H10
Calluna vulgaris-Erica cinerea heath

Synonymy
Scottish *Calluna* heath Smith 1911, Tansley 1939 *p.p.*; *Callunetum vulgaris* McVean & Ratcliffe 1962 *p.p.*, Birks 1973, Prentice & Prentice 1975, Meek 1975, 1976, Evans *et al.* 1977 *p.p.*, Hill & Evans 1978, Ferreira 1978; *Calluna-Erica cinerea* heaths Muir & Fraser 1940, Gimingham 1964*b*, 1972 *p.p.*; *Calluna vulgaris-Sieglingia decumbens* Association Birks 1973; *Carici binervis-Ericetum cinereae* Br.-Bl. & Tx (1950) 1952 *emend.* Birse 1980 *p.p.*; *Plantago maritima-Erica cinerea* Association Birse 1980.

Constant species
Calluna vulgaris, *Erica cinerea*, *Potentilla erecta*.

Rare species
Orobanche alba.

Physiognomy
The *Calluna vulgaris-Erica cinerea* heath is typically dominated by *Calluna vulgaris* but the cover, height and structure of the sub-shrub canopy vary quite markedly according to the incidence of burning and grazing and the degree of exposure. Where the community is more frequently burned, as where it makes some contribution to grouse-moor in parts of southern Scotland and locally around the east-central Highlands, pioneer and building phases of the heather tend to predominate but, with more sporadic firing, there can be patchworks of even-aged stands through to the mature and degenerate. Very commonly, however, there is also some grazing by stock and deer which helps keep the canopy more closely trimmed and, in extreme cases, exposure to wind and sun can reduce the bushes to a tight and even or wind-waved cover but a few centimetres high.

Further modest diversity comes from the frequent but varied contribution of *Erica cinerea*. This is generally subordinate to the heather in abundance though, being more shade-tolerant, it is well able to persist beneath taller *Calluna* canopies as a patchy second tier, the rather straggling branches that it often forms in mixed covers becoming semi-prostrate, rooting adventitiously and spreading laterally (Bannister 1965, Gimingham 1972). And, in certain circumstances, it can become locally abundant in this kind of heath, regenerating well after burning, for example, and, especially on south-facing slopes and where there is little grazing (Gimingham 1949), it can rival *Calluna* in its extent in the middle years of recovery. *Vaccinium myrtillus*, by contrast, is at most occasional here and only rarely of any abundance and *V. vitis-idaea* is decidedly scarce. *Empetrum nigrum* ssp. *nigrum* can occur, but it is very much confined to one particular kind of *Calluna-Erica* heath, and the restricted occurrence of all these sub-shrubs provides a good distinction between the community and the *Calluna-Vaccinium* heath. In this respect, then, the *Calluna-Erica* heath continues northwards the kind of vegetation seen in the *Calluna-Ulex gallii* heath and indeed the community provides a very occasional locus for *U. gallii* at the limit of its range in southern Scotland. Of other woody plants, *Erica tetralix* is sometimes found, particularly where the community forms mosaics with the *Scirpus-Erica* wet heath or its eastern counterpart, the *Ericetum tetralicis*, and rarely there are records for *Arctostaphylos uva-ursi*. Where the vegetation is recovering from burning, scattered plants of *Salix repens* or *S. aurita* can also find a temporary niche.

Despite the characteristic abundance of the constant sub-shrubs, two other floristic features often catch the eye. The first is the frequency of grasses, to a lesser extent sedges and dicotyledons, typical of Nardetalia swards, growing beneath and among the bushes. Of grasses, *Deschampsia flexuosa* is the most consistent throughout, with *Agrostis canina* (probably mostly ssp. *montana*) and *Nardus stricta* occasional to frequent in most kinds of *Calluna-Erica* heath but, in certain of the sub-communities, *Festuca ovina*, *Anthoxanthum odoratum*, *Agrostis capillaris* and *Molinia caerulea* also become very common, sometimes too with *Danthonia decumbens*, *Festuca rubra* or *F. vivipara*. The sedge component

is less varied but the Oceanic West European *Carex binervis* is very characteristic of this kind of heath, together with *C. pilulifera*. After burning, mixtures of these plants can become patchily abundant, and *D. flexuosa* and *C. pilulifera* are particularly able to establish themselves as temporary local dominants in such circumstances (Gimingham 1964*a*). In other cases, a more permanent and intimate grass-heath physiognomy, with these species ramifying an often rather short sub-shrub cover, is maintained by grazing. Other monocotyledons which find an occasional place in the community are *Carex panicea* and even *C. pulicaris* where this kind of heath extends some way on to less base-poor soils, *Luzula multiflora*, *L. campestris*, *Juncus squarrosus* and *Scirpus cespitosus*.

Dicotyledons are generally few in number, but *Potentilla erecta* is a constant and *Galium saxatile* fairly common and, in the grassier kinds of *Calluna-Erica* heath, species such as *Lotus corniculatus*, *Plantago lanceolata*, *Campanula rotundifolia*, *Succisa pratensis* and *Hypericum pulchrum* can be found occasionally, sometimes with further enrichment from oceanic or mildly basiphilous elements.

The second striking feature of many stands of the community is the contribution of the ground layer. Early stages of recovery from burning can have a local abundance of *Polytrichum piliferum*, *P. juniperinum* and encrusting *Cladonia* spp., while in exposed stands there is often a patchy carpet of *Racomitrium lanuginosum* and fruticose lichens over the bare ground. But more important than these through the community as a whole are bulky pleurocarpous mosses such as *Hypnum cupressiforme s.l.*, *Pleurozium schreberi* and *Hylocomium splendens*, with *Rhytidiadelphus triquetrus* and *R. loreus* also occurring occasionally. These species, together with *Dicranum scoparium*, typically become abundant with the maturing and opening up of the heather bushes, so frequent burning can repeatedly curtail their development, but they often make a more permanent contribution to grazed stands, where they can form a bulky mat among the more open network of sub-shrub branches and herbs.

Sub-communities

Typical sub-community: *Callunetum vulgaris* McVean & Ratcliffe 1962, Birks 1973, Prentice & Prentice 1975, Meek 1976, Evans *et al.* 1977, Hill & Evans 1978, all *p.p.*; *Calluna-Erica cinerea* heaths Gimingham 1964*b*, 1972 *p.p.*; *Carici binervis-Ericetum cinereae*, Typical subassociation *sensu* Birse 1980. In this, the most generally species-poor kind of *Calluna-Erica* heath, heather is typically dominant and is often overwhelmingly abundant in pioneer or building regrowth after burning. *Erica cinerea* is very frequent and it can show some local prominence among or beneath the heather or very occasionally replace it as the leading sub-shrub with recovery from fire, but usually it is of sparse cover and sometimes altogether absent. *Vaccinium myrtillus* occurs occasionally, though hardly ever as more than scattered shoots and *Empetrum nigrum* ssp. *nigrum* and *Erica tetralix* are scarce and usually found in stands that are obviously transitional to the *Racomitrium* sub-community.

Monocotyledons are typically few and generally of low cover though *Deschampsia flexuosa*, which is very frequent, sometimes shows local prominence. More striking here, though, is the preferential occurrence of *Molinia caerulea*, usually not more than patchily abundant but, with occasional *Scirpus cespitosus* and *Juncus squarrosus*, often bringing the vegetation close in its composition to degraded forms of *Scirpus-Erica* wet heath, with which this vegetation often forms mosaics. However, one good distinction between the two is provided by *Carex binervis*, better represented here than in any other kind of *Calluna-Erica* heath, though not usually with any abundance, being typically found as scattered shoots or in small clumps. *Agrostis canina*, *A. capillaris* and *Nardus stricta* also occur occasionally at low covers, but *Festuca ovina* and *Anthoxanthum* are characteristically uncommon and the grass-heath physiognomy of some other sub-communities is only rarely developed here. Apart from *Potentilla erecta* and occasional *Galium saxatile*, herbaceous dicotyledons are very sparse but there are sometimes scattered plants of *Blechnum spicant*.

The ground layer is generally also poor in species and of low cover. Younger stands can have patches of *Campylopus paradoxus*, *Polytrichum piliferum* and *P. commune*, together with encrusting lichens such as *Cladonia floerkeana*, growing over the bare peat and small amounts of *Racomitrium lanuginosum* can be found in more exposed situations, but the development of a mat of pleurocarps is usually limited to small wefts of *Hypnum cupressiforme* with occasional *Pleurozium schreberi*, a feature which reflects the scarcity of older, more open canopies of heather in this sub-community. Other particular features are ill-developed, although occasional *Diplophyllum albicans*, *Scapania gracilis* and little tufts of Sphagna can enhance the oceanic character of the vegetation.

***Racomitrium lanuginosum* sub-community:** *Callunetum vulgaris*, *Rhacomitrium* lichen-rich facies Prentice & Prentice 1975; *Callunetum vulgaris* Hill & Evans 1978; *Carici binervis-Ericetum cinereae*, *Rhacomitrium* subassociation *sensu* Birse 1980. *Calluna* is again the usual dominant here but its cover is not so consistently overwhelming as in the Typical sub-community. Indeed, although there is also frequently some *Erica cinerea*,

occasional *Vaccinium myrtillus* and, preferential here, quite common *Empetrum nigrum* ssp. *nigrum*, the sub-shrub canopy is altogether more open than usual and often dwarfed, with in extreme cases a patchy cover of wind-pruned, stunted bushes.

Among the sub-shrubs, grasses are especially sparse with just scattered tufts of *Deschampsia flexuosa* and very occasional *Nardus stricta*, *Agrostis canina*, *Festuca ovina* and *F. vivipara*. *Carex binervis* is rather rare, too, its place being often taken here by *C. pilulifera*, sometimes showing modest local abundance, and *C. panicea*. *Scirpus cespitosus* is also frequent and it can be patchily prominent. Of herbaceous dicotyledons, only *Potentilla erecta* shows any frequency, though *Huperzia selago* is preferentially common.

Much more prominent in this sub-community is the ground layer which often occupies substantial areas between the sub-shrubs. Although *Hypnum cupressiforme s.l.* remains frequent, the most important moss here is *Racomitrium lanuginosum* which can become especially abundant among degenerating bushes. Lichens, too, have their best representation in this sub-community with frequent *Cladonia uncialis* and *C. impexa*, and occasional *C. furcata*, *Cornicularia aculeata* and *Cetraria islandica*.

***Festuca ovina-Anthoxanthum odoratum* sub-community:** *Callunetum vulgaris* Birks 1973, Prentice & Prentice 1975, Evans *et al.* 1977, Hill & Evans 1978, all *p.p.*; *Carici binervis-Ericetum cinereae*, Typical subassociation *sensu* Birse 1980 *p.p.* *Calluna* is still often abundant in this sub-community, though its cover is quite frequently rivalled by that of *Erica cinerea*. *Vaccinium myrtillus* occurs occasionally, too, though in small amounts, and the sub-shrub canopy can be very extensive in total. But it is usually quite short, sometimes distinctly patchy, and commonly forms a mosaic with, or is thoroughly ramified by, a grassy turf. Most frequent in this element are *Festuca ovina*, *Anthoxanthum* and *Agrostis capillaris*, with occasional *A. canina*, *F. rubra*, *F. vivipara*, *Danthonia decumbens* and *Deschampsia flexuosa*, sometimes growing as tussocky clumps, sometimes as a more even-cropped sward, in which one or more of the grasses can show considerable local abundance or where there is a more balanced mixture of the species. *Carex binervis* and *C. pilulifera* are also both quite common and there are occasional scattered plants of *Luzula multiflora* and *L. campestris*. *Juncus squarrosus* and *Scirpus cespitosus*, by contrast, are both scarce here.

Dicotyledonous herbs, too, are much more numerous than in the above sub-communities. In addition to *Potentilla erecta* and *Galium saxatile*, both of which are very common, there are occasional records for *Campanula rotundifolia*, *Lotus corniculatus*, *Plantago lanceolata*, *P. maritima*, *Polygala serpyllifolia*, *Succisa pratensis*, *Hypericum pulchrum*, *Viola riviniana* and *Thymus praecox*.

Equally distinctive is the consistent role that the bulky pleurocarpous mosses have in this vegetation, with frequent *Hypnum cupressiforme s.l.*, *Pleurozium schreberi* and *Hylocomium splendens*, together with *Dicranum scoparium*, occurring among the more open parts of the canopy and among the grass culms as a patchy carpet.

***Thymus praecox-Carex pulicaris* sub-community:** *Callunetum vulgaris*, herb-rich facies McVean & Ratcliffe 1962, Ferreira 1978; *Calluna vulgaris-Sieglingia decumbens* Association Birks 1973; *Carici binervis-Ericetum cinereae*, *Viola riviniana* subassociation *sensu* Birse 1980; *Plantago maritima-Erica cinerea* Association Birse 1980 *p.p.* In its general structure and floristics, this kind of *Calluna-Erica* heath is very similar to the *Festuca-Anthoxanthum* type, with *Calluna* and *E. cinerea* both able to show prominence in the sub-shrub canopy, but with herbs and bryophytes also being of considerable structural importance. Here, however, there are some additional preferentials which make this the most species-rich and distinctive sub-community. Among the grasses, for example, *Danthonia decumbens* is particularly frequent and the commonest sedges are *Carex panicea* and, especially striking here, *C. pulicaris*. Frequent *Thymus praecox* and *Linum catharticum* continue the mildly basiphile aspect of the vegetation, and there are also frequent records for *Viola riviniana*, *Prunella vulgaris* and *Primula vulgaris* with occasional *Solidago virgaurea*, *Antennaria dioica*, *Blechnum spicant*, *Lathyrus montanus* and *Geum rivale*. On Skye, this vegetation provides the main locus for the rare Continental Southern *Orobanche alba* at the northern limit of its British range.

Among the bryophytes, *Dicranum scoparium* and the pleurocarps remain very common, but there is additionally frequent *Rhytidiadelphus triquetrus* and *Breutelia chrysocoma*. In more exposed situations, a local increase in *Racomitrium lanuginosum* and fruticose lichens can produce transitions to the *Racomitrium* sub-community.

Habitat

The *Calluna-Erica* heath is characteristic of acid to circumneutral and generally free-draining soils in the cool oceanic lowlands and upland fringes of northern and western Britain. In more exposed situations, it could perhaps be considered as a climatic or edaphic climax but, very often, grazing and burning play a considerable part in controlling its composition and structure.

The community includes most of the drier, non-maritime heath occurring through the more equable parts of the country beyond the northern limit of *Ulex gallii*. This gorse is found only very sparsely to the north

of the Solway, where mean annual maximum temperatures drop below 26 °C (Conolly & Dahl 1970) and beyond which February minima are usually less than the degree or so above freezing which this plant seems to demand (*Climatological Atlas* 1952). The *Calluna-Erica* heath does include stands of dry heath without the gorse at scattered localities down through northern England, Wales and the South-West Peninsula but, for the most part, this is a Scottish community. It is, however, quite strongly confined to the relatively mild regions of northern Britain, becoming distinctly scarce where the mean annual maximum temperature is below 22 °C and where February minima fall more than just below freezing. This, then, is the characteristic 'Atlantic heather moor' of Scotland, as Birse & Robertson (1976) called it, occurring at low to moderate altitudes, almost down to sea-level in some places but only occasionally penetrating over 400 m, through Dumfries & Galloway, the Western Isles, Orkney, Shetland and down the north-east coast to the Moray Firth. Through this region, *Erica cinerea*, which retains a measure of physiological activity through the winter (Bannister 1965, Gimingham 1972), can thrive on more free-draining soils and its vigour here, occurring together with *Molinia* and *Carex binervis*, is a good reflection of the broadly oceanic conditions.

For the Arctic-Alpine sub-shrubs *Vaccinium vitis-idaea* and *Empetrum nigrum*, on the other hand, the climate is not so congenial and even *V. myrtillus*, which becomes generally frequent in Britain where the annual rainfall exceeds 800 mm, is rather scarce here, despite the fact that precipitation is well above this almost everywhere in the range of the community. Its poor showing could be partly attributable to the high incidence of grazing in this vegetation (see below), but the particular combination of temperature and humidity may be less than optimal. Certainly, with the shift to higher altitudes, and particularly in the distinctly cooler and cloudier conditions through the east-central Highlands, these species all become very important in a switch to the *Calluna-Vaccinium* heath, which corresponds largely to what Birse & Robertson (1976) called 'Boreal heather moor'. The two communities do intergrade floristically and their altitudinal and geographical separation are far from absolute but, where they are both found in the same general areas, as in parts of the Grampians and the Southern Uplands, the *Calluna-Erica* heath is typically at lower altitudes than the *Calluna-Vaccinium* heath and/or on warmer slopes. Indeed, almost wherever the community penetrates over 300 m, it is to be found on south- or west-facing aspects, and it is probably the topoclimate on such slopes, locally tilting the balance in favour of *E. cinerea* and against *V. myrtillus*, that gives the *Calluna-Erica* heath its occasional representation at scattered localities well above 400 m through the Highlands proper.

The other climatic influences on the community are felt through exposure. In very windy situations, over brows and on open plateaus, both at higher altitudes and in the gale-ridden coastal lowlands of the west and in Shetland and Orkney, this kind of heath can have a very stunted and sometimes wind-waved cover of sub-shrubs and develop the extensive mat of *Racomitrium lanuginosum* and fruticose lichens characteristic of the *Racomitrium* sub-community. In very degraded heath of this kind, where frequent and intense burning or heavy grazing have contributed to the run-down of the vegetation, the typical canopy of the community can be very open and the rhizomatous *Empetrum nigrum* ssp. *nigrum* is sometimes able to spread, but *Erica cinerea* maintains its frequency, providing a distinction from the *Calluna-Racomitrium* and *Calluna-Cladonia* heaths of exposed situations through the Highlands.

On exposed coasts, maritime influence is an additional factor in the windy climate that affects the distribution of the community, although along the very rainy western seaboard of Scotland, high precipitation counteracts somewhat the deposition of salt-spray. Nonetheless, although the *Calluna-Erica* heath can be found almost down to sea-level on the tops of coastal cliffs in this part of the country (e.g. Birks 1973, Birse 1980), it is very often replaced in exposed sites, which are otherwise congenial, by the *Calluna-Scilla* heath. Transitional vegetation, in which species such as *Plantago maritima*, *Succisa pratensis* and *Danthonia decumbens* provide a floristic link, can be seen in the *Festuca-Anthoxanthum* and *Thymus-Carex* sub-communities. Over stabilised coastal sands, the community is likewise restricted to the inland edge of dune or machair systems, with the *Calluna-Carex* heath occupying similar soils to seaward.

Throughout its range, there is also a general edaphic limitation to profiles which are moderately to very base-poor and typically free-draining, though of course in the climate of this part of Britain, quite often moist. Surface pH, however, spans quite a broad range, being generally between 3.5 and 6, and in most kinds of *Calluna-Erica* heath, the mean is around 5. On steeper slopes, where the community can extend on to rockier ground around exposures, the soils can be very immature and fragmentary, little more than shallow humic rankers in pockets of rock, but generally they are deeper and better developed than this, sometimes brown earths, more usually brown podzolic profiles or podzols proper. Such soils are widespread over the pervious lime-poor bedrocks that make up so much of northern and western Britain but, within the range of the *Calluna-Erica* heath, particularly important substrates are provided by stretches of arenaceous rocks among the Ordovician and Silurian

deposits of the Southern Uplands, the Devonian Old Red Sandstone of north-east Scotland and Orkney, the granite intrusions of Dumfries, Arran and the Grampians, and a variety of other igneous and metamorphic rocks up through the Isles and round into Shetland.

Over such materials, the community is commonest on gentle to moderately steep hill-slopes, though it can be found on level ground provided the drainage remains reasonably free, and the general character of the soils is reflected in the prominence here, among the sub-shrubs, herbs and bryophytes, of calcifuges, many of a rather broad amplitude and some of the most distinctive, like *Carex pilulifera*, quite mesophytic. However, though some of the most frequent plants of the community are tolerant of quite moist soils, this kind of heath extends only a little way on to impeded profiles, such as the gley-podzols and stagnopodzols widely distributed through the range of the *Calluna-Erica* heath on gentle receiving slopes or over impervious bedrock and drift; and species able to stand a measure of stagnation, such as *Scirpus cespitosus*, *Erica tetralix* and *Juncus squarrosus*, find only rather sparse representation towards one edaphic extreme. Similarly, though some of the profiles accumulate a distinct humic top, the community does not normally occur over even the thin ombrogenous peats that, with the increasingly heavy rainfall towards the far north-west, extend on to the moderately steep slopes, even over pervious bedrocks, that further to the south would have the *Calluna-Erica* heath. In both of these situations, the community is typically replaced by the *Scirpus-Erica* wet heath, though the two kinds of vegetation intergrade widely and the boundary between them can be markedly affected by treatment. In extreme cases, the *Calluna-Erica* heath can spread over the dried and fretted margins of quite deep blanket peat that has been drained or cut: such a development appears to be in train on the most severely degraded stretches of blanket mire on Lewis and Harris (Hulme & Blyth 1984) and is well advanced on Shetland (Hulme 1985, Roper-Lindsay & Say 1986). In such transitional habitats, the heath can be of the Typical form or, particularly where there is exposure and wind erosion of the peat mantle down to underlying mineral material, of the *Racomitrium* sub-community.

Another edaphic limit is seen where there is a geological switch to calcareous bedrocks which, within the range of the *Calluna-Erica* heath, occurs most obviously along the Moine Thrust, where the Cambrian Durness Limestone crops out, and over some stretches of Tertiary basalts on Mull and Skye (Birks 1973, Birse 1980). The community can extend some considerable way on to the quite base-rich brown earths that have developed from such substrates, where the pH often rises above 6, and it is characteristically represented there by the *Thymus-Carex* type. The intimate mixtures of calcifuges and calcicoles in this vegetation recall the 'limestone heath' described from more southerly parts of Britain, with the additional interest in this case of a modest floristic element reflecting the oceanic climate, *Blechnum spicant* and *Primula vulgaris* in particular making rather a striking pair. Essentially similar vegetation to this has also been described from serpentine soils on Shetland, particularly on Unst (Birse 1980), where severe exposure makes some stands look transitional to the *Racomitrium* sub-community and encourages the development of a maritime component. And it has been noted, too, at scattered localities over limestones and calcareous metasediments through the Highlands (McVean & Ratcliffe 1962) and marking out limy partings in the Silurian shales of the Moorfoot cleughs (Ferreira 1978).

In very exposed situations, it is possible that the *Calluna-Erica* heath represents a fairly natural kind of climax vegetation, from which trees and shrubs are excluded by severe climatic and edaphic conditions, often combined now with a shortage of nearby seed-parents (Birse 1980). More often, though, it is treatments that maintain the community as a plagioclimax, burning and grazing having long been part of the agricultural economy in many parts of its range. In fact, management of the vegetation for grouse-rearing is not so important here as it is in the *Calluna-Vaccinium* heath, which is much more widespread than the community through the major grouse-moor areas of the Grampians and south-east Scotland. But periodic burning to control and regenerate the heather cover in hill-pasture for stock is of major significance in some areas, as in Dumfries & Galloway, and together with the grazing activities of the animals and, in certain regions, of deer too, this has a controlling influence on the floristics and physiognomy of the vegetation.

It is difficult to disentangle the different effects of the two kinds of treatment and, of course, in good pastoral management of the hill-grazings, the point is to use them together to maintain the health of the swards. And, in so far as accounts of burning experiments are ever explicit about the types of heath being treated, which is rarely, these have been mostly conducted on the communities widespread in the east-central Highlands, where the *Calluna-Erica* heath is rather poorly represented. But what we can say, is that, apart from its general effect of superimposing on to the floristic variation in the community the pattern of regeneration of heather universal in burned heaths, fire is particularly important here in providing *E. cinerea* with a repeated opportunity to maintain its representation. Even under the quite dense shade of a maturing *Calluna* canopy, *E. cinerea* can persist as an understorey in this vegetation but, with clearance of the ground in a burn, it can regenerate well

from seed, perhaps out-performing *Calluna* on the drier soils here and on warmer slopes, and, maintaining some activity through the winter in the oceanic climate, readily attains co-dominance in the middle years of recovery (Bannister 1964*b*, 1965, Gimingham 1972). Competitive interactions between these two in response to burning may account for much of the canopy diversity that is seen in Typical *Calluna-Erica* heath.

However, grazing of regenerating mixtures of *Calluna* and *E. cinerea*, even light grazing imposed for only a short time, can tip the balance back in favour of the heather which, in response to cropping, seems to adopt a plagiotropic habit, extending its cover laterally, while *E. cinerea* continues to grow erect (Gimingham 1949, 1972). And, of course, very heavy grazing after a burn can severely hinder regrowth of all the more palatable sub-shrubs, perhaps contributing in exposed sites to the kind of structure seen in some stands of the *Racomitrium* sub-community with its open canopy, its local spread of the unpalatable *Empetrum nigrum* ssp. *nigrum* and extensive carpets of *R. lanuginosum* or encouraging in Typical *Calluna-Erica* heath a greater abundance of species such as *Nardus stricta* or *Juncus squarrosus*.

With more judicious grazing applied for considerable periods of time, the major effect is to maintain among a fairly short sub-shrub canopy a continuing contribution from the kinds of grasses and bryophytes that, in ungrazed stands, are able to develop only in a patchy and temporary fashion during the early years of regeneration or among degenerating heather bushes, then to be largely extinguished. Local and somewhat attenuated floras of this kind can sometimes be seen in Typical *Calluna-Erica* heath but it is in the *Festuca-Anthoxanthum* sub-community and, over more base-rich soils, the *Thymus-Carex* type, that such a composition is most characteristic. The former kind of grassy heath is widespread through the range of the community, grazed usually now by sheep, sometimes by cattle and locally by horses, but is particularly important in the hill-pastures of south-west Scotland.

Zonation and succession

The community is typically found with grasslands, other kinds of heath and mires in zonations and mosaics where floristic variation is determined by differences in soils, local climate and treatments. Stable regimes of burning and grazing can hold any successional developments in check but, without some kind of treatment, many stands would probably progress to scrub and woodland.

In the simplest edaphic sequences, the *Calluna-Erica* heath occurs over the driest in series of base-poor soils disposed over the hill-slopes of the upland fringes. In those more oceanic parts of northern Britain where it is concentrated, it typically gives way, over gley-podzols and stagnopodzols which can accumulate a thick humic top over the periodically waterlogged sub-soil, to the *Scirpus-Erica* wet heath. There *Calluna* retains its high frequency, but *E. cinerea* is usually replaced by *E. tetralix*, and *Molinia* and *Scirpus cespitosus* become very common and often abundant, with more or less total eclipse of the smaller grasses and a replacement of the pleurocarpous mosses by at least some Sphagna. Such transitions are usually seen over ground of decreasing slope, either moving down from hillsides with shedding drainage on to more gentle receiving ground or uphill on to plateaus with intergrades to ombrogenous peat, but they can be very gradual and, where discontinuous mantles of drift result in patchy variations of drainage impedence, intimate mosaics of the two vegetation types can be seen, even over gently-undulating or flat ground. In such patterns as these, Typical *Calluna-Erica* heath is often found grading into Typical *Scirpus-Erica* heath or, in more exposed situations or where the ground has been much degraded, the *Racomitrium* sub-community can be seen juxtaposed with the *Cladonia* sub-community of the *Scirpus-Erica* heath. Quite widely, too, the zonation runs on into the *Scirpus-Eriophorum* blanket mire over thickening ombrogenous peat. The proportion of these communities in the sequences varies with the rainfall because, with the shift into the wetter reaches of north-west Scotland, the wet heath and blanket mire spread on to ground of increasing slope, thus restricting the contribution of the dry heath. Drainage of the peat can reverse this trend and the spread of *E. cinerea* through the wet heath and on into the *Cladonia* sub-community of the blanket mire in the more oceanic parts of Britain, as in the Outer Hebrides (Hulme & Blyth 1984) and Shetland (Hulme 1985, Roper-Lindsay & Say 1986), is a striking indication of the shift of the vegetation towards the *Calluna-Erica* heath where the bogs have been much cut over. Analagous sequences to the above can also be seen where the community extends into eastern Scotland, though here the wet heath is usually represented by the *Ericetum tetralicis* and the blanket bog by the *Calluna-Eriophorum* mire.

More often, though, in these latter zonations, the *Calluna-Erica* heath is itself replaced by the *Calluna-Vaccinium* heath, producing a boreal equivalent to the kinds of patterns normally seen in the oceanic west. However, as explained earlier, the two heath types do show some geographical overlap, when they are sometimes separated altitudinally, the *Calluna-Vaccinium* heath replacing the *Calluna-Erica* type with the move to higher ground, or according to aspect, when the communities can be found in closer proximity, but with the *Calluna-Vaccinium* heath taking over with the shift on to slopes facing north and east. Other local climatic complications can be seen among the dry-heath components of these kinds of sequences where sub-shrub vegetation runs right to the edge of sea-cliffs receiving appreciable

amounts of salt-spray. In extreme cases the *Calluna-Erica* heath can be totally replaced by some kind of *Calluna-Scilla* heath, but the two communities sometimes occur together, zoned according to the gradient of spray deposition and showing great continuity in their sub-shrub components, the effect of maritime influence being mainly felt among the associated herb flora, the particular character of which is also influenced by the nature of the soil. Such patterns are well seen on Skye (Birks 1973), along the Caithness cliffs and in Shetland (Birse 1980, Roper-Lindsay & Say 1986), where the *Festuca-Anthoxanthum* sub-community and, on more base-rich soils, the *Thymus-Carex* type, grade to the maritime heath. Analagous patterns occur towards the back of some coastal dune-systems, where the *Calluna-Erica* heath grades to *Calluna-Carex* heath towards the sea.

Zonations of these kinds, influenced primarily by differences in soils or climate or both, are all very often affected by treatments. In particular, burning, with its general tendency to favour vigorous regrowth of heather over the medium term, can blur boundaries between the *Calluna-Erica* heath and either the *Scirpus-Erica* wet heath or other types of drier sub-shrub vegetation, maritime or not, which occur adjacent to it, and it may take a considerable period of time before the floristic differences between the communities grow out to re-assert the zonation that has been cut across by fire. Grazing, too, can confuse patterns by, for example, favouring an abundance of herbaceous associates that are shared by the different kinds of heath: *Molinia* can increase generally across the junction of the *Calluna-Erica* heath and the *Scirpus-Erica* wet heath and, in transitions to maritime sub-shrub vegetation, finer-leaved grasses and small herbs may be encouraged throughout, producing a general grassy appearance that masks the increasing influence of salt-spray.

More generally important, however, is the effect which grazing, either alone or in conjunction with burning, has on mediating the transformation of this kind of heath to Nardo-Galion grasslands. After fire, very heavy grazing can precipitate a run-down of the heath to swards in which *Nardus stricta* or *Juncus squarrosus* play an important part or permit the spread of *Pteridium aquilinum*. But, less catastrophically than this, steady grazing pressure pushes the vegetation towards the *Festuca-Agrostis-Galium* grassland or, over more base-rich soils, the *Festuca-Agrostis-Thymus* grassland. The *Festuca-Anthoxanthum* and *Thymus-Carex* sub-communities are essentially intermediates along this developmental line and are very often found intermixed with the Nardo-Galion swards in mosaics which are determined by differences in grazing intensity. Many of these mixtures are stable and there is some pastoral advantage in having patches of the heath, which can provide a valuable winter bite, among the more generally nutritious grassland, but the long continuance of heavy pasturing, in areas like south-west Scotland, has certainly reduced the proportion of heaths in the mosaics (e.g. Hill & Evans 1978).

Release from grazing and burning, except where the heath occurs in very exposed situations, theoretically permits progression to scrub and woodland though, in many areas, natural seed-parents are now scarce. Over the characteristic soils here, the most likely developments are the *Quercus-Betula-Dicranum* woodland or, where the profiles are not quite so base-poor and oligotrophic, the *Quercus-Betula-Oxalis* woodland, with in both cases birch, mostly *Betula pubescens*, rather than oak being very much the predominant tree. Where the community extends into east-central Scotland, the *Pinus-Hylocomium* woodland is a possible climax of successions involving the *Calluna-Erica* heath, with the *Juniperus-Oxalis* scrub perhaps figuring as a precursor (Birse 1980). In various parts of the range, but particularly in the Dumfries and Galloway hills, ground which would be at least partly occupied by the community has been extensively afforested and conifers from the plantations can seed into the heath.

Distribution

The *Calluna-Erica* heath occurs widely through the more oceanic parts of Scotland with outlying stands in Wales and western England and around the east-central Highlands. It is particularly well seen in south-west Scotland, where the Typical and *Festuca-Anthoxanthum* sub-communities are common, and through some of the Western Isles and on Shetland where the Typical and *Racomitrium* sub-communities are distinctive. The *Thymus-Carex* type is much more local but good stands occur on Skye, Rhum and Uist, and at scattered localities through the Highlands and Southern Uplands.

Affinities

Although the distinctive character of some kinds of the *Calluna-Erica* heath has been recognised in accounts of Scottish sub-shrub communities (e.g. McVean & Ratcliffe 1962, Birks 1973, Ferreira 1978), this vegetation has been mostly subsumed within a broadly-defined *Callunetum* of the British sub-montane, and indeed, with frequent burning, it can be very difficult to separate the community from its boreal counterpart, the *Calluna-Vaccinium* heath. Gimingham (1972), following Muir & Fraser (1940), did distinguish two heath types roughly corresponding with the communities recognised in this scheme, grouping the *Calluna-Erica* heath among the generally oceanic sub-shrub types of Böcher (1943). But it was left to Birse (1980, see also Birse & Robertson 1976) to give a more precise and comprehensive definition of the community, which he saw as equivalent to the

Carici-binervis-Ericetum Braun-Blanquet & Tüxen 1950, 1952. As defined here, the *Calluna-Erica* heath takes in most of Birse's vegetation, but also includes what he saw as some distinctive heath from the Shetland serpentine (see also Roper-Lindsay & Say 1986). With the northern kinds of *Calluna-Scilla* and *Calluna-Carex* heaths, which replace it in more maritime situations, it forms a suite of sub-shrub communities of the cool oceanic parts of northern Britain, giving way southwards to related vegetation types with *Ulex gallii*. Birse (1980) grouped his emended *Carici-Ericetum* with these warm oceanic communities in the Ulicion gallii. An alternative view, echoing Braun-Blanquet's (1967) suggestion of a major split among Atlantic heaths along the northern boundary of *U. gallii*, would be to place the *Calluna-Erica* heath closer to communities described from Norway (Nordhagen 1928, Böcher 1940) and the Faroes (Böcher 1940).

Floristic table H10

	a	b
Calluna vulgaris	V (1–10)	V (1–8)
Erica cinerea	IV (1–10)	IV (1–6)
Potentilla erecta	IV (1–4)	IV (1–4)
Carex binervis	III (1–4)	I (1–2)
Molinia caerulea	III (1–5)	I (1–2)
Juncus squarrosus	II (1–4)	I (1–3)
Diplophyllum albicans	II (1–4)	I (1)
Campylopus paradoxus	II (1–3)	I (1)
Rhytidiadelphus loreus	II (1–4)	I (1–3)
Sphagnum capillifolium	I (1–4)	
Cladonia floerkeana	I (1–4)	
Sphagnum recurvum	I (1–8)	
Scapania gracilis	I (1–2)	
Racomitrium lanuginosum	II (1–6)	V (1–6)
Cladonia uncialis	I (1–4)	IV (1–5)
Scirpus cespitosus	II (1–4)	III (1–4)
Empetrum nigrum nigrum	I (1–5)	III (1–4)
Cladonia impexa	I (1–4)	III (1–6)
Carex panicea	I (1–3)	III (1–4)
Huperzia selago	I (1–2)	III (1–3)
Cornicularia aculeata	I (1–5)	II (1–3)
Cladonia furcata	I (1–3)	II (1–3)
Cetraria islandica	I (1–3)	II (1–3)
Alectoria nigricans		I (1–3)
Festuca ovina	I (1–4)	II (1–6)
Anthoxanthum odoratum	I (1–4)	I (1–3)
Galium saxatile	II (1–3)	I (1–3)
Agrostis capillaris	II (1–4)	I (1–3)
Pleurozium schreberi	II (1–4)	I (1–3)
Dicranum scoparium	II (1–4)	I (1–3)
Hylocomium splendens	I (1–6)	I (1–4)

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c	d	10
V (1–8)	V (1–8)	V (1–10)
V (1–10)	IV (1–6)	IV (1–10)
V (1–4)	V (1–4)	IV (1–4)
II (1–4)	I (1)	II (1–4)
I (1–4)	II (1–4)	II (1–5)
I (1)		I (1–4)
I (1–2)	I (1)	I (1–4)
I (1–4)		I (1–4)
I (1)		I (1–4)
		I (1–4)
		I (1–4)
		I (1–8)
		I (1–2)
I (1–4)	II (1–8)	III (1–6)
I (1–3)	I (1–4)	II (1–5)
I (1)	I (1)	II (1–4)
I (1–8)	I (1–3)	II (1–8)
I (1–4)	II (1–4)	II (1–6)
I (1)	II (1–4)	I (1–4)
		I (1–3)
I (1–2)		I (1–5)
I (1)		I (1–3)
		I (1–3)
		I (1–3)
V (1–6)	V (1–4)	III (1–6)
V (1–6)	V (1–4)	III (1–6)
III (1–4)	II (1–3)	II (1–4)
III (1–4)	II (1–4)	II (1–4)
III (1–4)	II (1–3)	II (1–4)
III (1–6)	II (1–3)	II (1–6)
III (1–6)	III (1–6)	II (1–6)

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Floristic table H10 *(cont.)*

	a	b	c	d	10
Campanula rotundifolia	I (1–3)	I (1–3)	II (1–3)	I (1)	I (1–3)
Succisa pratensis	I (1–4)	I (1–3)	II (1–4)	II (1–4)	I (1–4)
Hypericum pulchrum	I (1–3)	I (1–3)	II (1–3)	II (1–3)	I (1–3)
Festuca rubra	I (1–4)	I (1)	II (1–6)	II (1–3)	I (1–6)
Lotus corniculatus	I (1–3)	I (1–3)	II (1–4)	II (1–4)	I (1–4)
Luzula multiflora	I (1–3)	I (1–3)	II (1)	I (1)	I (1–3)
Polygala serpyllifolia	I (1–2)	I (1–3)	II (1–3)	II (1–3)	I (1–3)
Luzula campestris	I (1–3)		II (1–3)	II (1–3)	I (1–3)
Plantago maritima		I (1–3)	II (1–3)	II (1–2)	I (1–3)
Plantago lanceolata			II (1–4)	II (1–3)	I (1–4)
Thymus praecox	I (1)	I (1–3)	II (1–4)	V (1–4)	I (1–4)
Danthonia decumbens	I (1–3)	I (1–3)	II (1–4)	V (1–5)	I (1–5)
Viola riviniana	I (1–3)	I (1–3)	II (1–3)	V (1–4)	I (1–4)
Prunella vulgaris			I (1–2)	IV (1–3)	I (1–3)
Carex pulicaris			I (1–3)	IV (1–4)	I (1–4)
Blechnum spicant	II (1–4)	I (1–3)	II (1–4)	III (1–4)	II (1–4)
Rhytidiadelphus triquetrus	I (1–3)	I (1–3)	I (1)	III (1–4)	I (1–4)
Linum catharticum			I (1–3)	III (1–3)	I (1–3)
Primula vulgaris			I (1–2)	III (1–4)	I (1–4)
Breutelia chrysocoma			I (1–4)	III (1–4)	I (1–4)
Solidago virgaurea	I (1–3)	I (1–3)	I (1–3)	II (1–4)	I (1–4)
Deschampsia flexuosa	III (1–4)	III (1–4)	II (1–6)	II (1–3)	III (1–6)
Hypnum cupressiforme	III (1–6)	III (1–4)	II (1–4)	II (1–3)	III (1–6)
Agrostis canina	II (1–4)	II (1–4)	II (1–4)	II (1–4)	II (1–4)
Nardus stricta	II (1–4)	II (1–6)	II (1–3)	I (1)	II (1–6)
Vaccinium myrtillus	II (1–6)	II (1–4)	II (1–4)	I (1)	II (1–6)
Erica tetralix	II (1–4)	II (1–4)	I (1–3)	I (1)	II (1–4)
Carex pilulifera	I (1–4)	III (1–4)	II (1–4)	I (1–3)	II (1–4)
Festuca vivipara	I (1–4)	II (1–6)	II (1–4)	II (1–3)	II (1–6)
Polytrichum commune	I (1–4)	I (1–3)	I (1–3)		I (1–4)
Rhytidiadelphus squarrosus	I (1–3)	I (1–3)	I (1–3)	I (1–3)	I (1–3)

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Antennaria dioica	I (1–3)	I (1–3)
Polytrichum piliferum	I (1–3)	I (1–3)
Vaccinium vitis-idaea	I (1–3)	I (1–4)
Narthecium ossifragum	I (1–3)	I (1–3)
Pteridium aquilinum	I (1–4)	
Cladonia coccifera	I (1–4)	I (1–3)
Mnium hornum	I (1–3)	
Leontodon autumnalis		
Number of samples	84	37
Number of species/sample	16 (5–49)	19 (9–35)
Shrub/herb height (cm)	20 (3–50)	13 (3–31)
Ground layer height (mm)	25 (10–50)	21 (10–50)
Shrub/herb cover (%)	87 (5–100)	60 (15–95)
Ground layer cover (%)	6 (0–70)	36 (25–45)
Altitude (m)	315 (60–780)	403 (120–688)
Slope (°)	15 (0–85)	7 (0–80)
Soil pH	4.8 (3.5–5.7)	5.4 (3.9–6.2)

a Typical sub-community
b *Racomitrium lanuginosum* sub-community
c *Festuca ovina-Anthoxanthum odoratum* sub-community
d *Thymus praecox-Carex pulicaris* sub-community
10 *Calluna vulgaris-Erica cinerea* heath (total)

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I (1–3)		I (1–3)
I (1–3)		I (1–3)
I (1–4)		I (1–4)
I (1–3)	I (1)	I (1–3)
I (1–3)	I (1–3)	I (1–4)
		I (1–4)
I (1–3)	I (1–3)	I (1–3)
I (1–3)	I (1–3)	I (1–3)
55	13	189
24 (13–58)	36 (12–50)	20 (5–58)
15 (3–50)	15 (7–30)	17 (3–50)
15 (10–30)	25 (20–30)	22 (10–50)
91 (30–100)	99 (90–100)	89 (5–100)
23 (0–90)	20 (0–70)	18 (0–90)
221 (7–520)	181 (16–390)	295 (7–780)
18 (0–80)	21 (5–30)	15 (0–85)
5.1 (3.4–5.6)	6.4 (6.1–6.6)	5.1 (3.4–6.6)

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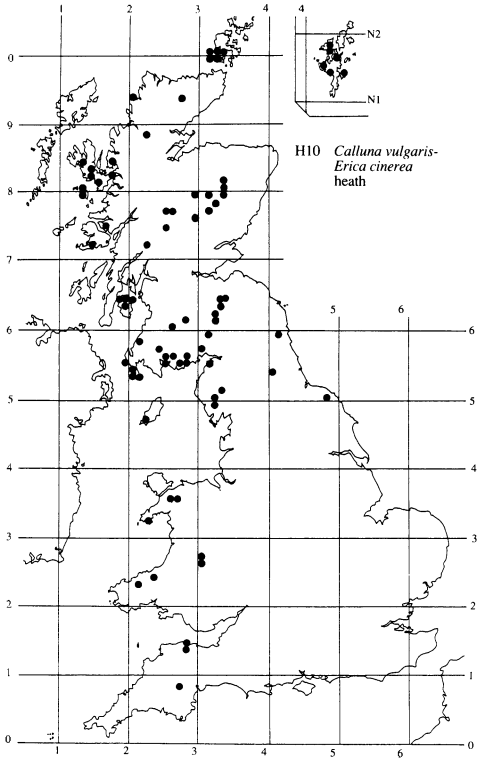

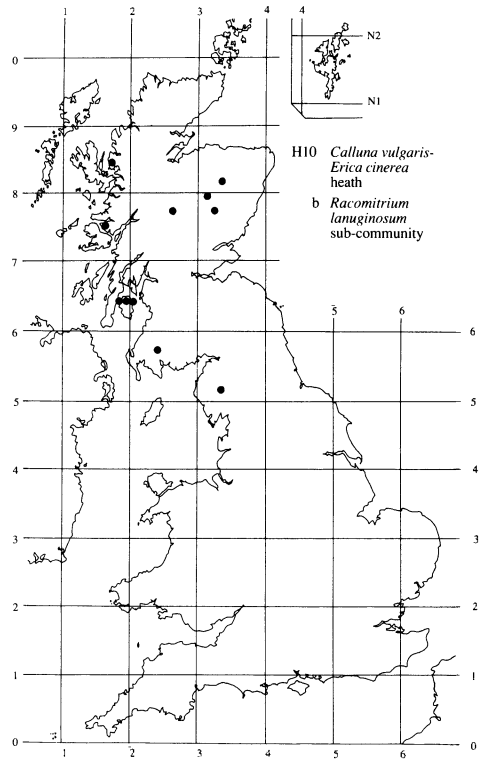

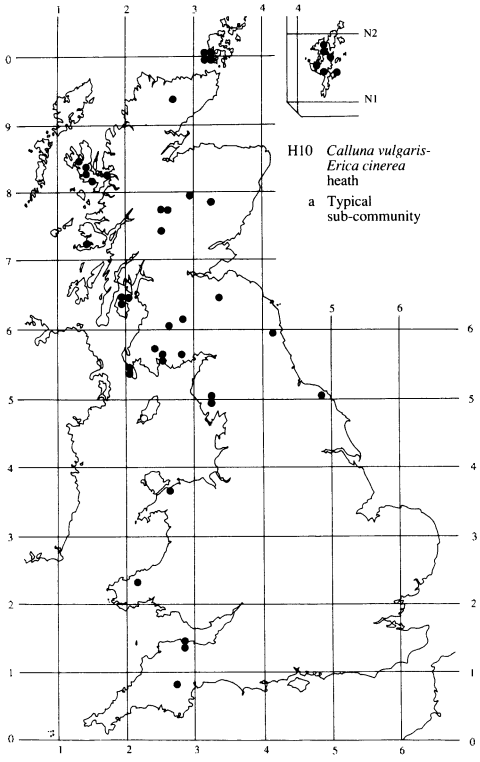

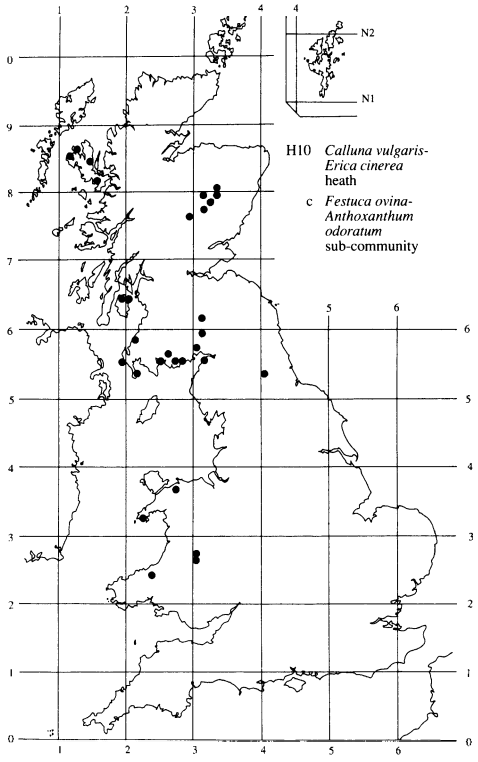

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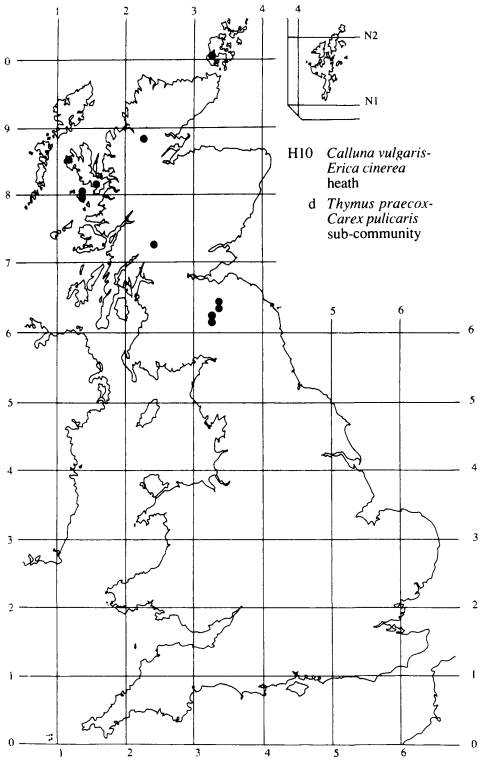

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