

# CG1

## *Festuca ovina*-*Carlina vulgaris* grassland

### Synonymy

Natural pasture Moss 1907 *p.p.*; Carboniferous Limestone Grassland Hope-Simpson & Willis 1955 *p.p.*; *Helianthemum apenninum* localities Proctor 1956, 1958; *Helianthemum canum* localities Proctor 1956 *p.p.*; *Helianthemum canum*-*Thymus drucei* Association Proctor 1958 *p.p.*; *Arabis stricta* localities Pring 1961; Carboniferous Limestone Grassland Gittins 1965a *p.p.*; *Thymo-Festucetum* Williams & Varley 1967 *p.p.*; *Poterio-Koelerietum vallesianae* Shimwell 1968a; *Helianthemum apenninum*-*Euphorbia portlandica* Nodum Shimwell 1968a; *Helianthemo-Koelerietum cristatae* Shimwell 1968a *p.p.*; *Draba aizoides* localities Kay & Harrison 1970 *p.p.*; Carboniferous Limestone Grassland Ratcliffe 1977 *p.p.*; Devonian Limestone Grassland Ratcliffe 1977 *p.p.*; Typical Limestone Grassland 3a South Gower Coast Report 1981.

### Constant species

*Carlina vulgaris*, *Dactylis glomerata*, *Festuca ovina*, *Hieracium pilosella*, *Lotus corniculatus*, *Plantago lanceolata*, *Sanguisorba minor*, *Thymus praecox*.

### Rare species

*Arabis stricta*, *Aster linosyris*, *Bupleurum baldense*, *Carex humilis*, *Cerastium pumilum*, *Draba aizoides*, *Euphorbia portlandica*, *Gentianella anglica*, *Helianthemum apenninum*, *H. canum*, *H. × sulfureum*, *Hypochoeris maculata*, *Koeleria vallesiana*, *Potentilla tabernaemontani*, *Scilla autumnalis*, *S. verna*, *Sedum forsterianum*, *Senecio cineraria*, *Veronica spicata*, *Scorpiurium circinatum*, *Tortella nitida*.

### Physiognomy

The *Festuca*-*Carlina* grassland has a characteristically short and open tussocky turf which, even where it forms extensive stands, is usually interrupted by fractured rock outcrops and small patches of bare soil and which is

often disposed in more fragmentary fashion over narrow ledges and in crevices. *Festuca ovina* (or, in one of the sub-communities, *F. rubra*) is almost always an abundant component of the sward and either *Koeleria macrantha* or *K. vallesiana* is also very frequent throughout, though usually in smaller amounts. There are often some rather small tufts of *Dactylis glomerata*, perhaps of the form variously described as var. *abbreviata*, var. *maritima* or ssp. *hispanica* (see Tutin *et al.* 1980). Generally, however, it is not perennial grasses but the woody chamaephytes *Thymus praecox* and *Helianthemum* spp., together with the deep-rooted hemicryptophyte *Sanguisorba minor*, which give the vegetation its distinctive stamp. Each of these can be abundant and combinations of them frequently co-dominate with either *F. ovina* or *F. rubra*.

*Hieracium pilosella* and *Lotus corniculatus* are constant throughout and these, too, may be abundant; *Anthyllis vulneraria*, though its occurrence is rather more uneven, can also be locally prominent. There are very frequently some scattered rosettes of *Plantago lanceolata* and, less commonly, *Leontodon taraxacoides*, *Galium verum* and *Daucus carota* (including some records for ssp. *gummifer*) occur in small quantities. Although many stands occur close to the sea, strictly maritime species are rare in the community as a whole.

There are two further general features of this vegetation. The first is the frequency of those ephemeral species which are characteristic of more calcicolous open habitats. The most frequent and showy of these (though it is rarely abundant) is the biennial *Carlina vulgaris*. Less common, but sometimes present in abundance on the fine patchwork of areas of bare soil, are some of the following annuals or paucennial: *Euphrasia officinalis* agg., *Centaureum erythraea*, *Blackstonia perfoliata*, *Medicago lupulina*, *Crepis capillaris*, *Arenaria serpyllifolia* and the grasses *Bromus hordeaceus* ssp. *feronii* and *Desmazeria rigida*; the national rarities *Cerastium pumilum* and *Gentianella anglica* also occur

occasionally in such situations. It is a marked feature of many of these species that their abundance can vary very considerably from one year to the next at the same locality (e.g. Grubb *et al.* 1982; see also below) and this may play some part in their rather uneven occurrence and prominence through the various sub-communities. They are, however, as a group much more consistently common here than in the *Festuca-Avenula* grassland. In contrast to the *Festuca-Hieracium-Thymus* grassland, however, where some of these ephemerals may also be prominent, they are very rarely accompanied here by such species as *Senecio jacobaea*, *Erigeron acer* or *Fragaria vesca*.

The second characteristic is easily overlooked but nonetheless distinctive. It is the preferential occurrence here of *Weissia* spp., which are found with varying frequency in the different sub-communities as sometimes extensive patches on the bare soil and in crevices. This is a difficult genus and plants have invariably been referred to *W. microstoma* (var. *microstoma sensu* Smith 1978). Most of the other bryophytes occurring in the community are equally characteristic of the *Festuca-Avenula* grassland, though they rarely form such extensive and luxuriant covers as are sometimes attained there. *Homalothecium lutescens*, *Pseudoscleropodium purum*, *Hypnum cupressiforme*, *Fissidens* spp. (mostly *F. cristatus*) and *Tortella tortuosa* all occur occasionally. *Cladonia rangiformis* is found in most sub-communities and is sometimes abundant, when it gives a typically crisp character to the turf. There is sometimes also a little *C. pocillum*.

Although the general character of the swards included here is xeric, there can be discerned among the various sub-communities a shift towards more mesic vegetation (see Table). In moving from the former to the latter, *Helianthemum apenninum* and *H. canum* are replaced by *H. nummularium* and *Koeleria vallesiana* by *K. macrantha*. Among the associates, *Sedum acre* and the Mediterranean-Atlantic moss *Tortella nitida* are strongly associated with the former (although *T. nitida* may have been under-recorded in certain areas). In the more mesic sub-communities there is a rise to prominence of Mesobromion species, such as *Carex flacca*, *C. caryophyllaea*, *Briza media*, *Avenula pratensis*, *Linum catharticum* and *Ranunculus bulbosus*, which brings the composition of some stands very close to the *Festuca-Avenula* grassland.

Against this general floristic background, most of the sub-communities show peculiarities which are largely attributable to the coincidental occurrence of various national rarities. Most of these have a markedly discontinuous present-day distribution in Britain, being wholly or largely confined to the kind of dry, open, calcicolous vegetation of which this community is the major example. Over Europe as a whole, these species show mostly an Oceanic Southern (*Bupleurum baldense*,

*Helianthemum apenninum*, *Koeleria vallesiana*, *Scilla autumnalis*) or a Continental Southern distribution (*Aster linosyris*, *Carex humilis*, *Helianthemum canum*, *Trinia glauca* and perhaps also here *Cerastium pumilum*).

### Sub-communities

***Carex humilis* sub-community:** *Helianthemum apenninum* localities Proctor 1956 p.p.; *Poterio-Koelerietum vallesianae caricetosum humilis* Shimwell 1968a. Both *Helianthemum apenninum* and *Koeleria vallesiana* are constant here but usually the most distinctive feature of the vegetation is the abundance of *Carex humilis* which may rival or exceed *F. ovina* in cover. These species, with *Thymus praecox*, *Sanguisorba minor* and *Hieracium pilosella*, generally form the bulk of the sward, occurring as an open turf or as smaller, broken stands over rock ledges or isolated individuals rooted in crevices. Mesobromion species are generally quite absent and *Plantago lanceolata* is very rare here too, though in some stands very close to the sea, scattered rosettes of *P. coronopus* may be found. Tall flowering stems of *Teucrium scorodonia* are sometimes prominent and locally *Sedum acre* may be abundant. On patches of bare soil, the characteristic pauciennials of the community occur together with *Weissia* cf. *microstoma*. *Tortella nitida* and, preferential to this sub-community, *Scorpiurium circinnatum*, are also occasional.

***Scilla autumnalis-Euphorbia portlandica* sub-community:** *Helianthemum apenninum* localities Proctor 1956 p.p.; *Helianthemum apenninum-Euphorbia portlandica* Nodum Shimwell 1968a; Devonian Limestone Grassland Ratcliffe 1977 p.p. *Festuca ovina* is usually the most abundant plant here and, together with a little *Dactylis glomerata* and *Koeleria macrantha* (never *K. vallesiana*), forms the grassy ground to the open or fragmentary sward. *H. apenninum*, *T. praecox* and *S. minor* can again each be prominent and, in addition, *Anthyllis vulneraria* is constant here and locally abundant. The most distinctive feature, however, is the frequent occurrence of scattered plants of *Scilla autumnalis*, *Euphorbia portlandica* and *Inula conyza* and, with the more usual *Sedum acre*, occasional *S. forsterianum*. *Trinia glauca*, though most typical of the next sub-community, is found in some stands and *Aster linosyris* and *Bupleurum baldense* occur rarely. Widely naturalised on and around the cliffs where this vegetation occurs are *Centranthus ruber* and the more recent escape from seaside gardens, *Senecio cineraria*, a west Mediterranean ragwort which has established itself at scattered localities all around the south-western coast. Again, *W.* cf. *microstoma* and *T. nitida* can be prominent on bare soil and rock outcrops.

***Trinia glauca* sub-community:** *Helianthemum apenninum* localities Proctor 1958 p.p.; *Poterio-Koelerietum vallesianae trinetosum glaucae* Shimwell 1968a. The community constants, which are all frequent in this sub-community, are here joined by a variety of Mesobromion species, notably *Avenula pratensis*, *Briza media*, *Scabiosa columbaria*, *Carex flacca* and *Linum catharticum*. The turf generally retains its open rocky character, however, and there is frequently some *Koeleria vallesiana*, sometimes with a little *K. macrantha* and, very rarely, their hybrid. *Helianthemum apenninum* is somewhat less common, though it may be abundant and, along the contact zone with *Festuca ovina*-*Avenula pratensis* grassland, in which *H. nummularium* is common, the hybrid *H. × sulfureum* occurs (Proctor 1956, 1958). This is the main vegetation type in Britain for *Trinia glauca*, which is abundant in some stands, and two other national rarities which occur much more locally here are *Aster linosyris* and *Potentilla tabernaemontani*. The most frequent bryophytes are *Homalothecium lutescens* and *Weissia* cf. *microstoma* but some stands have an unusually lush cover of *Pseudoscleropodium purum*, *Frullania tamarisci* or *Neckera crispa*.

***Helianthemum canum* sub-community:** *Helianthemum canum* localities Proctor 1956 p.p.; *Helianthemum canum-Thymus drucei* Association Proctor 1958 p.p.; Carboniferous Limestone Grassland Gittins 1965a p.p.; *Helianthemo-Koelerietum cristatae typicum* and *helictotrichetosum pratensis*, typical variant Shimwell 1968a. In general floristics and physiognomy, this sub-community is very similar to the last, with the same mixture of community constants and Mesobromion species. Here, however, *Koeleria vallesiana* is absent while *K. macrantha* is constant and *Helianthemum apenninum* is totally replaced by *H. canum*. There is, moreover, not quite so sharp a degree of vicarism between the rare *Helianthemum* and *H. nummularium*: the two may occur together here, though *H. canum* is generally the more abundant. *Trinia glauca* is absent but *P. tabernaemontani*, *A. linosyris*, *Hypochoeris maculata* and *Veronica spicata* occur in some stands. Certain species more characteristic of northern calcicolous grasslands make an appearance here: there is frequently a little *Agrostis capillaris* in the turf and, among the bryophytes, *Hylacomium splendens*, *Ditrichum flexicaule*, *Dicranum scoparium* and *Rhytidadelphus squarrosus* are occasional to frequent.

***Koeleria macrantha* sub-community:** includes *Arabis stricta* localities Pring 1961 and *Arabis stricta* nodum Shimwell 1968a. This is the sub-community which approaches most closely the more mesic vegetation of the *Festuca ovina*-*Avenula pratensis* grassland. The Mesobromion component characteristic of the two preceding sub-communities is here augmented by *Cen-*

*taurea nigra*, *Leontodon hispidus*, *Ranunculus bulbosus* and *Cirsium acaule*; *Koeleria vallesiana* and the rare *Helianthemum* spp. are quite absent. The generally open, rocky nature of the turf is still present, however; the hemicryptophytes are frequently extremely diminutive (e.g. Lousley 1950) and pauciennials and *Weissia* cf. *microstoma* occur frequently and sometimes in abundance on bare soil patches. Particular stands may be rich in *Anthyllis vulneraria* or *Hippocrepis comosa* and *Danthonia decumbens* or *Festuca rubra* are occasionally prominent. The characteristic rarities of the community are generally absent but the fragmentary vegetation in which *Arabis stricta* occurs in Britain is probably best considered here. Its most frequent associates and the physiognomy of the vegetation are those typical of this community and there are occasional records for *Carex humilis*, *Trinia glauca* and *Potentilla tabernaemontani* at the sites where it occurs.

***Festuca rubra*-*Scilla verna* sub-community:** *Helianthemo-Koelerietum cristatae* Sub-association of *Asperula cynanchia* & *Bromus ferronii* Shimwell 1968a; Typical Limestone Grassland 3a South Gower Coast Report 1981. The community constants and a variety of Mesobromion species form the ground of the vegetation here, although the sub-community occurs outside the distribution limits of *Avenula pratensis* and *Cirsium acaule*. Also, *Festuca rubra* replaces *F. ovina* here and there is consistently a small amount of *Cynosurus cristatus* in the turf. Mixtures of small tussocks of these grasses (and some *Koeleria macrantha*) and the woody chamaephytes *Thymus praecox* and *Helianthemum nummularium*, with occasional *H. canum*, generally remain the most abundant species of the vegetation which, as usual, is disposed in an open or fragmentary form over rocky slopes, ledges and crevices. However, a long list of preferential or differential species, many of which are common in maritime cliff vegetation, make this the richest of the sub-communities. *Scilla verna* is frequent here and there are occasionally scattered plants of *Armeria maritima*, *Plantago maritima* and *P. coronopus*. Then, among the pauciennials of the more open areas of the sward and crevices, the more usual species of the community are joined by *Aira caryophyllea*, *A. praecox*, *Cerastium diffusum* ssp. *diffusum*, *Bromus hordeaceus* ssp. *ferronii* and the annual clovers, *Trifolium dubium*, *T. scabrum* and *T. striatum*. It is in the more open stands of this sub-community that *Draba aizoides* occurs most frequently in Britain, usually rooted deeply in rock crevices and especially conspicuous when its bright yellow flowers emerge in early spring (Kay & Harrison 1970).

### Habitat

The *Festuca*-*Carlina* grassland is almost wholly confined to steep and rocky, though stable, slopes over hard limestones where a southerly to westerly aspect and

excessive drainage of shallow rendzinas accentuate the warm and sunny character of an oceanic regional climate. Heavy grazing is often a contributory factor in keeping the vegetation in its characteristically open state.

The distribution of the community is limited to limestones which fall within the 'warm temperate, humid and mild' region in Walter & Lieth's (1967) classification of British climate. Here, though there are between 120 and 160 wet days  $\text{yr}^{-1}$  with an annual precipitation of from 800 to 1000 mm, a disproportionate amount of the rain falls within the winter quarter when generally mild temperatures make frosts and snow rare (*Climatological Atlas* 1952, Manley 1952, Chandler & Gregory 1976). The growing season starts earlier (about mid-March) and lasts longer (260 days or more) than in other limestone areas of Britain (Smith 1976). Moreover, although spring and summer temperatures are not as generally high as on inland exposures in the south-east, these seasons are drier than there and considerably sunnier, with 7 or more hours of bright sunshine daily in mid-summer. The region is windy and gales are common.

This regional climate is modified on a local scale by the influence of topography. Almost without exception, stands of the community are confined to slopes which have a general southerly aspect, from south-east through to west. On these slopes, and especially on the steeper areas where the community is most often found and which present a more or less normal face to summer sunshine, the effects of insolation on the soil and vegetation are maximised, especially when combined with the rather low summer rainfall. With long exposure to hot sun, the soil dries and much of the heat in its surface layers is transferred back to the air: temperatures of 35–40 °C have been recorded in the boundary layer of this kind of vegetation (Berry Head, Devon using small screen: C.D. Pigott, unpub.) and still, summer days in these localities can be scorching. Taken with the generally mild winter weather, this makes their topoclimate probably the nearest approach on the British limestones to conditions characteristic of the Mediterranean.

The soils beneath the community are always free- to excessively-draining, of generally high base-status (pH 6.4–8.1) and with some free calcium carbonate (e.g. Proctor 1956, 1958, Shimwell 1968a, 1971a, b). In many cases, they are so shallow, stony and fragmentary as to amount to nothing more than crevice protorendzinas in a largely rock-dominant landscape. Elsewhere, they occur as more extensive stretches of deeper profiles, though still having the dark-grey to blackish colour and highly organic and undifferentiated structure of typical rendzinas. At various sites throughout the range of the community, however, the profiles have a distinct reddish hue which indicates the liberation of iron oxides in relatively dehydrated (haematitic) forms and a some-

what sandy or silty texture below which suggests the inheritance of long-weathered Permo-Triassic fragments and/or the incorporation of blown sand or loess (e.g. Smithson 1953, Findlay 1965; see also Pigott 1962). This range of soils has been described under a variety of names (e.g. Roberts 1958, Ball 1960, Findlay 1965) but is now mapped largely as the Crwbin Series (*Soil Survey* 1983). The most important edaphic features, as far as the vegetation is concerned, are that the soils are maintained in a generally immature, calcareous state by the slow but continual weathering of the bedrock and that they have a strong tendency to summer parching. They are also almost certainly deficient in major nutrients, especially nitrogen, but only systematic assay and controlled application of fertilisers could confirm this.

As Pigott & Walters (1954) and Proctor (1956, 1958) have stressed, the habitat of this kind of vegetation is essentially stable, despite its being so open and rocky. The community is found only on harder limestones, most commonly the Palaeozoic Devonian Limestone in Devon and Carboniferous Limestone in Wales and the Mendips and is always associated with fractured rock outcrops and cliffs rather than mobile talus. It is noticeably absent from most of the Chalk within the range of the typical regional climate, where this generally softer rock often crumbles away to a highly unstable margin along the tops of south-facing cliffs along the Channel coast. In such situations, the community is replaced on shallow rendzina soils on the warmest slopes by fragmentary and often ephemeral stands of the *Arenaria* sub-community of the *Armeria-Cerastium* therophyte vegetation, or simply by the eroding fringe of downland stands of the *Festuca-Avenula* grassland which periodically shed chunks into the sea below. On some especially hard chalk strata, though, as on the anticlinal folds that run across the Isle of Wight and into Dorset, north of Swanage, the community does occur on the typical slopes and aspects. It is, however, always in the form of the *Koeleria macrantha* sub-community, the type which is closest to a Mesobromion sward and which lacks the distinctive preferential rarities of this vegetation.

It is these harsh climatic, topographic and edaphic conditions which probably play the major role in maintaining the vegetation in its permanently open state. Perennial grasses, though often abundant in their total cover, occur typically as small discrete tussocks and never form the basis of the kind of thicker, plusher sward characteristic of deeper rendzina soils on more shaded aspects. Under these circumstances, the plants which benefit are those which are sensitive to competition for light and yet able, in one way or another, to survive the exigencies of summer droughting. Mat-forming chamaephytes favouring open habitats are often especially prominent: *Thymus praecox*, for example, is known to depend on high illumination for good growth and



flowering (Pigott 1955), and the rare *Helianthemum* spp. show an often marked vicarism with *H. nummularium* at the switch to thicker turf over more mesic soils which suggests that they are excluded from the latter by shading (Proctor 1956, 1958). *Draba aizoides* is another species intolerant of shading (Kay & Harrison 1970) and *Arabis stricta* is unable to establish itself in closed swards (Pring 1961). *Aster linosyris* shows a markedly significant reduction in achene fertility if pollinated inflorescences are shaded, although some of its British populations are self-incompatible clones whose plants never set seed (Pigott 1977; see below).

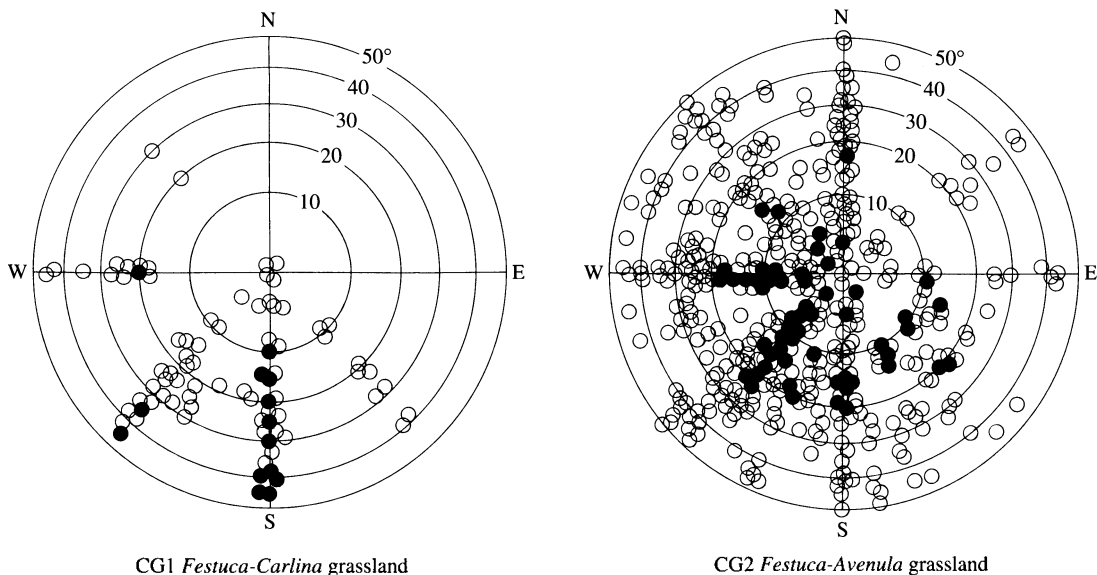
Some of these species, such as *Helianthemum canum* (Griffiths & Proctor 1956) and *D. aizoides* (Kay & Harrison 1970), though their growth is checked by drought, have a remarkable ability to recover rapidly and completely from periods of water stress. Others perhaps avoid the worst effects of parching by having extensive root systems which can penetrate very deeply into soil-filled crevices or fissures in the bedrock (e.g. Anderson 1927, Salisbury 1952, Pigott 1955, Proctor 1956). Interestingly, *Sanguisorba minor*, the only Mesobromion species which is constant and abundant throughout this community is noted for its extremely long tap-root system.

There is some evidence, too, that the phenology of certain of these perennials is geared to the topoclimatic conditions. Growth begins early and is concentrated in the spring and early summer as temperatures rise, sometimes with a further burst in autumn as precipi-

tation increases. The timing of flowering is also often early: *D. aizoides* begins as early as February, *Arabis stricta* and *Carex humilis* from March onwards (Figure 20), *Helianthemum apenninum* from late April with *H. canum* a little later. The summer months are, for such species as these, thus marked by what may approach the pattern of vegetative dormancy and fruit-ripening typical of Mediterranean plants.

Among the ephemerals which are so characteristic of the community, there are different responses to the same uncongenial conditions. In general, these are species that are able to exploit the network of gaps within the stable but open vegetation cover, growing on the accumulations of wind-blown organic and mineral detritus within crevices, areas that are too small or temporary for colonisation by perennials, or on the patches of bare soil within the turf itself, niches that may be periodically renewed by the occasional death of perennials in times of very severe droughting. Some of these species, e.g. *Centaureum erythraea*, *Bromus hordeaceus* ssp. *ferronii*, *Desmazeria rigida* and the rarities *Cerastium pumilum* and *Gentianella anglica*, behave as winter annuals, their seeds germinating in the autumn rains and the seedlings surviving the generally mild winter to flower before the onset of the driest and hottest weather which they consequently survive as seed. Others, such as *Carlina vulgaris*, *Blackstonia perfoliata*, *Medicago lupulina* and *Crepis capillaris* are sometimes or always biennial, germinating in either autumn or spring and flowering and fruiting in the following year. Grubb *et al.* (1982) have suggested that the widely differing maximum levels of abundance of species such as these in this kind of vegetation may be related to the varied size of the available gaps in the turf, the larger and

Figure 20. Polarographs showing the distribution of samples with *Carex humilis* (solid) among two kinds of calcareous grassland.



more slow-growing species (like *Carlina vulgaris*) requiring more space than the smaller annuals. In some cases, however, other factors may account for the relative rarity of these pauciennials: in some dune vegetation, for example, the abundance of *C. vulgaris* seems to be strongly influenced by seed predation by small mammals (Grieg-Smith & Sagar 1981).

Although the openness of this vegetation is probably primarily controlled by the physical characteristics of the habitat, grazing of the herbage by sheep and rabbits is also likely to be of importance in maintaining the cover of grasses at relatively low levels and so favouring the abundance of chamaephytes and the relatively high frequency of pauciennials. The former, though they may be sometimes nibbled (e.g. *Thymus praecox*: Pigott 1955) or have their seed-set limited by the removal of inflorescences (e.g. *Helianthemum canum*: Griffiths & Proctor 1956), are probably partly protected by their very prostrate habit. The latter perhaps benefit by the grazing-out of grass tussocks and the creation of scuffed areas of bare soil. These effects are likely to be of greater significance around the less rocky fringes of stands of the community where access is easier: on narrow ledges and in remoter crevices, the vegetation is probably out of reach of sheep at least. On these margins, heavy grazing may help maintain the community under more mesic edaphic conditions than are usual: on the Great Orme in Gwynedd, for example, the *Helianthemum canum* sub-community occurs in stands of quite substantial size under very heavy sheep-grazing over somewhat deeper soils than normal (Proctor 1958).

In some localities, especially where the community occurs close to coastal resorts, where large summer populations are attracted to the fine views afforded by the cliffs over which it grows or to the pleasing 'rock-garden' effect of the vegetation itself, trampling can be considerable. The unevenness of the terrain can afford some protection to craggier stands and some sensitive species, such as *Draba aizoides* and *Arabis stricta*, are generally confined to such situations. Others, such as the rare *Helianthemum* spp. and *Thymus praecox*, are resistant to a certain amount of trampling and will persist in more accessible stands. *Cynosurus cristatus*, a grass which is usually no more than very occasional in the community, is markedly frequent and sometimes abundant in stands of certain sub-communities where trampling is considerable, as in the *Trinia* sub-community on the Mendips around Weston-super-Mare and the *Festuca-Scilla* sub-community on the south Gower coast. Heavy trampling has undoubtedly contributed to the now rather scruffy appearance of some stands of the *Scilla-Euphorbia* sub-community around Torquay and Brixham in Devon.

Some of the floristic variations between the different sub-communities are perhaps related to present-day

differences in these climatic, topographic and biotic variables. As outlined above, there is a trend among the vegetation types included here from the more extreme (the *Carex humilis* and the *Scilla-Euphorbia* sub-communities) to swards which are very similar to the *Festuca ovina-Avenula pratensis* grassland (the *Koeleria* sub-community) in which an increase in Mesobromion species may be partly related to the occurrence of somewhat deeper soils over less rocky terrain in slightly damper and less sunny climates. In this respect, the slight ecological differences between *H. apenninum* and *H. canum* are of interest. The former is very much confined in Britain to the more extreme kinds of sward in this community; the latter has a wider geographical and phytosociological distribution, occurring not only in more mesic swards here but also in the *Sesleria-Galium* grassland in the considerably cooler, wetter and duller climate of the Pennine Carboniferous Limestone. Its topographic vicarism with *H. nummularium* is also somewhat less marked than that of *H. apenninum*, although this may be affected by grazing intensity (Proctor 1956, 1958). Then, again, in the *Carex humilis*, and, especially, the *Festuca-Scilla* sub-community, there is a more obvious maritime influence where the occasional occurrence of species such as *Plantago coronopus*, *P. maritima* and *Armeria maritima* may reflect a greater input of salt-spray in stands very close to the sea. Only detailed comparative studies of the physical environments of the different sub-communities can elucidate the extent of such influences.

It seems, however, very probable that some of the floristic variation within the community, and especially that involving the coincidental occurrence in the various sub-communities of different members of the group of Oceanic Southern and Continental Southern rarities, is related, not only to present-day ecological variation, but also, and perhaps primarily, to the accidents of historical survival. The habitat of the community as a whole is one of those kinds of environment that Pigott & Walters (1954) saw as likely to have retained its open and calcareous character, by virtue of its topographic and edaphic features, in the face of the forest advance and soil leaching that occurred as the Post-glacial progressed. Indeed, it is not impossible that the localities where the community occurs, or perhaps more restricted rockier areas within them, have remained in largely the same physiographic form as they are today, since the Late-glacial. On this hypothesis, they could have provided refuges for vegetation which, with the close of the Glacial, spread to become much more widely distributed than now, but which, with the later advance of a tree cover and the development of deeper and less calcareous soils over less extreme topographies, became progressively more restricted. Such a view could account not only for the present confined and disjunct

distribution of the community and the rarity in Britain of some of its most distinctive species, but also for the somewhat anomalous pattern of presence and absence of these species in moving from one locality to another. Which of these rarities survived where, may be the largely fortuitous result of an uneven process of forest advance and irregular isolation of remaining areas of open ground. Some support for this proposal is given by the fact that, in the equivalent kinds of vegetation in Continental Europe, species which here seem to replace one another in different sites occur together more frequently and consistently in communities that are both richer and more widely distributed than the *Festuca-Carlina* grassland. Such Continental communities also sometimes have consistent records for species which still survive in Britain but which here are not confined to the *Festuca-Carlina* community, but also occur in other kinds of disjunctly-distributed open vegetation (e.g. *Veronica spicata* and *Potentilla tabernaemontani* (part of the European *P. verna* agg.)) or are wholly restricted to the latter (e.g. *Phleum phleoides* and *Scleranthus perennis*). What we seem to have in this community is therefore part of the remnants of a flora which is still widespread in parts of the unglaciated area of Europe but which has been sorted and fragmented through history in Britain and is now confined to a small number of scattered sites which remain ecologically suitable.

We cannot reconstruct the detailed history of the localities where the community survives or of the vegetation itself. The pollen record provides little information about the former distribution of its preferentials or differentials: although *Helianthemum* pollen is very widespread in Late-glacial deposits (Godwin 1975), it is not separable reliably into its species. What does seem clear, however, is that, as forest was cleared for agriculture, there was no large-scale reappearance of habitat conditions suitable for expansion of the community. Grazing, especially where very heavy, may have permitted some extension of stands around the margins of rockier areas but the community still retains its essentially disjunct distribution and strict confinement to steep, warm and dry slopes.

Moreover, even stands which occur in close proximity to one another have not been colonised by species which occur nearby: thus *Carex humilis* remains abundant on Brean down in Somerset, yet totally absent from Uphill, less than two kilometres away; conversely, *Trinia glauca*, which is common on the latter site, is not present on the former. Colonies of some other species remain similarly localised, yet good growth in cultivation has been recorded for certain of them well outside their present natural ranges (e.g. *H. apenninum* (Proctor 1956), *Aster linosyris* (C.D. Pigott, pers. comm.)). In some cases, therefore, there may be hindrances to even small-scale migration which compound the isolation of tracts of the suitable habitat. Certain species, like *H.*

*apenninum* (Proctor 1956), *H. canum* (Griffiths & Proctor 1956), *Draba aizoides* (Kay & Harrison 1970) and *Arabis stricta* (Pring 1961), though they fruit well, have no special dispersal mechanism: seeds seem to be scattered to within but a short distance of the parent plants and cannot establish in the closed swards that often separate stands of the community. There may also be difficulties in survival for young seedlings of perennials in the parched conditions of the summer following germination. Again, seeds or seedlings may be heavily predated, as in *D. aizoides*, where snails are a major cause of seedling mortality in the first winter (Kay & Harrison 1970). It would be wrong to presume a common reason for slow migration of these species and only detailed programmes of experimentation, with perhaps seeding-in or transplantation of species into stands of the community from which they are absent, could provide a firm answer to their behaviour.

An additional complexity here is that some of the distinctive species of the community show ecotypic responses to what must now be very long periods of isolation of their populations. *Helianthemum apenninum*, for example, though very uniform in its British localities, retains in cultivation a prostrate habit that differs markedly from the erect form of this species in its nearest Continental locality along the Seine valley in France (Proctor 1956, 1958). Other species vary from one British locality to another, though differences may be hard to discern in the often exposed conditions in which the plants grow in the wild. Plants of *H. canum* from different British sites show a certain amount of this kind of variation and they also differ in their somewhat hairier leaves from the *H. canum* which survives in the Teesdale locality of the *Sesleria-Galium* grassland (forms sometimes described as var. *vineale* Pers. or ssp. *levigatum* Griffiths & Proctor 1956, Proctor 1957). *Aster linosyris* from the Mendips in Somerset and Berry Head in Devon has, in cultivation, a sub-erect form with the plants attaining heights of 30–35 cm; erect and taller plants, 40–45 cm high, are produced from the populations on the Great Orme in Gwynedd (and Humphrey Head in Cumbria where this species occurs in the *Sesleria-Galium* grassland) (C.D. Pigott, pers. comm.). The Humphrey Head and some, at least, of the Great Orme populations are also known to be self-incompatible clones, though they readily produce fertile achenes when plants propagated from root cuttings are brought together with other populations (Pigott 1977). By contrast, the Berry Head population fruits well in the wild, being either self-fertile or composed of a group of strains of mixed incompatibilities.

*Veronica spicata* is another species which shows considerable variation, both between and within its populations in stands of this community and of those other vegetation types in which it survives, such that some of the more robust and larger-leaved western forms which

can be found in the *Festuca-Carlina* grassland have been considered as the separate species, *V. hybrida* L. A more satisfactory solution, proposed by Pigott & Walters (1954; see also Tutin *et al.* 1972), seems to be to regard such differences as largely ecotypic responses within a single species whose populations have been widely separated in habitats which have a generally open and calcareous character but which perhaps differ slightly in certain features. As with the community as a whole, a great deal remains to be known about the interplay between historical and ecological factors that have produced such distinctive patterns of distribution.

### Zonation and succession

Stands of the *Festuca-Carlina* grassland generally occur as relatively small islands of open, rocky vegetation within more extensive tracts of closed swards or patchworks of grassland, heath and scrub. Much of this variation is explicable in terms of an edaphic transition in moving from the limestone exposures with their often fragmentary and highly calcareous soils to areas of deeper and moister soils which, in the absence of heavy grazing, become invaded by ericoids or other shrubs.

In many places, and especially where exposures of bedrock are low and much fractured, the community may cover entire outcrops. In some sites, however, the cliffs are more substantial and here the *Festuca-Carlina* grassland may become fragmented in the crevices and on the ledges of the rock face and give way over the more massive exposures to fern-dominated stands of the *Asplenium trichomanes*-*Fissidens cristatus* community in narrow fissures. Some of the species of the *Festuca-Carlina* grassland, such as certain of the paucennials and *Draba aizoides*, can survive in this more chasmo-phytic vegetation. Elsewhere, on more unstable areas of bare limestone, where there is clitter and shifting accumulations of wind-blown organic and mineral detritus, there can be a transition to the more ephemeral vegetation of the Thero-Airion.

On grazed sites (which are the majority), the most common transition around stands of the community is to some form of the *Festuca ovina*-*Avenula pratensis* grassland, frequently, on these warm, south-facing slopes, the *Helianthemum nummularium*-*Filipendula vulgaris* variant of the Typical sub-community. As the soil cover becomes more continuous and slightly deeper (though remaining calcareous and base-rich), the sward thickens up and there is a switch to a more obviously grass-dominated turf with an increase in Mesobromion dicotyledons and a reduction in the frequency of paucennials. Often, such junctions are marked by a strong vicarism between either *H. apenninum* or *H. canum* and *H. nummularium*, patterns which have been strikingly depicted by Proctor (1958). In those sub-communities where *Koeleria vallesiana* occurs (the *Carex humilis* and *Trinia glauca* sub-communities), there may be a similar

abrupt switch to *K. macrantha*; elsewhere, this latter species runs right through the grasslands to even the most strongly parched stands of the *Festuca-Carlina* community.

Variations in the sub-surface configuration of the limestone or local accumulations of loess or head can complicate such transitions. Then, more calcifuge communities developed over the deeper and initially less calcareous or superficially leached and acidified soils, can occur in close contact with the *Festuca-Carlina* grassland. This kind of mosaic is very characteristic where the *Festuca-Scilla* sub-community occurs on the Gower cliffs in West Glamorgan (South Gower Coast Report 1981).

In the more maritime sites, as in Gower and on Brean Down, there is the additional complexity imposed by gradients, running more or less normal to the coastline, of salt-spray deposition. Here, stands of the *Festuca-Scilla* and *Carex humilis* sub-communities may have occasional records for certain maritime species and give way towards the sea to the *Festuca-Armeria* grassland or directly to the crevice vegetation of the *Crithmo-Spergularietum* on sea-splashed rocks. Likewise, transitions to Thero-Airion and heath communities further up the cliffs may involve more maritime vegetation types like the *Armeria-Cerastium* therophyte community or the *Calluna-Scilla* heath.

It is doubtful whether grazing is necessary to maintain the openness of the more extreme habitats of the community, where topographic and climatic conditions are probably sufficient to prevent the development of a closed sward, subsequent invasion of shrubs and the formation of a closed woody canopy. However, bird-sown seed of shrubs can germinate in rock crevices and, if grazing is relaxed on the slopes where the community occurs, stands can be encroached upon by scrub relatively quickly: thus, Proctor (1958) noted a marked change in some stands of the *Scilla-Euphorbia* sub-community on Anstey's Cove in Devon in only three years following the demise of rabbits from myxomatosis. *Ligustrum vulgare* seems to be the most characteristic early invader, but *Crataegus monogyna*, *Rubus fruticosus* agg. and, at some sites, the Himalayan introduction *Cotoneaster microphylla*, have also been recorded. In the sunny gaps within this patchy cover, tussocks of *Brachypodium sylvaticum* can grow up together with prominent plants of *Teucrium scorodonia*, *Geranium sanguineum* and *Centaurea scabiosa* with, in the shade beneath the shrubs, sprawls of *Hedera helix*. In time, such vegetation probably develops into the kind of wind-cut spinose scrub characteristic of many ungrazed sea cliffs. In some cases, where such scrub is encroaching more slowly from areas of deeper soil, it may grade to the *Festuca-Carlina* grassland through an intermediate zone of rank *Avenula pubescens* grassland with its characteristic mixture of Mesobromion herbs, tall grasses and dicotyledons and



seedling shrubs or, in more maritime situations, through the *Festuca rubra*-*Daucus carota* ssp. *gummifer* grassland (South Gower Coast Report 1981). Some of the chamaephytes and pauciennials of the *Festuca-Carlina* grassland seem to be able to persist for some time in more open areas but they are soon overwhelmed by the taller herbage.

### Distribution

The community is characteristically limited to scattered sites on harder limestones around the southern and western coasts of England and Wales. The most widely distributed type is the *Koeleria macrantha* sub-community which occurs over Carboniferous Limestone in north Wales and the Mendips and extends the occurrence of the community on to harder Chalk strata in Dorset, the Isle of Wight and Sussex. All the remaining sub-communities are much more strictly confined to geographically isolated localities: the *Carex humilis* sub-community to Brean Down in Somerset, the *Trinia* sub-community to various sites between Brean and Axbridge along the southern Mendips, the *Festuca-Scilla* sub-community to cliffs along the south Wales coast from St Govan's Head to Gower, the *Helianthemum canum* sub-community to the north Wales coast between Anglesey and the Vale of Clwyd, all these over Carboniferous Limestone, and, over Devonian Limestone, the *Scilla-Euphorbia* sub-community to the area around Tor Bay in Devon.

### Affinities

The vegetation types included in this community represent the nearest approach among British calcicolous grasslands to the Continental *pelouses sèches calcaires* and *felsigen Trockenrasen* of the sub-alliance Xerobromion. Open, rocky swards of this kind are found more widely in mainland Europe where limestones (including Chalk) occur in climatic conditions which are attained in this country in but a few scattered localities, but which there characterise whole regions. As in Britain, however, the communities still have their maximum expression on the warmest, south-facing slopes, especially where the annual precipitation exceeds 900 mm (Shimwell 1971a). Vegetation of this kind has been described from north-west France (Allorge 1921–2, Litardière 1928, Hagène 1931, Liger 1952, Bournérias 1968; see also Stott 1970), south-west Germany (Volk 1937, Krause 1940), the Jura (Pottier-Alapetite 1943), the Auvergne (Luquet 1937) and the Alpes Maritimes (Braun-Blanquet 1961). In these regions, those rarities of the *Festuca-Carlina* grassland which are of very sporadic occurrence in Britain become a more consistent feature of the vegetation, providing a strong link with the steppe-grasslands of eastern Europe (in the order Festucetalia vallesiacae) and, to the south, with the calcicolous *garrigue* scrub of the Mediterranean (Proctor 1958, Shimwell 1971a).

Lying, as it does, on a far fringe of the distribution of this kind of vegetation in Europe, the *Festuca-Carlina* community has more in common with the swards of the Mesobromion than have the mainstream Xerobromion associations of mainland Europe and it could be argued that only the more extreme types should be separated off from vegetation of the former alliance. This was the solution proposed by Shimwell (1968a, 1971a), but if his suggestion were to be followed consistently, the *Trinia glauca* sub-community of his *Poterio-Koelerietum* (equivalent to the *Trinia* sub-community here) would belong better alongside the *Helianthemum canum* vegetation of the Welsh localities which he placed in the Mesobromion: apart from the absence of *Trinia glauca* itself, the replacement of *Helianthemum apenninum* by *H. canum* and of *Koeleria vallesiana* by *K. macrantha*, the vegetation is very similar indeed. While recognising the transition within the sub-communities to the Mesobromion (a trend which Shimwell himself acknowledged), it seems preferable to keep these vegetation types together in a single distinct community. All are characterised by some floristic and physiognomic features that separate them from the closed swards of the *Festuca ovina-Avenula pratensis* grassland and all occupy distinctly more extreme habitats. Moreover, grouping them in this way provides a unified framework for considering the effects of those historical factors that have apparently played some part in determining the structure and distribution of each.

Two other floristic affinities deserve mention. First, the *Festuca-Carlina* grassland is replaced on warm, rocky slopes on the more northerly Carboniferous Limestone around Morecambe Bay by the *Helianthemum canum-Asperula cynanchia* sub-community of the *Sesleria-Galium* grassland. Apart from the rather particular conditions of Upper Teesdale, this is the only vegetation type in Britain in which *Sesleria albicans* occurs with any of the Oceanic Southern or Continental Southern rarities, a situation which contrasts strikingly with mainland Europe where *S. albicans* is a constant species in a number of Xerobromion communities. The peculiar British distribution of this grass is taken up below.

Second, the *Festuca-Carlina* community shares with the *Festuca-Hieracium-Thymus* grassland a distinctly open structure and an abundance of pauciennials. In that vegetation type, however, the fragmentary nature of the sward is attributable to very heavy grazing by sheep or (especially in the past) rabbits and the instability of the habitat is reflected by the additional frequency of weed species which are never prominent in the *Festuca-Carlina* community. Such swards can develop on all aspects and, though on south-facing slopes the effects of insolation may accentuate the openness of the cover, they do not depend on topoclimatic conditions for the maintenance of their distinctive physiognomy.

## Floristic table CG1

	a	b	c
<i>Sanguisorba minor</i>	V (2–7)	V (3–5)	V (1–7)
<i>Thymus praecox</i>	V (3–5)	V (1–6)	V (1–7)
<i>Festuca ovina</i>	V (3–8)	V (4–8)	V (3–8)
<i>Hieracium pilosella</i>	IV (1–7)	II (1–2)	V (1–5)
<i>Lotus corniculatus</i>	IV (1–5)	II (1–4)	V (1–5)
<i>Carlina vulgaris</i>	IV (1–3)	II (1–2)	III (1–2)
<i>Dactylis glomerata</i>	IV (1–3)	V (1–3)	IV (1–4)
<i>Plantago lanceolata</i>	I (3)	V (1–4)	IV (1–5)
<i>Helianthemum apenninum</i>	V (1–5)	V (3–6)	III (1–5)
<i>Koeleria vallesiana</i>	V (1–5)		V (1–5)
<i>Koeleria macrantha</i>	I (1–3)	III (2–4)	II (1–3)
<i>Helianthemum nummularium</i>			I (1–3)
<i>Helianthemum canum</i>			
<i>Carex humilis</i>	V (4–8)		
<i>Teucrium scorodonia</i>	II (1–3)		I (1–2)
<i>Scorpiurium circinnatum</i>	II (1–2)		I (1)
<i>Scilla autumnalis</i>		IV (1–3)	
<i>Euphorbia portlandica</i>		III (1–3)	
<i>Inula conyza</i>		III (1–4)	I (1–2)
<i>Sedum forsteranum</i>		II (2)	
<i>Carex flacca</i>		I (1–2)	III (1–5)
<i>Carex caryophylla</i>	I (1)	II (1–3)	II (1–3)
<i>Briza media</i>			IV (1–7)
<i>Avenula pratensis</i>		I (1)	IV (1–5)
<i>Linum catharticum</i>	I (1)	II (2–3)	III (1)
<i>Polygala vulgaris</i>			I (1)
<i>Cirsium acaule</i>			II (1–5)
<i>Centaurea nigra</i>			I (1)
<i>Ranunculus bulbosus</i>	I (1)		I (1)
<i>Leontodon hispidus</i>			
<i>Asperula cynanchica</i>	I (2)		I (2–3)
<i>Gentianella amarella</i>			I (1)
<i>Plantago media</i>			I (1)
<i>Campanula rotundifolia</i>			

d	e	f	l
V (1-5)	V (1-6)	V (1-5)	V (1-7)
V (1-5)	V (1-5)	V (1-7)	V (1-7)
V (1-7)	IV (2-8)	II (1-8)	V (1-8)
IV (1-3)	V (1-5)	IV (1-3)	IV (1-7)
IV (1-3)	IV (1-5)	IV (1-7)	IV (1-7)
IV (1-3)	IV (1-3)	IV (1)	IV (1-3)
II (1)	III (1-4)	IV (1-4)	IV (1-4)
V (1-3)	IV (1-5)	IV (1-3)	IV (1-5)
			II (1-6)
			II (1-5)
V (1-5)	IV (1-6)	V (1-5)	III (1-6)
III (1-7)	III (2-4)	IV (1-5)	III (1-7)
IV (1-7)		II (1-6)	II (1-7)
	I (6-7)		I (4-8)
I (1-3)		I (1)	I (1-3)
		I (1)	I (1-2)
			I (1-3)
		II (1)	I (1-3)
	I (1)		I (1-4)
			I (2)
IV (1-5)	IV (2-6)	V (1-5)	III (1-6)
IV (1-3)	III (1-5)	III (1-3)	III (1-5)
IV (1-3)	V (2-7)	II (1)	III (1-7)
III (1-3)	IV (1-4)		III (1-5)
IV (1-3)	V (1-4)	II (1)	III (1-4)
II (1)	II (1-2)	II (1-3)	II (1-3)
	III (1-5)		II (1-5)
I (1)	III (2-3)		I (1-3)
I (1)	III (1-4)	III (1-3)	II (1-4)
	III (1-7)	III (1-5)	II (1-7)
	II (1-3)	II (1-2)	I (1-3)
I (1)	II (1-2)		I (1-2)
	I (1-4)		I (1-4)
II (1-2)	I (3)	I (1)	I (1-3)

# Floristic table CG1 (cont.)

	a	b	c
<i>Trinia glauca</i>		II (2–3)	V (1–3)
<i>Scabiosa columbaria</i>	I (1–2)	II (1–4)	IV (1–3)
<i>Helianthemum</i> × <i>sulfureum</i>			II (1)
<i>Festuca rubra</i>		I (2)	
<i>Aira caryophyllea</i>	I (3)	I (1)	
<i>Cerastium diffusum diffusum</i>	I (2)	I (1)	II (1–3)
<i>Cynosurus cristatus</i>			II (1–5)
<i>Scilla verna</i>			
<i>Trifolium scabrum</i>	I (1–2)	I (3)	I (2)
<i>Plantago coronopus</i>	II (1–3)		
<i>Trifolium dubium</i>			I (3)
<i>Trifolium repens</i>			
<i>Armeria maritima</i>			
<i>Plantago maritima</i>			
<i>Echium vulgare</i>			
<i>Aira praecox</i>			
<i>Acinos arvensis</i>			
<i>Trifolium striatum</i>			
<i>Draba aizoides</i>			
<i>Euphrasia officinalis</i> agg.	III (1–3)	II (1–2)	II (1–3)
<i>Galium verum</i>	III (1–3)	I (2–3)	IV (1–5)
<i>Leontodon taraxacoides</i>	II (1–3)	III (1–2)	II (1–5)
<i>Daucus carota</i>	II (1–3)	III (1–4)	II (1–3)
<i>Centaureum erythraea</i>	III (1–3)	I (2)	II (1)
<i>Weissia</i> spp.	II (1–5)	III (1–8)	II (1–3)
<i>Blackstonia perfoliata</i>	III (1–3)		II (1)
<i>Pseudoscleropodium purum</i>	II (1–3)	I (1)	II (1–8)
<i>Bromus hordeaceus ferronii</i>	III (1)	III (1–4)	II (1–3)
<i>Taraxacum officinale</i> agg.	III (1–2)	I (1)	I (1–7)
<i>Anthyllis vulneraria</i>		V (1–4)	II (3–7)
<i>Cladonia rangiformis</i>	III (1–3)	III (1–3)	II (1–3)
<i>Centaurea scabiosa</i>	II (1–3)	II (1–5)	II (2–4)
<i>Homalothecium lutescens</i>	II (1)		IV (1–5)
<i>Bellis perennis</i>		II (1–5)	
<i>Desmazeria rigida</i>	I (1)	III (1–3)	II (1)



d	e	f	l
II (1-3)	I (2)	II (1-3)	I (1-3) II (1-4) I (1)
III (1) I (1) I (1-3)	II (3-7)  I (1-3)	V (3-8) III (1-5) III (1-3) III (1-5) III (1-5) II (1-3) II (1-3) II (1-3) II (1-3) II (1-5) II (1) II (1-3) II (1) I (1-5) I (1-3) I (2-3)	II (2-8) II (1-5) II (1-3) I (1-5) I (1-5) I (1-3) I (1-3) I (1-3) I (1-3) I (1-5) I (1) I (1-3) I (1) I (1-5) I (1-3) I (2-3)
IV (1-3) III (1-3) III (1-3) I (1)  II (1-3) I (1) II (1)	III (1-4) II (1-4) I (4) II (1-3) II (1) III (1) IV (1) II (1-4)	III (1-3) II (1) II (1-3) II (1-3) II (1-2)  I (1) II (1-3) III (1-5) II (1-3) III (1-5)  I (1-2) I (1) III (1-4)	III (1-4) II (1-5) II (1-5) II (1-4) II (1-3) II (1-8) II (1-3) II (1-8) II (1-5) II (1-7) II (1-7) II (1-3) II (1-5) II (1-5) II (1-5) II (1-5) I (1-3)
II (1-3) I (1) II (1)	I (1-2) I (1) I (1-3)		
III (1-3) II (1-4)			
I (3) II (1) I (2)	II (1-2) II (1)		

<i>Medicago lupulina</i>	I (1)		III (1)
<i>Sedum acre</i>	III (1–3)	II (1–3)	IV (1–3)
<i>Cerastium pumilum</i>	II (1–2)	I (2)	II (1)
<i>Tortella nitida</i>	II (1–3)	III (1–3)	
<i>Hypochaeris radicata</i>			III (1–3)
<i>Hippocrepis comosa</i>	I (1–5)	II (1–2)	I (1–5)
<i>Crepis capillaris</i>	II (1–3)		II (1)
<i>Arenaria serpyllifolia</i>	I (1–2)	II (1–3)	II (1)
<i>Hypnum cupressiforme</i>	I (2)	II (3–4)	I (1–3)
<i>Fissidens</i> spp.	II (1–2)		I (2)
<i>Trisetum flavescens</i>	I (1–5)		II (1–5)
<i>Holcus lanatus</i>	I (1)		I (1)
<i>Viola hirta</i>	II (1–3)		I (3)
<i>Avenula pubescens</i>	I (1–3)		I (1–7)
<i>Poa pratensis</i>	I (1)		I (1–3)
<i>Filipendula vulgaris</i>		I (2)	II (1–3)
<i>Tortella tortuosa</i>	I (1)		I (3)
<i>Danthonia decumbens</i>	I (1)		I (1–3)
<i>Phleum pratense bertolonii</i>	I (2)		II (1–5)
<i>Rhinanthus minor</i>	I (1)		I (7)
<i>Brachypodium sylvaticum</i>		I (2)	I (1)
<i>Anacamptis pyramidalis</i>	I (1)		
<i>Agrostis capillaris</i>	I (1)		II (1–5)
<i>Dicranum scoparium</i>			I (1)
<i>Prunella vulgaris</i>			II (1)
<i>Ditrichum flexicaule</i>		I (3)	
<i>Aster linosyris</i>			I (3)
<i>Potentilla tabernaemontani</i>			I (1–3)
<i>Cerastium fontanum</i>			
Number of samples	15	12	19
Number of species/sample	24 (12–38)	22 (18–32)	30 (12–42)

- a *Carex humilis* sub-community
- b *Scilla autumnalis*-*Euphorbia portlandica* sub-community
- c *Trinia glauca* sub-community
- d *Helianthemum canum* sub-community
- e *Koeleria macrantha* sub-community
- f *Festuca rubra*-*Scilla verna* sub-community
- l *Festuca ovina*-*Carlina vulgaris* grassland (total)

II (1)			I (1)
I (1-2)		I (1)	II (1-3)
I (3)			I (1-3)
			I (1-3)
I (1)		III (1-5)	II (1-5)
I (1)	II (2-6)		I (1-6)
II (1)	I (1)		I (1-3)
I (1-3)		II (1)	I (1-3)
II (1-3)	II (1-7)		I (1-7)
II (1-3)	I (1-3)	I (1)	I (1-3)
I (1)	I (1)	I (1)	I (1-5)
I (1)	I (2-3)		I (1-3)
	II (1-3)		I (1-3)
	I (1-2)	II (1-3)	I (1-7)
	I (1)	II (1)	I (1-3)
I (2-4)	I (4)		I (1-4)
II (1-2)		I (1)	I (1-3)
I (1)	II (3-7)	II (1-5)	I (1-7)
	I (2)		I (1-5)
		II (1-3)	I (1-7)
I (1-3)	II (1-9)	I (1-5)	I (1-9)
	I (1)		I (1)
II (1-3)		I (1)	I (1-5)
II (1-3)	I (1-2)	I (1)	I (1-3)
I (1)	II (1-4)	I (1)	I (1-4)
II (1-2)		II (1-3)	I (1-3)
I (3)			I (3)
I (1-3)			I (1-3)
I (1)	I (1)	I (1)	I (1)
26	25	22	119
24 (12-33)	23 (14-31)	35 (28-50)	27 (12-50)

