I (1–4)
I (1-2)	I (1-2)	I (1–3)	I (1–3)
1 (2-4)	I (2-3)	I (2-3)	I (2-5)
, ,	I (2-4)	I (3)	I (2-4)
I (2)	I (2-3)	I (3)	I (2-4)
			I (2-4)
			I (2–8)
	I (3)		I (2-3)
47	40	85	336
47 19 (10–25)	40 18 (11–29)	85 15 (6–20)	336 19 (6–31)
19 (10–25)	18 (11–29)	15 (6–20)	19 (6–31)
19 (10–25) 7 (3–17)	18 (11–29) 7 (3–20) 99 (90–100)	15 (6–20) 12 (2–75)	9 (2–75)
19 (10–25) 7 (3–17) 100 (90–100)	18 (11–29) 7 (3–20)	15 (6–20) 12 (2–75) 97 (55–100)	19 (6–31) 9 (2–75) 99 (55–100)

