CG10

Festuca ovina-Agrostis capillaris-Thymus praecox grassland

Synonymy

Agrostis-Festuca grassland auct. angl. p.p.; Basic grassland Ratcliffe 1959; Species-rich Agrosto-Festucetum McVean & Ratcliffe 1962; Saxifrageto-Agrosto-Festucetum McVean & Ratcliffe 1962; Festuca ovina/ Agrostis tenuis Type D grassland King 1962; Festuca-Agrostis Type 9 grassland King & Nicholson 1964; Festuco-Poetum Shimwell 1968a p.p.; Herb-rich Agrostis-Festuca grassland Ward et al. 1972; Festuco-Nardetum Jones 1973 p.p.; Achilleo-Festucetum tenuifoliae Birse & Robertson 1976; Thymo-Agrosto-Festucetum Evans et al. 1977; Trifolio-Agrosto-Festucetum Evans et al. 1977 p.p.; Thymo-Festucetum boreale Evans et al. 1977 p.p.; Viola-Festuca-Agrostis nodum Huntley 1979 p.p.; Galium sterneri-Helictotrichon pratense community Birse 1980; Galium verum-Koeleria cristata community Birse 1980.

Constant species

Agrostis capillaris, Campanula rotundifolia, Festuca ovina, F. rubra, Plantago lanceolata, Potentilla erecta, Prunella vulgaris, Thymus praecox, Viola riviniana, Hylocomium splendens.

Rare species

Alchemilla filicaulis ssp. filicaulis, A. wichurae, Carex capillaris, C. montana, C. rupestris, Draba incana, Galium sterneri, Minuartia verna, Myosotis alpestris, Omalotheca supina, Sagina saginoides, Salix herbacea, Sibbaldia procumbens, Tofieldia pusilla.

Physiognomy

The Festuca-Agrostis-Thymus grassland occurs as generally closed swards, often close-cropped by heavy grazing, in which the most obvious distinguishing feature, compared with the Sesleria albicans grasslands and lowland calcicolous communities, is the consistent prominence of various Nardo-Galion species. Among the grasses, for example, Agrostis capillaris is as frequent

and abudant as Festuca ovina (sometimes recorded here as F. tenuifolia but rarely as F. vivipara) and these two species together often comprise the basis of the turf. Festuca rubra is also very frequent, though it is usually not so abundant as F. ovina. Common, too, but somewhat unevenly represented in the different subcommunities, are Nardus stricta, Anthoxanthum odoratum and Danthonia decumbens and each of these can also be locally prominent. Much more patchy and rarely at high cover are Poa pratensis/subcaerulea (inadequately distinguished in some data), in drier stands Agrostis canina ssp. montana and Deschampsia flexuosa and in damper sites A. canina spp. canina and D. cespitosa.

Some sedges are frequently present but, again, there is a shift in emphasis among these species as compared with lowland swards. Carex flacca, for example, is never more than occasional and C. caryophyllea, though frequent in one sub-community, is scarce in the others. As in other upland calcicolous grasslands, certain kinds of Festuca-Agrostis-Thymus sward are characterised by the presence, together and at high frequency, of C. pulicaris and C. panicea. C. pilulifera is occasional in drier stands, C. binervis in wetter and the Arctic-Alpine rarity C. capillaris is very occasionally found.

Thymus praecox is the commonest dicotyledonous associate and it is often abundant, but that other important chamaephyte of lowland calcicolous swards, Helianthemum nummularium, though it typically occurs in this vegetation at many of its upland, northern stations, is scarce in the community as a whole. Also constant are Viola riviniana, Plantago lanceolata, Campanula rotundifolia and Prunella vulgaris with, less frequently, Ranunculus acris, Lotus corniculatus and Euphrasia officinalis agg. (including E. nemorosa, E. confusa, E. scottica and, very rarely, the Arctic rarity, E. frigida where taxa have been distinguished). Among this component, too, Nardo-Galion species can be important. Potentilla erecta is a constant throughout and Galium saxatile and Luzula campestris (rarely L. multiflora) are frequent in

one sub-community. There is very commonly a little Calluna vulgaris in the sward, often hard-grazed scattered plants or occasionally a low patchy cover, but Vaccinium myrtillus, V. vitis-idaea and Empetrum nigrum, which are a marked feature of some upland calcicolous communities, are characteristically scarce here.

Among the less frequent associates worthy of note are Galium sterneri, which has many of its eastern Scottish and Welsh localities in this vegetation, and the Continental Northern G. boreale. Also present occasionally are various Alchemilla spp., including some national rarities. A. glabra is the commonest species, though it is more frequent in some sub-communities than others. A. alpina also occurs but it is not a consistent feature of the community, one difference between these swards and those of the closely-related Festuca-Agrostis-Alchemilla grassland. Much less common here are A. xanthochlora and A. filicaulis ssp. vestita, the Arctic-Subarctic A. wichurae, and the Arctic-Alpine A. filicaulis ssp. filicaulis. Other rare species sometimes encountered are Minuartia verna and Potentilla crantzii but, apart from at a very few exceptional localities (see below), montane rarities are not a feature of this vegetation.

Bryophytes are frequent and often abundant among the herbage and within crevices in bedrock exposures, though the consistently common species are few. Hylocomium splendens is the most obvious of these with Pseudoscleropodium purum, Rhytidiadelphus squarrosus, R. triquetrus and Hypnum cupressiforme somewhat less frequent. More patchy, though sometimes conspicuous, are Dicranum scoparium, Ctenidium molluscum, Ditrichum flexicaule, Tortella tortuosa, Racomitrium lanuginosum, Thuidium tamariscinum, T. delicatulum and Frullania tamarisci. Lichens are infrequent but there is occasionally some Peltigera canina and Cetraria islandica.

Sub-communities

Trifolium repens-Luzula campestris sub-community: Species-rich Agrosto-Festucetum McVean & Ratcliffe 1962 p.p.; Festuca ovina/Agrostis tenuis Type D grassland King 1962; Festuca-Agrostis type 9 grassland King & Nicholson 1964; Festuco-Poetum cynosuretosum Shimwell 1968a p.p.; Herb-rich Agrostis-Festuca grassland Ward et al. 1972 p.p.; Festuco-Nardetum galietosum saxatilis Jones 1973; Achilleo-Festucetum tenuifoliae, Subassociation with Thymus drucei Birse & Robertson 1976; Thymo-Agrosto-Festucetum typicum and plantaginetosum p.p. Evans et al. 1977; Trifolio-Agrosto-Festucetum Evans et al. 1977 p.p.; Agrostis-Festuca basic grassland Ferreira 1978; Viola-Festuca-Agrostis nodum Huntley 1979 p.p.; Galium sterneri-Helictotrichon pratense community Birse 1980; Galium verum-Koeleria cristata community

Birse 1980. The general appearance of the vegetation here is of a usually short, close-grazed sward in which grasses play a predominant role: Festuca rubra and Anthoxanthum odoratum are more frequent and abundant than in the other sub-communities and, with F. ovina and A. capillaris, they often comprise the bulk of the cover. The most obvious floristic feature of the vegetation, however, is the occurrence together of Nardo-Galion associates and species characteristic of less-improved Cynosurion grasslands. Among the former, Luzula campestris and Galium saxatile join Potentilla erecta as constants and there is occasionally some Carex pilulifera and Polygala serpyllifolia. Lathyrus montanus and Viola lutea are scarce but also distinctive. Among the bryophytes, Rhytidiadelphus squarrosus becomes constant here and is sometimes abundant, Dicranum scoparium is frequent and Hypnum jutlandicum and Pleurozium schreberi occasional. Trifolium repens is the commonest of the more mesophytic species but is frequently accompanied by Cerastium fontanum, Achillea millefolium, Carex caryophyllea and Veronica officinalis. Galium verum, Rumex acetosa and Holcus lanatus also occur occasionally and, among the bryophytes, Lophocolea bidentata s.l. and Plagiomnium undulatum. Species of improved Cynosurion swards, notably Lolium perenne, are generally absent but there is sometimes a little Cynosurus cristatus. Minuartia verna and, in south Wales, Carex montana and, at its most southerly British station, Salix herbacea, have been recorded in this vegetation.

Within this general framework, stands may show a range of small-scale variation which has been described by a number of authors (notably Birse 1980) under distinct taxa. In some cases, for example, the vegetation appears slightly more calcicolous with a reduction in the cover of Nardo-Galion associates and the occurrence together of Helianthemum nummularium and Koeleria cristata (both scarce species in the community as a whole). Then, stands from higher altitudes may be enriched by the joint presence of Polygonum viviparum and Alchemilla alpina or, again, in wetter sites, there may be the signs of floristic transitions to the more sedge-rich vegetation of the Carex pulicaris-Carex panicea subcommunity. Each of these kinds of trend can be further affected by the intensity of grazing, with a relaxation of which some of the herbaceous dicotyledons, like the larger Alchemilla spp., may grow more bushy.

Carex pulicaris-Carex panicea sub-community: Speciesrich Agrosto-Festucetum McVean & Ratcliffe 1962 p.p.; Festuco-Poetum sub-alpinum Shimwell 1968a p.p.; Herb-rich Agrostis-Festuca grassland Ward et al. 1972; Festuco-Nardetum caricetosum pulicaris Jones 1973 p.p.; Achilleo-Festucetum tenuifoliae, Subassociation with Thymus drucei Birse & Robertson 1976 p.p.; Thymo-Festucetum boreale Evans et al. 1977 p.p.;

Moist Agrostis-Festuca basic grassland Ferreira 1978; Viola-Festuca-Agrostis nodum Huntley 1979 p.p. Although there are a few, mostly low frequency, preferentials here, the floristics are essentially intermediate between those of the two other sub-communities. In the first place, various of the Nardo-Galion and Cynosurion species characteristic of the Trifolium-Luzula subcommunity remain occasional (e.g. Anthoxanthum odoratum, Galium saxatile, Dicranum scoparium, Rhytidiadelphus squarrosus, Trifolium repens, Cerastium fontanum) and they occur intermixed with plants which attain their maximum frequency and cover in the Saxifraga-Ditrichum sub-community (notably Selaginella selaginoides and Ctenidium molluscum). Second, there is a rise to prominence here of a block of species which remain equally frequent in the Saxifraga-Ditrichum subcommunity. The commonest of these are Carex pulicaris, C. panicea, Linum catharticum and Succisa pratensis with Carex flacca, Geum rivale, Alchemilla glabra and A. alpina occasional.

Among the preferentials, Agrostis canina ssp. canina is the most frequent but Cirsium palustre, Hypericum pulchrum, Primula vulgaris, Filipendula ulmaria and Plantago maritima are also sometimes found and the rare Alchemilla wichurae has been recorded here.

Saxifraga aizoides-Ditrichum flexicaule sub-community: Saxifrageto-Agrosto-Festucetum McVean & Ratcliffe 1962; Festuco-Nardetum caricetosum pulicaris Jones 1973 p.p.; Viola-Festuca-Agrostis nodum Huntley 1979 p.p.; Galium sterneri-Helictotrichon pratense community, Carex capillaris Subassociation Birse 1980. The shift away from species characteristic of drier Nardo-Galion swards continues here with Festuca rubra, Anthoxanthum odoratum and Calluna vulgaris being reduced in both frequency and abundance and Galium saxatile and Luzula campestris virtually disappearing. Carex pulicaris and C. panicea, on the other hand, remain constant as in the previous sub-community, though they are generally more abundant here, often comprising, with Festuca ovina, Agrostis capillaris and Thymus praecox, the basis of the sward. These species are joined, first, by a variety of plants characteristic of damper, though not always base-rich, habitats: Selaginella selaginoides is constant, Pinguicula vulgaris frequent and Carex demissa occasional. Saxifraga aizoides is an especially distinctive member of this group: it is constant here and particularly conspicuous when its yellow flowers add a splash of colour to the vegetation in summer. This species is also a member of the second preferential component of this sub-community, comprising Arctic-Alpines: another saxifrage, S. oppositifolia, with its much earlier purple flowers, is not quite so frequent though it, too, can be locally abundant; Polygonum viviparum is common, Thalictrum alpinum and Silene acaulis occasional. Carex capillaris and the Northern Montane Antennaria dioica are also sometimes found. Third, there are species which are of fairly widespread occurrence in lowland calcicolous swards and less common in upland communities but which here show a resurgence in response to the increased baserichness that comes from the flushing of this vegetation: Briza media, Avenula pratensis and Leontodon taraxacoides. Finally, there is a prominent bryophyte component that reflects this combination of increased soil moisture and base-richness: Ctenidium molluscum, Ditrichum flexicaule and Tortella tortuosa are all constant and Plagiochila asplenoides occasional.

Some of the distinctive vegetation described from The Cairnwell in Perthshire by Coker (1969) is probably best considered as a variant of this sub-community. At this locality, there are some rather open swards which, though noticeably poor in some of the common species of the Festuca-Agrostis-Thymus grassland (e.g. Agrostis capillaris, Prunella vulgaris, Ranunculus acris, Plantago lanceolata, Carex pulicaris, C. panicea), have more in common with the Saxifraga-Ditrichum sub-community than any other montane calcicolous vegetation. As well as S. aizoides and D. flexicaule themselves, there are constant records for Saxifraga oppositifolia, Polygonum viviparum, Selaginella selaginoides, Linum catharticum, Bellis perennis, Tortella tortuosa and Ctenidium molluscum. Thalictrum alpinum and Antennaria dioica, which are occasionally found in the Saxifraga-Ditrichum subcommunity, and Potentilla crantzii, a scarce species there, all increase in frequency here. Festuca vivipara joins or replaces F. ovina and the common eyebright is the rare Arctic E. frigida. As well as Thymus praecox, there are usually some patches of Hieracium pilosella and Galium sterneri, and Carex flacca attains constancy. Other noteworthy species include Empetrum nigrum ssp.hermaphroditum and Botrychium lunaria and there are occasional records for the Arctic-Alpine rarities Carex rupestris, Draba incana (in a dwarf form sometimes distinguished as var. nana: Clapham et al. 1962), Omalotheca supina, Sibbaldia procumbens, Sagina saginoides and Tofieldia pusilla. Bryophytes are abundant with, in addition to the Saxifraga-Ditrichum species, frequent Encalypta streptocarpa, Rhytidium rugosum and Fissidens adianthoides. Cetraria islandica occurs in small amounts.

Habitat

The Festuca-Agrostis-Thymus grassland is essentially a sub-montane community of fairly base-rich and often moist brown earths developed over a wide variety of calcareous bedrocks and coarse-textured superficial deposits. It is typically a plagioclimax vegetation maintained by the grazing of stock (usually sheep) with some deer, rabbits and hares.

The community can be found at altitudes up to 750 m (exceptionally up to 1000 m) and, though it descends almost to sea-level in north-west Scotland, it is generally restricted to areas which have the cool, moist and cloudy climate typical of the British uplands. Annual precipitation is usually in excess of 1000 mm, in places more than twice this figure (*Climatological Atlas* 1952), with at least 160, and at some localities more than 200, wet days yr⁻¹ (Ratcliffe 1968). The mean annual summer maximum temperature is always less than 26 °C, and, at higher altitudes and to the north-west, less than 23 °C (Conolly & Dahl 1970). On the higher mountains, winters can be very bitter and stormy, with more than 50 days of morning snow-lie (Ratcliffe 1968).

Within this extensive climatic zone, the community is characteristically confined to exposures of more calcareous soil parent materials and the scattered distribution of the typically small (usually less than 1 ha) stands is a fairly precise reflection of the local occurrence of these deposits within landscapes which are generally dominated by more acidic rocks and widespread thick drift. However, the bedrocks are very varied. The most widely distributed and locally extensive calcareous sedimentary rocks in the uplands are the various strata of the Carboniferous Limestone but the Festuca-Agrostis-Thymus grassland is not as common over these deposits as might perhaps be expected: it occurs at scattered localities in north and south Wales and in the northern Pennines but, over much of the last area, it is replaced by the Sesleria-Galium grassland and otherwise restricted by substantial extents of boulder clay. Drift likewise limits its occurrence on the Cambrian/Ordovician Durness Limestone on Skye (Birks 1973), though it is more extensive on the mainland exposures of this rock along the Moine Thrust, to the north and south of Inchnadamph. It also occurs in this area on the Jurassic Limestone of Skye (Birks 1973). Elsewhere on sedimentary rocks, it is confined to those occasional more calcareous strata which occur within masses of largely non-calcareous deposits, like some of the Ordovician/ Silurian shales exposed in the deeply-cut cleughs of the Moorfoot Hills (Ferreira 1978), parts of the Devonian Old Red Sandstone in the Brecon Beacons and certain strata of the Carboniferous sandstone which are extensively weathered in corries and gullies on Hoy in Orkney (Prentice & Prentice 1975).

Some more basic igneous rocks also provide a suitable substrate. The community can be found, for example, on the Devonian andesite lavas of the Cheviots (King 1962, Lunn 1976), on more calcareous parts of the Borrowdale Volcanics in Cumbria, on dolerites and pumice tuffs in the Eryri massif (Ratcliffe 1959a) and on Cader Idris (Edgell 1969) in north Wales and on Tertiary basalts in Skye (Birks 1973) and Mull (Jermy & Crabbe 1978). In Scotland especially, the *Festuca-Agrostis*-

Thymus grassland also occurs on more calcareous metamorphic rocks, at a few localities on the Archaean Lewisian gneiss in the north-west Highlands and on the variously-modified metasediments of the Moine and, particularly, the Dalradian Assemblage, where it is well developed on schists and epidiorites (McVean & Ratcliffe 1962, Ratcliffe 1977, Huntley 1979).

Over all these rock types, the community occurs where there is sufficient influence of the parent material to maintain the soils in a moderately calcareous and base-rich state despite the high potential for leaching in the generally wet climate. Such conditions are met around exposures and on steeper slopes by the weathering of the bedrock and solifluction within the mantle but sub-surface irrigation with lime-rich waters often plays an important part. Many of these soils are therefore kept moist throughout the year though the permeability of the underlying rocks means that drainage is usually free. Provided a balance is maintained between a marked reduction in base-status on the one hand and excessive waterlogging on the other, the Festuca-Agrostis-Thymus grassland can also occur on soils derived partly from superficial deposits. It is, for example, especially characteristic at some sites of accumulations of colluvium and it can be found, too, on riverside flats of alluvium and glacio-fluvial material. Many of the soils incorporate some glacial drift and, though this is often stony till, the presence of more fine-textured deposits may increase the tendency for drainage impedence.

The typical profiles developed under these conditions are various kinds of brown earth with mull humus, a good loamy structure and an active soil fauna in which lumbricids are often conspicuous (e.g. McVean & Ratcliffe 1962, King 1962, King & Nicholson 1964, Eddy et al. 1969, Birks 1973, Birse & Robertson 1976, Birse 1980). Such soils are moderately calcareous with a superficial pH of 5–7. They have been mapped in the Southern Uplands of Scotland within the Sourhope Series (Muir 1956, Ragg 1960, King 1962) and in England and Wales included within a variety of typical brown earths (*Soil Survey* 1983).

These more general climatic and edaphic features are reflected in the community as a whole in two major ways. First, the rise to prominence of species which are more indifferent to soil reaction and of Nardo-Galion associates can be seen as a response to the increased dilution of the effect of the bedrock by slight surface eluviation and contamination with superficials, features which are generally absent from southern lowland calcicolous grasslands. Second, the calcicolous element in these latter communities, characteristic of drier soils in a more continental climate, is here replaced by species typical of moister soils in a cool and humid upland climate. The relative importance of these two trends within this vegetation type, varying primarily in relation

to the amount of flushing, governs many of the floristic differences visible in the sub-communities.

The drier soils are characterised by the Trifolium-Luzula sub-community. In extreme cases, as around bedrock exposures and on steeper, less stable slopes, they may approach shallow lithomorphic profiles which, with little or no flushing and low drift influence, are dry and free-draining. Where the bedrock is more calcareous, the soils are rendzina-like and species such as Helianthemum nummularium and Koeleria macrantha may appear in vegetation which marks the closest approach within this community to the southern, lowland Mesobromion swards (e.g. Ferreira 1978, Birse 1980). However, where the rocks are less calcareous or the rainfall sufficiently high to induce some reduction in calcium content and base-status in even these very shallow soils, the profiles are more like rankers and Nardo-Galion calcifuges then become more conspicuous in the turf. There is, though, never more than the slightest suggestion of a switch to a mor humus economy and podzolisation is never encountered under this vegetation. The Trifolium-Luzula sub-community extends on to deeper soils over colluvium and drift, provided there is no marked increase in the amount or regularity of flushing or in the extent of drainage impedence.

Where such flushing is more pronounced, the community will extend on to moister and often less freedraining soils in the form of the Carex pulicaris-Carex panicea and Saxifraga-Ditrichum sub-communities, provided that the irrigating waters are calcareous. The soils under these vegetation types frequently show signs of B horizon gleying and their surface pH is somewhat higher than that of the Trifolium-Luzula sub-community, often approaching pH 7. In the Scottish Highlands, McVean & Ratcliffe (1962) recorded calcium levels of almost 7 g kg⁻¹ in soils under the Saxifraga-Ditrichum sub-community, compared with 1.4 g kg⁻¹ for the Trifolium-Luzula sub-community. Such features are marked in the vegetation by the increasing prominence of more calcicolous species able to tolerate high soil moisture, e.g. Carex pulicaris, Linum catharticum, Briza media, Avenula pratensis and certain bryophytes, among others characteristic of a wider range of flushed habitats in the uplands, e.g. Carex panicea, Selaginella selaginoides. The kind of regular and substantial irrigation that is marked by the development of the Saxifraga-Ditrichum sub-community is typically localised and stands of this vegetation type are generally small, rarely exceeding 10 m² in extent.

In one sense, the Carex pulicaris-Carex panicea subcommunity can be seen as a transition between the drier and wetter kinds of Festuca-Agrostis-Thymus sward but the Saxifraga-Ditrichum sub-community is also distinct in that it is generally restricted to somewhat higher altitudes within the east-central Highlands. This may be simply a reflection of the distribution of the most thoroughly flushed sites occupied by this community because, as is well known, the Arctic-Alpine species which are best represented within it (Saxifraga aizoides, S. oppositifolia, Silene acaulis, Thalictrum alpinum) can descend almost to sea-level in the north-west Highlands where the Carex pulicaris-Carex panicea sub-community is widespread (McVean & Ratcliffe 1962).

The distinctive kind of Saxifraga-Ditrichum vegetation noted from The Cairnwell (Coker 1969: see above) can be seen as a high-altitude variant developed over particular types of Dalradian metamorphic rocks. These crop out at just below 900 m on this hill and weather to a deposit which resembles the Teesdale sugar-limestone in its structure and susceptibility to wind erosion and frost-heave. The annual precipitation here is high, at about 1250 mm, and the soils are flushed but some of the wetness of the ground is due to the long snow-lie (November to June) over the east- and north-facing slopes where this vegetation occurs.

For the most part, the Festuca-Agrostis-Thymus grassland is a plagioclimax vegetation type which has been produced and maintained by the grazing of stock, deer, rabbits and hares. The most likely original forbears of the community, especially the drier swards of the Trifolium-Luzula sub-community, are probably the widespread north-western Quercus-Betula-Oxalis woodland and perhaps also the more restricted Fraxinus-Sorbus-Mercurialis woodland on more base-rich soils but, at high altitudes and latitudes, it is likely that some stands have been derived from Dryas vegetation (McVean & Ratcliffe 1962).

At the present time, the community commonly occurs as part of the extensive hill-grazings of upland Britain, exploited as pasture for sheep with some cattle. Over much of Wales, the Lake District, the northern Pennines and Southern Uplands of Scotland, such a pastoral economy, though sporadic at first, is probably very ancient (e.g. Pearsall & Pennington 1947, Steven & Carlisle 1959, Welch & Rawes 1964, Rawes & Welch 1964, 1969) and has existed in more highly organised forms, like the 'heft' or 'heaf' systems of the Scottish Borders and Pennines, for more than two centuries (e.g. Trow-Smith 1957, King & Nicholson 1964, Welch & Rawes 1964, 1969). Traditionally, in such areas, sheep have been reared in largely self-maintaining flocks, kept on the hills for much of the year at stocking rates varying from one sheep per 4 ha (in parts of the Scottish Highlands: Hunter 1961) to up to 13 sheep ha⁻¹ (as at Moor House in Cumbria: Rawes & Welch 1969). Typically, there is no manuring apart from the dung and urine of the stock.

On these unenclosed uplands, the stock generally have unhindered access to a wide variety of vegetation types but, though Festuca-Agrostis swards, including

this grassland, are not as productive as some other communities (e.g. Rawes & Welch 1969), there is some evidence to suggest that they are preferentially grazed, especially in summer (Hunter 1954, 1962, Rawes & Welch 1964, 1969). Defoliation maintains the vegetation in its typically close-cropped state, favouring, at least in the drier swards, mixtures of grasses, light-demanding species such as *Thymus praecox* and hemicryptophytes which can survive as tight rosettes.

Zonation and succession

The community is very frequently found in zonations of vegetation types related to geological and edaphic variation and, at some localities, forms part of altitudinal sequences influenced primarily by climate. Sometimes, such patterns are complicated by seral changes mediated by grazing.

The most widespread kind of edaphically-influenced zonation is found where the typically small exposures of calcareous rocks which carry this community give way to less calcareous rocks which generally make up the bulk of the surrounding landscape (Figure 23). At such junctions, there is a switch to less base-rich brown earths or, in regions of higher rainfall, to various kinds of podzol, and this is marked by transitions from the Trifolium-Luzula or Carex pulicaris-Carex panicea subcommunities to less calcicolous vegetation such as the Festuca-Agrostis-Galium grassland or various kinds of upland heath. Ordered sequences of such communities have been systematically related to variables such as calcium content and pH of the soil in the Southern Uplands (e.g. Heddle & Ogg 1936, Nicholson & Robertson 1958, King 1962) and patchworks of these vegetation types are a very common feature of many upland areas, such as north Wales (Ratcliffe 1959a, Edgell 1969), the Lake District, the northern Pennines (Eddy et al. 1969) and on the Dalradian rocks of the east-central Highlands (McVean & Ratcliffe 1962, Ratcliffe 1977). Very often, such patterns are complicated by an overlay of drift which masks the immediate influence of the underlying bedrock and increases drainage impedence. Then grasslands dominated by such species as Nardus stricta, Juncus squarrosus or Deschampsia cespitosa and wet heaths or ombrogenous mires may be added to the mosaics. The resulting close juxtaposition of these different vegetation types over complex mountain topographies is well illustrated in the vegetation maps of the Carneddau (Ratcliffe 1959a) and Cader Idris (Edgell 1969) in north Wales and a more straightforward pattern has been described from the dip slopes of Carboniferous sandstones with intruded Whin Sill along Hadrian's Wall by Lock & Rodwell (1981).

Where there is flushing with base-rich waters within stands of the *Festuca-Agrostis-Thymus* grassland, a different kind of sequence occurs. Then, the *Trifolium*-

Figure 23. Zonations of grasslands and heaths on lime-rich bedrocks with superficials.

CG9b Sesleria-Galium grassland, Typical sub-community

CG10a Festuca-Agrostis-Thymus grassland, Trifolium-Luzula sub-community

CG11a Festuca-Agrostis-Alchemilla grass-heath, Typical sub-community

CG13a Dryas-Carex heath, Hieracium-Ctenidium sub-community

U4a Festuca-Agrostis-Galium grassland, Typical sub-community

U4d Festuca-Agrostis-Galium grassland, Luzula-Rhytidiadelphus sub-community

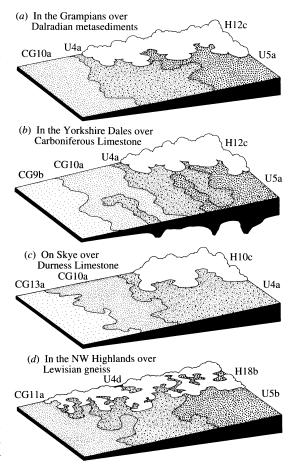
U5a Nardus-Galium grassland, species-poor sub-community

U5b Nardus-Galium grassland, Agrostis-Polytrichum sub-community

H10c Calluna-Erica heath, Thymus-Carex sub-community

H12c Calluna-Vaccinium heath, Galium-Festuca sub-community

H18b Vaccinium-Deschampsia heath, Alchemilla-Carex sub-community



Luzula sub-community gives way to either the Carex pulicaris-Carex panicea or, with more continuous or pronounced irrigation, the Saxifraga-Ditrichum, subcommunity. This, in turn, may be a transition to soligenous mire, the Pinguiculo-Caricetum dioicae, or, particularly in the Scottish Highlands, the Carici-Saxifragetum aizoidis. Sometimes, both these vegetation types are involved in complex patterns around stronglyflushed sites within stands of Festuca-Agrostis-Thymus grassland (e.g. McVean & Ratcliffe 1962). Where dripping rock outcrops intrude into the vegetation, the Saxifraga-Ditrichum sub-community may pass sharply to Cratoneurion spring vegetation or to Saxifraga-Alchemilla banks: such patterns have been well described from cliffs within Dalradian schists and epidiorites (McVean & Ratcliffe 1962, Huntley 1979), from banks on Hoy (Prentice & Prentice 1975) and around springs on the Jurassic and Durness limestones of Skye (Birks 1973) and they occur more fragmentarily in the Lake District and Upper Teesdale (e.g. Eddy et al. 1969, Jones 1973).

Where there are considerable expanses of more baserich rocks and soils in the uplands or repeated sets of exposures at progressively higher altitudes, the Festuca-Agrostis-Thymus grassland can be seen in climaticallyrelated sequences. Essentially, it seems to be the submontane counterpart of the dwarf-herb vegetation of the Festuca-Alchemilla-Silene community (McVean & Ratcliffe 1962) and it gives way to this vegetation at altitudes above about 750 m at certain sites in the Scottish Highlands. Frequently, such transitions also involve the Festuca-Agrostis-Alchemilla grass-heath, which extends to somewhat higher levels than the Festuca-Agrostis-Thymus grassland and is perhaps typical of somewhat less base-rich soils. On wetter soils, where there is more extensive flushing, greater drainage impedence or some effect of snow-lie, the community may give way above to montane Deschampsia-Galium grassland.

The pastures within which the Festuca-Agrostis-Thymus grassland occurs are usually sufficiently heavily grazed to prevent any succession to the woodland which, in the majority of sites, would be the natural climax vegetation. It is very likely, however, that variations in such factors as the breed of stock, the social behaviour of the animals, and the palatability and seasonal availability of the herbage, play a considerable part in local differences in the grassland mosaics in which the community occurs, complicating the soil- and climate-related patterns. Changes in grazing may also mediate some successional developments between the grassland types: the spread of Nardus stricta in these swards, for example, may be encouraged by very intensive grazing, especially if it is uncontrolled (Heddle & Ogg 1936, Harris 1939) and involves more selective stock such as breeding ewes, rather than mixtures of cattle and wethers (Roberts 1959). Other unpalatable species, such as *Prunella vulgaris*, *Cirsium* spp. and bryophytes, may also increase locally with heavy grazing (Rawes & Welch 1969) or there may be a run-down, on very heavily trampled sites, to vegetation with some resemblances to Lolio-Plantaginion communities in which *Poa annua* is conspicuous (e.g. Ratcliffe 1959a).

Some indication of early changes with a cessation of grazing have been provided by enclosure experiments at Moor House in the northern Pennines (Welch & Rawes 1969). At this site, it was grasses, such as Festuca rubra, F. ovina, Agrostis capillaris, Deschampsia cespitosa and D. flexuosa (the last a rare grass under normal circumstances here), which showed a marked increase, at the expense of most of the important herbaceous dicotyledons of the community and the bryophytes and lichens. Despite the occasional occurrence of certain ericoids in this community, there was no development of heath vegetation in this experiment.

On inaccessible ledges, it is often the increase in height and cover of tall dicotyledons which is the most noticeable response to lack of grazing, especially where such sites are kept moist by dripping water. Then Deschampsia cespitosa may also increase and the vegetation take on the appearance of tall-herb ledge communities. Transitions to this kind of vegetation have been recorded from the Welsh mountains (Ratcliffe 1959, Edgell 1969) and from Dalradian rocks in Scotland (e.g. McVean & Ratcliffe 1962, Huntley 1979) where the communities approach those of the Cicerbition alpini. At lower altitudes, woody species may invade such sites, as at Craig y Ciliau in the Brecon Beacons where endemic Sorbi are a notable feature (Ratcliffe 1977). In the complex topography of the Moorfoot cleughs, Festuca-Agrostis-Thymus grassland, tall-herb vegetation and scattered trees of Sorbus aucuparia, Fraxinus excelsior and Betula pubescens occur in jumbles of vegetation on the exposed rock faces (Ferreira 1978). In such sites, it is probably the Fraxinus-Sorbus-Mercurialis woodland that is the natural development of ungrazed stands of the community.

At higher altitudes and latitudes, *Dryas octopetala* vegetation may be another derivative of ungrazed *Festuca-Agrostis-Thymus* grassland (McVean & Ratcliffe 1962). Gradations to the *Dryas-Silene* community have been reported from ungrazed ledges on Dalradian rocks at The Cairnwell (Coker 1969), Creag Mhor (Ratcliffe 1977) and Caenlochan (Huntley 1979) in the east-central Highlands and on the Durness Limestone above Inchnadamph (Ratcliffe 1977). At lower altitudes in the north-west of Scotland, the community also occurs in close juxtaposition with *Dryas-Carex* heath as on the Durness Limestone on Skye, where there are also woodland fragments in a pavement landscape which

resembles the karst scenery of the Pennine Carboniferous (Birks 1973). Fencing experiments on the mainland Durness Limestone should help reveal the relationships between the *Festuca-Agrostis-Thymus* grassland and these less heavily grazed communities (Ratcliffe 1977).

Stands of the community which occur on deeper and better-drained colluvial soils on gentler slopes which are often adjacent to enclosed valley-bottom land are very susceptible to agricultural improvement by the addition of fertilisers. Although the effects of such treatment have not been followed, it is likely that the *Trifolium-Luzula* sub-community typical of such sites would progress to some kind of *Lolio-Cynosuretum*, provided grazing were maintained.

Distribution

The community occurs at scattered localities throughout much of the British uplands, always reflecting the distribution of more calcareous bedrocks and superficials. The *Trifolium-Luzula* sub-community is the most widespread form, occurring over the whole range, though less commonly at the higher altitudes and towards the north-west coast of Scotland. Here it is often replaced by the Carex pulicaris-Carex panicea subcommunity which also occurs in the east-central Highlands and at a few more montane localities in north Wales and northern England. The Saxifraga-Ditrichum sub-community is much more restricted to the Scottish Highlands, where it is largely confined to the Dalradian schists between Breadalbane and Clova with a notable outlier on Hoy in Orkney. The variant of this vegetation with Encalypta streptocarpa and Cetraria islandica has been recorded only from The Cairnwell in Perthshire.

Affinities

The Festuca-Agrostis-Thymus grassland has been recognised as a clearly-defined vegetation type since the classic descriptions of Scottish Highland stands by McVean & Ratcliffe (1962), though there has always been some hesitation as to its affinities with other communities and its position within higher classificatory units. Some studies, mostly concentrating on the contribution which the more widely distributed drier swards make to upland hill-grazing, have given the community an informal place alongside more calcifugous and mesotrophic pastures in a compendious 'Agrostis-Festuca' complex (e.g. King 1962, King & Nicholson 1964, Evans et al. 1977). Other accounts have been more precise. Some of these have described ranges of vegetation similar to that included within McVean & Ratcliffe's species-rich Agrosto-Festucetum and Saxifrageto-Agrosto-Festucetum (e.g. Eddy et al. 1969, Birks 1973, Prentice & Prentice 1975, Huntley 1979); others, sampling in different geographical areas, have shifted the perspective somewhat and characterised vegetation types, clearly very similar but sometimes named in a way which implies marked differences in floristics (e.g. Shimwell 1968a, Jones 1973, Birse & Robertson 1976, Birse 1980).

The present account, though it includes data from throughout the range of these vegetation types and takes in samples produced from many of the accounts, returns to the broad framework proposed by McVean & Ratcliffe (1962), though it unites their two communities (a possibility they acknowledged) and distinguishes an intermediate taxon. That being said, the precise affinities of the Festuca-Agrostis-Thymus grassland remain a problem. It is not so much a simple matter of these swards being anthropogenic (many anthropogenic communities have much clearer relationships) but rather that a fairly uniform kind of pastoral treatment has produced here a convergent development of vegetation which bears signs not only of its agricultural origin but also of the quite considerable variation in, or delicate balance between, different levels of base-status and soil moisture. The community thus coheres in a somewhat amorphous fashion, taking in vegetation which leans in a number of directions.

Taken as a whole, the Festuca-Agrostis-Thymus grassland is clearly not a Mesobromion community, though some of the drier calcicolous swards included here as part of the Trifolium-Luzula sub-community were separated off by Birse (1980) as part of the Seslerio-Mesobromion. In general, however, the bulk of this vegetation has been classified outside the Festuco-Brometea and two uneasy solutions have been proposed. Some authors (Birks 1973, Birse 1980), while recognising the mixed nature of the vegetation, have stressed the affinities to Nardo-Galion communities within the Nardo-Callunetea, seen especially clearly in the drier and less base-rich swards of the Trifolium-Luzula sub-community. Others have emphasised similarities to certain Continental sub-montane Molinio-Arrhenatheretea communities, though they have varied in their suggestions of an appropriate alliance, some (e.g. Eddy et al. 1969, Prentice & Prentice 1975) favouring the Cynosurion in which Jurko (1969, 1971) placed certain Czechoslovakian mountain pastures, others (e.g. McVean & Ratcliffe 1962, following Nordhagen 1943) the Nardeto-Agrostion capillaris, yet others (e.g. Shimwell 1968a and Jones 1973, following Gjaerevøll 1956) the Ranunculo-Anthoxanthion.

Floristic table CG10

	a	b	c	10
Festuca ovina	V (4-8)	V (1–9)	V (1-6)	V (1–9)
Agrostis capillaris	V (1–8)	V (1-5)	V (1-7)	V (1–8)
Thymus praecox	V (1-5)	V (1-4)	V (1-5)	V (1-5)
Viola riviniana	V (1-5)	V (1-4)	V (1-3)	V (1-5)
Potentilla erecta	IV (1-5)	IV (1–4)	IV (1-3)	IV (1-5)
Plantago lanceolata	IV (1-5)	IV (1–7)	III (1–4)	IV (1–7)
Hylocomium splendens	IV (1-8)	III (1–4)	III (14)	IV (1–8)
Campanula rotundifolia	IV (1–4)	III (1–4)	III (1–3)	IV (1–4)
Festuca rubra	IV (1–6)	III (1–6)	III (1–4)	IV (1–6)
Prunella vulgaris	III (1–4)	IV (1–4)	V (1-4)	IV (1–4)
Anthoxanthum odoratum	V (1-7)	III (1–8)	II (1–3)	III (1–8)
Trifolium repens	V (1–6)	II (1–5)	II (1)	III (1–6)
Rhytidiadelphus squarrosus	V (1-6)	II (1–6)	II (1-3)	III (1–6)
Galium saxatile	IV (1-4)	II (1-3)	I (1-3)	II (1–4)
Luzula campestris	IV (1-4)	I (1-3)		II (1-4)
Dicranum scoparium	III (1–4)	II (1-3)	I (1-3)	II (1–4)
Veronica officinalis	III (1–3)	II (1–3)	I (1)	II (1–3)
Cerastium fontanum	III (1–3)	II (1–3)	I (1)	II (1–3)
Achillea millefolium	III (1–4)	I (1–3)	$\widetilde{\mathbf{I}(1)}$	II (1–4)
Carex caryophyllea	III (1–4)	I (1–3)	I (1)	II (1–4)
Polygala serpyllifolia	II (1–3)	II (1–3)	` '	I (1-3)
Galium verum	II (1-4)	I (1–3)	I (1-3)	I (1–4)
Plagiomnium undulatum	II (1–3)	I (1)	I (1)	I (1-3)
Pleurozium schreberi	II (1–4)	I (1)	I (1)	I (1-4)
Lophocolea bidentata s.l.	II (1–3)	I (1-3)	()	I (1-3)
Rumex acetosa	II (1–4)	I (1)		I (1–4)
Hypnum jutlandicum	II (1–5)	I (4)		I (1–5)
Carex pilulifera	II (1–4)	I (1–4)		I (1–4)
Hieracium pilosella	II (1-4)	I (1–3)		I (1–4)
Holcus lanatus	II (1-4)	I (1-3)		I (1–4)
Agrostis canina montana	II (1–4)	- ()		I (1-4)
Carex pulicaris	I (1–4)	IV (1–6)	IV (1-4)	III (1-6)
Carex panicea		IV (1-4)	IV (1-4)	II (1–4)
Linum catharticum		IV (1-4)	IV (1-4)	II (1-4)
Succisa pratensis	I (1-4)	III (1–4)	II (1–4)	II (1–4)
Alchemilla glabra	I (1–3)	II (1–4)	III (1–4)	II (1-4)
Alchemilla alpina	I (1–4)	II (1–4)	II (1–4)	I (1-4)
Carex flacca	I (1–3)	II (1-4)	II (1–4)	I (1–4)
Geum rivale	, ,	II (1–3)	II (1–3)	II (1–3)
Agrostis canina canina	I (1-3)	III (1–7)	II (1-3)	I (1-7)
Cirsium palustre	I (1)	II (1–3)	I (1-3)	I (1-3)
Hypericum pulchrum	I (1-3)	II (1–3)	I (1-3)	I (1–3)
Plantago maritima	I (1-4)	II (1–4)	I (1–4)	I (1-4)
Primula vulgaris		II (1–4)	I (1)	I (1–4)
Filipendula ulmaria		II (1-3)	I (1)	I (1–3)
Alchemilla wichurae		I (1–4)		I (1–4)
Thelypteris limbosperma		I (1-3)		I (1-3)

Selaginella selaginoides	I (1–2)	III (1-3)	V (1-3)	III (1-3)
Ctenidium molluscum	I (1–6)	III (1 -4)	V (1–4)	III (1–6)
Saxifraga aizoides	I (1-3)	II (1-4)	IV (1–4)	II (1–4)
Bellis perennis	I (1–4)	II (1–4)	IV (1–4)	II (1–4)
Ditrichum flexicaule	I (1–3)	I (1)	IV (1-4)	II (1–4)
Tortella tortuosa	I (1-3)	I (1–3)	IV (1-3)	I (1-3)
Briza media	I (1–4)	II (1 -4)	III (1–4)	I (1-4)
Polygonum viviparum	I (1-4)	II (1 -4)	III (1–4)	I (1-4)
Saxifraga oppositifolia		II (1-3)	III (1–4)	I (1-4)
Pinguicula vulgaris		I (1)	III (1-3)	I (1-3)
Plagiochila asplenoides	I (1)	I (1)	II (1-3)	I (1-3)
Leontodon autumnalis	I (1-4)	I (1–3)	II (1-3)	I (1–4)
Racomitrium canescens	I (1-3)	I (1-3)	II (1-3)	I (1-3)
Antennaria dioica	I (1-3)	I (1-4)	II (1-3)	I (1–4)
Avenula pratensis	I (1-4)	I (1-4)	II (1–3)	I (1–4)
Carex demissa	I (1-3)	I (1-3)	II (1–4)	I (1–4)
Thalictrum alpinum		I (1–4)	II (1–6)	I (1-6)
Silene acaulis		I (1-4)	II (1–4)	I (1-4)
Nardus stricta	III (1–4)	III (1-7)	III (1–5)	III (1–7)
Ranunculus acris	III (1–4)	III (1–4)	III (1–3)	III (1–4)
Calluna vulgaris	III (1–4)	III (1–4)	II (1–3)	III (1–4)
Pseudoscleropodium purum	III (1–4)	III (1–3)	II (1–3)	III (1–4)
Lotus corniculatus	III (1–6)	III (1–5)	II (1–3)	III (1–6)
Danthonia decumbens	III (1–4)	II (1–6)	III (1–4)	III (1–6)
Rhytidiadelphus triquetrus	II (1–4)	II (1–4)	III (1–4)	II (1–4)
Euphrasia officinalis agg.	II (1–4)	II (1–3)	II (1–3)	II (1–4)
Deschampsia cespitosa	II (1–5)	I (1–8)	III (1–3)	II (1–8)
Hypnum cupressiforme	II (1–4)	II (1–3)	I (1-3)	II (1–4)
Hieracium spp.	I (1-3)	II (1)	II (1)	I (1–3)
Frullania tamarisci	I (1-2)	II (1–3)	II (1–3)	I (1-3)
Thuidium tamariscinum	II (1-6)	I (1-4)	I (1)	I (1–6)
Racomitrium lanuginosum	$\mathbf{I}(\mathbf{l})$	II (1–4)	I (4)	I (1-4)
Thuidium delicatulum	I (1-2)	II (1–3)	I (1)	I (1–3)
Breutelia chrysocoma	I (1-4)	I (1–4)	I (1-3)	I (1–4)
Luzula multiflora	I (1-3)	I (1)	I (1-3)	I (1-3)
Vaccinium myrtillus	I (1-4)	I (1-4)	I (1-3)	I (1–4)
Rhytidiadelphus loreus	I (1-4)	I(1)	I (1)	I (1–4)
Vaccinium vitis-idaea	I (1)	I (1-4)	I (1)	I (1–4)
Ptilidium ciliare	I(1)	I (1)	I (1)	I (1)
Blechnum spicant	I(1)	I (1)	I (1)	I(1)
Deschampsia flexuosa	I (1-4)	I (1-3)	I (1-3)	I (1–4)
Alchemilla filicaulis vestita	I (1-3)	I (1–4)	I (5)	I (1–5)
Peltigera canina	I (1–4)	I (1-3)	I (1–3)	I (1–4)
Drepanocladus uncinatus	I (1–4)	I (1-3)	I (1-3)	I (1-4)
Galium boreale	I (1)	I (1-3)	I (1–4)	I (1-4)
Fissidens osmundoides	I (1–3)	I (1-3)	I (1-3)	I (1-3)
Alchemilla filicaulis filicaulis	I (1-3)	I (1-3)	I (1-3)	I (1-3)
Helianthemum nummularium	I (1-6)	I (4-7)	I (1-4)	I (1-7)
Botrychium lunaria	I (1-2)	I (1-3)	I (1)	I (1-3)
Fissidens adianthoides	I (1–3)	I (1-3)	I (1–3)	I (1-3)
Calliergon cuspidatum	I (1-3)	I (1-3)	I (1-3)	I (1-3)
Hypochoeris radicata	I (4)	I (1-3)	I (1-3)	I (1–4)
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Floristic table CG10 (cont.)

	a	b	c	10
Pteridium aquilinum	I (1-4)	I (1-3)	I (1-3)	I (1-4)
Euphrasia scottica	I (1-3)	I (1-3)	I (1–3)	I (1-3)
Carex nigra	I (1)	I (1–4)	I (1-3)	I (1-4)
Bryum pseudotriquetrum	I (1-3)	I (1–3)	I (1-3)	I (1-3)
Gentianella campestris	I (1-3)	I (1-3)	I (1-3)	I (1-3)
Oxalis acetosella	I (1-3)	I (1-3)		I (1-3)
Luzula sylvatica	I (1-3)	I (1-3)		I (1–3)
Molinia caerulea	I (1-4)	I (1–4)		I (1-4)
Rhizomnium punctatum	I (4)	I (1-3)		I (1-4)
Galium sterneri	I (1-3)	I (1–3)		I (1-3)
Erica cinerea	I (1-3)	I (1-5)		I (1-5)
Scapania undulata	I (1-3)	I (1–3)		I (1-3)
Koeleria macrantha	I (1–4)	I (1)		I (1-4)
Poa pratensis	I (1–4)	I (1-3)		I (1-4)
Cynosurus cristatus	I (1-3)	I (1-2)		I (1-3)
Carex binervis	I (1–4)	I (1)		I (1-4)
Lathyrus montanus	I (1–3)	I (1-3)		I (1-3)
Potentilla sterilis	I (1-4)	I (1)		I (1-4)
Aira praecox	I (1-3)	I (1-3)		I (1-3)
Alchemilla xanthochlora	I (1–3)	I (1-3)		I (1-3)
Empetrum nigrum nigrum	I (1–3)	I (1-3)		I (1-3)
Mnium hornum	I (1-3)	I (1-4)		I (1–4)
Ranunculus repens	I (1–3)	I (1-3)		I (1-3)
Bryum pallens	I (1-3)	I (1-3)		I (1–3)
Cardamine pratensis	I (1-3)	I (1)		I (1-3)
Euphrasia confusa	I (1-3)	I (1–3)		I (1-3)
Juncus squarrosus	I (1–7)	I (1–3)		I (1-7)
Senecio jacobaea	I (1-3)		I (1-3)	I (1-3)
Empetrum nigrum hermaphroditum		I (1-3)	I (1-3)	I (1-3)
Potentilla crantzii		I (1-3)	I (1–6)	I (1–6)
Cetraria islandica		I (1–3)	I (1–3)	I (1-3)
Solidago virgaurea		I (1-3)	I (1-3)	I (1-3)
Angelica sylvestris		I (1-3)	I (1-3)	I (1-3)
Rubus idaeus		I (1–3)	I (1)	I (1-3)
Number of samples	78	34	12	124
Number of species/sample	30 (14–47)	36 (12–48)	40 (23–64)	32 (12–64)

a Trifolium repens-Luzula campestris sub-community

b Carex pulicaris-Carex panicea sub-community

c Saxifraga aizoides-Ditrichum flexicaule sub-community

¹⁰ Festuca ovina-Agrostis capillaris-Thymus praecox grassland (total)

