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Festuca ovina-*Avenula pratensis* grassland

Synonymy

Natural pasture Moss 1907, 1913; *Festucetum ovinae* Moss 1911 *p.p.*; *Festucetum ovinae calcareum* Tansley & Rankin 1911 *p.p.*; Chalk grassland *auct. angl. p.p.*; Limestone grassland *auct. angl. p.p.*; *Xerobrometum britannicum* Braun-Blanquet & Moor 1938; *Festucetum* Balme 1954, Cornish 1954; *Festuco-Agrostidetum* Balme 1954 *p.p.*; *Thymo-Festucetum* Williams & Varley 1967 *p.p.*; *Festuca ovina-Helictotrichon pratense* community Lloyd 1968; *Cirsio-Brometum* Shimwell 1968a *p.p.*; *Helictotricho-Caricetum flacca* Shimwell 1968a; *Helianthemo-Koelerietum cristatae* Shimwell 1968a *p.p.*; *Caricetum montanae* Shimwell 1968a *p.p.*; Species-rich *Festuca ovina* grassland Lloyd 1972; Species-rich Carboniferous Limestone grassland Lloyd 1972; *Agrosti-Campanuletum rotundifoliae* van der Meulen & Wiegiers 1972 *p.p.*; *Festuca ovina/rubra* grassland Wells 1975; *Carex humilis* grassland Wells 1975, Smith 1980; *Festuca ovina/Poterium sanguisorba/Lotus corniculatus* grassland Wells *et al.* 1976; *Cirsio-Brometum* Shimwell *emend.* Willems 1978; Fine-leaved fescue grassland Smith 1980; Mixed Gramineae grassland Smith 1980.

Constant species

Avenula pratensis, *Briza media*, *Carex flacca*, *Festuca ovina*, *Hieracium pilosella*, *Koeleria macrantha*, *Leontodon hispidus*, *Linum catharticum*, *Lotus corniculatus*, *Plantago lanceolata*, *Sanguisorba minor*, *Scabiosa columbaria*, *Thymus praecox*.

Rare species

Aceras anthropophorum, *Ajuga chamaepitys*, *Astragalus danicus*, *Bunium bulbocastanum*, *Carex ericetorum*, *C. humilis*, *C. montana*, *Cerastium pumilum*, *Cirsium tuberosum*, *Euphrasia pseudokernerii*, *Galium pumilum*, *G. sternerii*, *Gentianella anglica*, *G. germanica*, *Herminium monorchis*, *Hypochoeris maculata*, *Iberis amara*, *Linum perenne* ssp. *anglicum*, *Ophrys fuciflora*, *O. sphegodes*, *Orchis simia*, *O. ustulata*, *Orobanche picridis*, *Phyteuma*

tenerum, *Polygala amara*, *P. calcarea*, *Pulsatilla vulgaris*, *Salvia pratensis*, *Senecio integrifolius* ssp. *integrifolius*, *Seseli libanotis*, *Silene nutans*, *Spiranthes spiralis*, *Teucrium botrys*, *Thesium humifusum*, *Thymus pulegioides*, *Veronica spicata*.

Physiognomy

The *Festuca ovina*-*Avenula pratensis* grassland typically comprises rich and intimate mixtures of grasses and herbaceous dicotyledons in a continuous, closed sward. Though many of its species, even some of the numerous low-frequency associates, can be locally prominent, there is generally no consistent pattern of dominance in the vegetation, even at the sub-community level. This is especially so under the close sheep- or rabbit-grazing characteristic of many stands of the community. Under such conditions, the vegetation occurs as even expanses of very short, tight and springy turf, its individual plants often extremely diminutive and its richness and variety on a strikingly small scale. Such features, together with the attractive appearance of many of the plants when in bloom and the occurrence of a large number of national rarities, give the community an aesthetic appeal which has been long extolled (e.g. Defoe 1724, White 1788, Cobbett 1830, Hudson 1900, 1910).

Predominant among the grasses are fine-leaved species which form a compact ground. *Festuca ovina* is the most frequent of these and usually the most abundant; *F. rubra* is much less common throughout (cf. Tansley 1939), though when it does occur (and it is especially characteristic of certain kinds of *Festuca-Avenula* grassland), it may rival or exceed *F. ovina* in cover. Also constant, though usually less abundant than *F. ovina*, are *Avenula pratensis* (except in south Wales), *Koeleria macrantha* and *Briza media*. A number of other grasses, some of them coarser in physiognomy, occur frequently or occasionally, though they are mostly preferential for particular sub-communities, e.g. *Dactylis glomerata*, *Avenula pubescens*, *Holcus lanatus*, *Cynosurus cristatus*, *Trisetum flavescens* and also *Agrostis stolonifera* which,

in these data, is much less widespread throughout the community than some earlier surveys might suggest (e.g. Tansley & Adamson 1925, 1926, Duffey *et al.* 1974). As the *Festuca-Avenula* grassland has been defined in this scheme, both *Bromus erectus* and (especially) *Brachypodium pinnatum* are typically infrequent and never abundant, though even small scattered tussocks can be conspicuous where they are avoided (as they often are: see below) by grazing animals. The only sedges to occur with any frequency are *Carex flacca*, which is constant and often abundant, and *C. caryophylla*, which is somewhat more uneven in its occurrence within the different sub-communities, but generally less prominent than *C. flacca*.

Among the dicotyledons, hemicryptophytes predominate, their often tiny rosettes or sprawls of shoots scattered among the ground of grasses. *Sanguisorba minor*, *Plantago lanceolata*, *Lotus corniculatus*, *Leontodon hispidus*, *Scabiosa columbaria*, *Prunella vulgaris*, *Campanula rotundifolia* and *Galium verum* are uniformly frequent throughout. Less common overall and, in some cases, preferential for different sub-communities are *Ranunculus bulbosus* (easily missed in its aestival state when just a small hole betrays the site of the stem-tuber), *Pimpinella saxifraga*, *Filipendula vulgaris*, *Trifolium pratense*, *Plantago media*, *Centaurea nigra*, *Primula veris*, *Polygala vulgaris* and *Viola hirta* (including the rare and later-flowering forms sometimes distinguished as ssp. *calcareo*: e.g. Clapham *et al.* 1962, cf. Tutin *et al.* 1968).

Chamaephytes are typically few, but both *Thymus praecox* and *Helianthemum nummularium* are frequent in the community and each can be locally abundant, their fine woody shoots forming sometimes quite extensive prostrate mats or low tangled cushions among the shoots of their neighbours. Under light grazing on the south-eastern Chalk (and mostly therefore in the *Cirsium-Asperula* and *Holcus-Trifolium* sub-communities), *T. praecox* frequently develops a distinctive bushy habit (the 'Chalk Down race' of Pigott 1955) which suggests some genotypic affinity with Continental populations. *T. pulegioides* also occurs at low frequency in some sub-communities but this species has probably been under-recorded in the data. It is widely distributed and locally plentiful throughout much of the range of the community, though somewhat different from *T. praecox* in its ecological preferences (Pigott 1955; see below).

Within the turf, therophytes occur on patches of bare soil which are, in normal circumstances, small and scattered. Most frequent through the community as a whole are the smaller species *Linum catharticum*, *Gentianella amarella* and *Euphrasia officinalis* agg. (almost always *E. nemorosa*, or, more rarely (see below), *E. pseudokernerii*, where species have been distinguished). *Medicago lupulina* is also common in some sub-communities but, in general, larger paucienials like *Carlina*

vulgaris and *Picris hieracioides* are infrequent. As a group, therophytes are not as consistently important in this community as in the *Festuca-Carlina* grassland, though, where they are able to take advantage of more disturbed conditions, they may show the marked fluctuations in numbers of individuals noted by Grubb *et al.* (1982).

Bryophytes occur with varying frequency and abundance in the different sub-communities. The commonest and most characteristic species are the pleurocarpous mosses *Pseudoscleropodium purum* and *Homalothecium lutescens* which sometimes form very extensive carpets among the herbage. *Calliergon cuspidatum* and *Campyllum chrysophyllum* and, on patches of bare soil, *Weissia* cf. *microstoma*, *Fissidens cristatus* and *Ctenidium molluscum* are much less frequent overall. Lichens are typically very rare.

Over much of its range, the *Festuca-Avenula* grassland is characterised by a further group of species, most of which have some sort of Continental distribution over Europe as a whole and reach their north-western limit in this country roughly along a line from the Humber to the Severn. The bulk of these species, many of which are national rarities here, have their major locus in this community and, to a lesser extent, in the invaded derivatives dominated by rank grasses such as *Bromus erectus*, *Brachypodium pinnatum* and *Avenula pubescens*. The general absence of these species on lowland limestones to the north of the Humber-Severn line is largely what defines those kinds of *Festuca-Avenula* swards which have generally been considered as a quite separate vegetation type but which are here included as the *Dicranum scoparium* sub-community without, it is suggested, disrupting the overall integrity of the community. To the south and east, this group of species is characteristic of the bulk of *Festuca-Avenula* grasslands, except in the coarser swards of the *Holcus-Trifolium* sub-community, where their reduced representation is of different origin from their absence from the north and west.

Foremost among the species is *Cirsium acaule* which is very frequent and often abundant as scattered rosettes or clonal colonies which, expanding vegetatively by branching rhizomes, may form patches up to 2 m in diameter, perhaps 60–80 years old and with as many as 50 rosettes m⁻² (Pigott 1968). *Asperula cynanchica* is likewise very frequent, though its distribution and phytosociological affinities are a little more diverse: unlike *C. acaule*, it extends on to northern limestones around Morecambe Bay where it occurs in the *Sesleria-Galium* grassland (and also to Eire in rather similar vegetation). Less common, though sometimes abundant and very conspicuous when flowering, is *Hippocrepis comosa* whose mainland British distribution and phytosociology are similar to those of *A. cynanchica*. Like

Thymus praecox, it is a chamaephyte which, with reduced grazing, occurs in a bushier form; here, however, this morphological difference appears to have some basis in different levels of ploidy (Fearn 1973). Finally, among these more widespread species, though much less frequent than any of the above, is *Onobrychis viciifolia*, a plant which is probably native here (Clapham *et al.* 1962, Perring & Walters 1962) but which was very widely cultivated (and hence dispersed) in the nineteenth century as a mainstay autumn fodder crop for downland sheep, especially along the Cotswolds and over the East Anglian and western Chalk (Salisbury 1964, Smith 1980).

Among the nationally rare species within this group, those most widespread, frequent and characteristic of the community are *Polygala calcarea*, *Senecio integrifolius* ssp. *integrifolius*, *Thesium humifusum*, the distinctive robust eyebright *Euphrasia pseudokernerii*, and the diminutive orchids *Orchis ustulata* and *Herminium monorchis*. Each of these has its own peculiarities of distribution. Some, for example, are absent from the Isle of Wight, others are poorly represented along the North Downs (e.g. Rose 1957, 1973) or in East Anglia (e.g. Salisbury 1932) and the Oceanic West European *Thesium humifusum* is distinctly more plentiful on the western Chalk of Wiltshire and Hampshire (e.g. Wells 1975). In general, however, the range of these species is included within that of the *Festuca-Avenula* grassland and their major phytosociological locus is within this community. Two further rarities which are also widespread across part of the range of the community and occasionally encountered within it but which occur also in other vegetation types are *Spiranthes spiralis* (found, too, in some dune and heath communities) and the much more robust orchid *Himantoglossum hircinum*, a species which has displayed a remarkable extension of its British range since early in this century (Good 1936) and which is more characteristic of transitions to scrub. Like the more common *Ophrys apifera*, which shows a similar partial geographical and phytosociological overlap with the *Festuca-Avenula* grassland, these orchids and those others found in this community may show some fluctuation in their numbers from year to year but, as Wells (1967a, 1981) has shown, this uncertainty of appearance is by no means as simple or uniform throughout the group as some accounts suggest. Finally, among these more widely distributed species, but more local, are *Galium pumilum* and the pauciennials *Gentianella anglica* and *Cerastium pumilum*, the last two especially characteristic of more open and sometimes disturbed swards.

Of more restricted distribution, though in some cases quite widespread and plentiful within their regions, are *Phyteuma tenerum* (especially on the South Downs), *Aceras anthropophorum* (concentrated on the North

Downs), *Pulsatilla vulgaris* (the Cotswolds, Northamptonshire, the eastern Chilterns and Cambridgeshire: Wells & Barling 1971) and *Carex humilis* and *Cirsium tuberosum* (the western Chalk: Wells 1975, Wells *et al.* 1976). Much more local and, in some cases, extremely rare though still characteristic of the *Festuca-Avenula* grassland, are the three orchids *Ophrys sphegodes*, *O. fuciflora* and *Orchis simia*. Another great rarity, *Orchis militaris*, is also sometimes found on the margins of open swards of this kind though it is more usually associated with ranker grasslands and scrub.

Three rare species with markedly disjunct distributions are sometimes encountered in *Festuca-Avenula* grassland. *Hypochoeris maculata* (Pigott & Walters 1954, Wells 1976) has a much narrower phytosociological range in Britain than on the Continent: although it occurs at one locality in vegetation approaching maritime heath, it is more usually found in calcicolous grasslands, not only in the open rocky turf of the *Festuca-Carlina* and *Sesleria-Galium* communities but also in closely-grazed *Festuca-Avenula* swards and in ungrazed stands of the last which now have considerable amounts of *Bromus erectus*, the expansion of which it seems to be able to tolerate for many years. Much more usually confined in this country to the open vegetation of the *Festuca-Carlina* and *Festuca-Hieracium-Thymus* grasslands is *Veronica spicata* (including *V. hybrida*), but this species too occurs in those *Festuca-Avenula* swards which most closely approach their physiognomy and floristics. The third species of this group, *Carex montana*, has somewhat more diverse phytosociological affinities in this country but it can be found in *Festuca-Avenula* grassland, as a local dominant at some sites, in south Wales and the Mendips (the *Caricetum montanae typicum* of Shimwell 1968a, 1971b; see also David 1977).

Last, among these rarities which are generally restricted to the south-east, there are species which are more typical of disturbed places but which are occasionally recorded in more open *Festuca-Avenula* swards or intact grassland of this kind which has a history of interference. Most have their real home on disturbed calcareous soils such as are found in and around arable fields on the Chalk and in quarries: these are *Iberis amara*, *Bunium bulbocastanum*, *Gentianella germanica* (all especially characteristic of the Chiltern scarp: e.g. Dony 1953, 1967), *Ajuga chamaepitys* and *Teucrium botrys* (the last perhaps introduced as recently as the mid-nineteenth century with lucerne seed: Salisbury 1964). *Salvia pratensis*, possibly also a seed contaminant, in this case of grass mixtures (Lousley 1950), is another species sometimes found in these more open situations in the community. *Seseli libanotis*, like *B. bulbocastanum* a rather persistent perennial umbellifer, is a little different from the rest of the group. Although very occasionally found in *Festuca-Avenula* grassland, it

seems most typical of open bushy vegetation which, in the absence of grazing, is progressing to rank grassy scrub (e.g. Dony 1953, Perring *et al.* 1964).

The general picture, in moving northwards up the eastern limestones of Northamptonshire and Lincolnshire, into Derbyshire, Yorkshire and north Wales, is that these species become rarer and then mostly disappear. Spanning this divide, however, are four rarities which occur locally throughout the range of the *Festuca-Avenula* grassland (and its very heavily grazed or ungrazed derivatives) as well as, in some cases, extending on to more distantly related calcicolous swards further north. *Astragalus danicus* and *Carex ericetorum* are both species with a Continental Northern distribution through Europe and *Linum perenne* ssp. *anglicum* is an endemic which has a similar range in Britain. *A. danicus* is the most widespread and the most diverse in its phytosociological relationships: as well as occurring in more mainstream calcicolous swards towards the south of its range, along the eastern coast of Scotland it moves into maritime heath and dune vegetation. Both *C. ericetorum* and *L. perenne* ssp. *anglicum* are more restricted geographically and ecologically. The former has in recent decades been shown to be more widespread than previously thought, having perhaps been formerly mistaken for *C. caryophylla*, from which, when vegetative, it is scarcely distinguishable (e.g. David 1981). It occurs at scattered localities in this community, in the more open vegetation of the *Festuca-Hieracium-Thymus* grassland and in *Bromus erectus* and *Brachypodium pinnatum* derivatives. *L. perenne* ssp. *anglicum* (Ockenendon 1968) is most often found in mainstream *Festuca-Avenula* grassland, though, to the north on the Durham Magnesian Limestone, it also occurs in the *Sesleria-Scabiosa* community. Finally, among this group, there is *Silene nutans*, a species more common to the north of the range of the *Festuca-Avenula* grassland in Derbyshire and north Wales and one seeming to favour more rocky sites (where it also occurs in a distinctive kind of *Arrhenatheretum*) or slumping cliffs (where it can be encountered in various kinds of more calcicolous maritime vegetation).

These, then, are the rare species which, with various degrees of exclusivity, are characteristic of the *Festuca-Avenula* grassland. Some, as outlined above, are largely confined to it and, within it, are especially associated with particular sub-communities. Numbers of them are sometimes found, in various assortments, in individual stands of these sub-communities. Their occurrence adds greatly to the floristic interest and value of the sward and, in many cases (see below), is strongly suggestive of the antiquity of the grassland. As a rule, however, none of these species is of major importance in diagnosing different kinds of *Festuca-Avenula* grassland: in general, sub-communities and variants can be distinguished and

the floristic variation which they encompass understood without primary recourse to them.

Sub-communities

***Cirsium acaule-Asperula cynanchica* sub-community:** *Festucetum ovinae calcareum* Tansley & Rankin 1911; Chalk grassland *auct. angl. p.p.*; *Xerobrometum britannicum* Braun-Blanquet & Moor 1938; *Festucetum Cornish* 1954; *Cirsio-Brometum* Shimwell 1968a *p.p.* and *emend.* Willems 1978 *p.p.*; Fine-leaved *Festuca ovina* grassland Smith 1980. This is the kind of *Festuca-Avenula* grassland which most British authors have recognised as the core of 'Chalk grassland'. In its typical form, it comprises a short, even and tight carpet of closed turf, characteristically species-rich, frequently with up to 25 species, sometimes more than 40, per m², extremely diminutive plants of several being packed, in extreme cases, into a single square centimetre. All the community constants are well represented with, in addition, constant *Cirsium acaule*, frequent *Asperula cynanchica* and occasional *Hippocrepis comosa*. Although there is no consistent pattern of dominance, some species frequently show local prominence by virtue of vegetative expansion. *C. acaule*, for example, with its clonal colonies, is sometimes especially conspicuous and chamaephytes, such as *Thymus praecox*, *Helianthemum nummularium*, *Hippocrepis comosa* and *Hieracium pilosella*, or proto-hemicryptophytes, like *Asperula cynanchica*, *Lotus corniculatus* and *Galium verum*, have spreading shoots which can ramify even a very closely grazed ground of fine-leaved grasses and rosette species. These, and other less frequent associates, can also appear temporarily conspicuous with the sequential appearance of their often showy flowers during the spring and summer months, when whole stretches of sward can become tinged with yellow, white or purple as the season progresses (Wells 1971, Smith 1980). In essence, however, the turf has a distinctive fine-grained structure in which variations in abundance seem to be attributable largely to strictly local vegetative success in the face of very intense competition maintained by heavy grazing. Where grazing is relaxed or where there are changes in the balance of different grazing animals, then some consistent alterations of physiognomy and floristics ensue and some stands may show features which are intermediate between this sub-community and other vegetation types (see Habitat below).

This sub-community and, to a lesser extent, that of *Succisa-Leucanthemum*, are the types of *Festuca-Avenula* grassland in which the group of largely Continental rarities is best represented and their differing geographical ranges result in a further element of variation in swards from one region to another in each of the three variants recognised. These variants comprise a

typical form, which preserves the floristics and physiognomy of the sub-community with no strong preferential features, and the following more distinct types.

***Filipendula vulgaris*-*Helianthemum nummularium* variant:** Chalk grassland Thomas *et al.* 1957 *p.p.*; *Helianthemum-Koelerietum cristatae helictotrichetosum*, *Sieglingia-Filipendula* variant Shimwell 1968a; Chalk grassland, *Poterium sanguisorba*-*Helianthemum chamaecistus* and *Poterium sanguisorba-Filipendula vulgaris* facies Ratcliffe 1977. Over the *Festuca-Avenula* grassland as a whole, *Filipendula vulgaris* ranks as no more than an occasional associate, but in this variant it attains constancy and both *Sanguisorba minor* and, especially, *Helianthemum nummularium* have unusually high frequencies. None of these species is consistently abundant but, in June, when their flowers begin to open, they give the sward a very distinctive appearance. *Koeleria macrantha*, too, is somewhat more common than normal and these features bring the floristics of this variant closest, among all the *Festuca-Avenula* grasslands, to the Xerobromion swards of the *Festuca-Carlina* community, though here the turf is always closed and lacks the prominent therophyte element of that grassland. Interestingly, *Veronica spicata* and *Helianthemum canum*, rarities more usually associated with open calcicolous vegetation in Britain, occur in north Wales in stands of *Festuca-Avenula* grassland which are best referred to this variant, though they lie very much to the margin of the ranges of the sub-community preferentials *Cirsium acaule*, *Asperula cynanchica* and *Hippocrepis comosa*.

A further distinctive feature of this variant is that, unusually in the *Festuca-Avenula* grassland, *Festuca ovina* is frequently, sometimes wholly, replaced by *F. rubra*. Under the heavy grazing typical of these swards, however, this species does not assume the gross tussocky form that is so characteristic of its growth in many vegetation types and careful examination may be needed to distinguish the two species in the short turf. *Danthonia decumbens* is locally prominent in some stands (e.g. Shimwell 1968a, 1971b, Wells 1975).

***Pseudoscleropodium purum*-*Prunella vulgaris* variant:** Chalk grassland Tansley & Adamson 1925 *p.p.*, 1926 *p.p.*, Hope-Simpson 1941 *p.p.*, Watson 1960 *p.p.*; *Festucetum* Cornish 1954 *p.p.* Both *H. nummularium* and *F. vulgaris* are markedly infrequent here but *Prunella vulgaris* becomes constant and *Bellis perennis*, *Senecio jacobaea* and *Ranunculus bulbosus*, though less common, are preferential for this variant. (The last species may have been recorded more frequently here than in other variants partly because plants retain their leaves longer into the summer in the distinctive environmental conditions: see Habitat below.) Usually, however, the most obvious feature of this vegetation is the high frequency, and often the abundance, of bryophytes, especially pleurocarpous mosses which can form

extensive carpets among the herbage. *Pseudoscleropodium purum*, though frequent throughout the *Festuca-Avenula* grassland, rises to constancy here and *Homalothecium lutescens* becomes frequent. Less common are *Ctenidium molluscum*, *Rhytidiadelphus triquetrus*, *Hylocomium splendens*, *Neckera complanata* and, much more rarely, *N. crispa*. Less obviously preferential, though sometimes unusually abundant in this variant, are *Calliergon cuspidatum*, *Campyllum chrysophyllum*, *Hypnum cupressiforme*, *Rhytidiadelphus squarrosus*, *Eurhynchium striatum* and *E. swartzii*. On patches of bare soil, there can be tufts of *Fissidens* spp., most commonly *F. cristatus* but sometimes *F. taxifolius*, *Weissia* spp., especially *W. microstoma*, and, less commonly, *Rhodobryum roseum*. Hepatics are much less common or varied but *Frullania tamarisci*, *Scapania aspera* and *Porella laevigata* are sometimes present. The very rare occurrences of *Racomitrium lanuginosum* in southern lowland calcicolous grasslands mostly belong here though, at one of the most renowned, on War Down in Hampshire (Tansley & Adamson 1925, Hope-Simpson 1941b), enclosure, the early extermination of rabbits and afforestation have destroyed the open sward in which it flourished (Tallis 1958).

***Succisa pratensis*-*Leucanthemum vulgare* sub-community:** Typical Chalk grassland Grose 1957; *Cirsium tuberosum* stands Grose 1957 *p.p.*; *Cirsio-Brometum* Shimwell 1968a *p.p.* and *emend.* Willems 1978 *p.p.*; *Festuca ovina/rubra* grassland Wells 1975; *Carex humilis* grassland Wells 1975; Chalk grassland, *Serratula tinctoria-Betonica officinalis-Succisa pratensis*, *Scabiosa columbaria-Succisa pratensis*, *Phyteuma tenerum-Scabiosa columbaria-Succisa pratensis* and *Chrysanthemum leucanthemum* facies Ratcliffe 1977. This sub-community shares with the first a good representation of all the community constants and frequent records for *Cirsium acaule*, *Asperula cynanchica* and *Hippocrepis comosa* and, like that vegetation, it occurs typically as a short, closed sward. Here, however, a variety of species become markedly more frequent and this makes samples consistently more species-rich. Some of these species such as *Trifolium pratense*, *Carex caryophyllaea*, *Prunella vulgaris*, *Dactylis glomerata*, *Plantago media*, *Medicago lupulina*, *Cynosurus cristatus* and *Agrostis stolonifera* are common, too, in the *Holcus-Trifolium* sub-community. Others occur preferentially here. Most notable among these are *Succisa pratensis*, *Leucanthemum vulgare*, *Campanula glomerata*, *Serratula tinctoria* and *Stachys betonica*; less firmly restricted to this sub-community are *Centaurea nigra* and *Avenula pubescens*. Most of these species can show a local abundance in particular stands and, in late summer, the blue or reddish-purple inflorescences which most of them possess give this vegetation a very distinctive look.

The most peculiar feature of this sub-community, however, is the occurrence in some stands of *Carex humilis*. This species occurs rarely in most kinds of *Festuca*-*Avenula* grassland, as well as being very characteristic of one kind of the *Festuca*-*Carlina* community. Here, however, it is unusually common and, though easily missed if present as scattered isolated tufts, it frequently forms small patches and may be the most abundant plant in whole stretches of sward. Then, it gives a definite dark yellow-green tinge to the herbage when seen from a distance. Its presence, however, does not seem to be accompanied by any other consistent differences in the composition of the turf.

Some other national rarities are also especially characteristic of this sub-community, having distributions which are concentrated in the relatively restricted area in which it occurs. The most frequent of these are *Thesium humifusum* and *Polygala calcarea*. Much rarer is *Cirsium tuberosum* which is found at some of its stations in vegetation of this kind, sometimes as pure populations, sometimes as hybrids with *Cirsium acaule*, with which it readily interbreeds, producing plants which are intermediate in many features, as well as introgressed crosses very close to the species in their appearance (Grose 1957, Pigott 1968). It is more tolerant of invasion of *Festuca*-*Avenula* grassland by rank grasses such as *Bromus erectus* and *Arrhenatherum elatius* than is *C. acaule* (Pigott 1968) and is sometimes also found in vegetation dominated by these species. *Hypochoeris maculata* occurs in vegetation very similar to this sub-community at one of its Cornish localities, over stabilised dune-sand at Porthtowan (Wells 1976).

***Holcus lanatus*-*Trifolium repens* sub-community:** Closed *Festucetum* Balme 1953; Hurley downland permanent pasture Norman 1956; Neutral grassland Gittins 1965a; *Helictotricho*-*Caricetum flacca*, Sub-association of *Holcus lanatus* and *Trifolium repens* Shimwell 1968a; *Agrostis*-*Campanuletum rotundifoliae* van der Meulen & Wiegers 1972 p.p.; *Cirsio*-*Brometum anthoxanthetosum* Willems 1978 p.p. Although all the community constants remain well represented here, *Cirsium acaule* and, even more markedly, *Asperula cynanchica* and *Hippocrepis comosa*, are much reduced in frequency. *Helianthemum nummularium* is also distinctly uncommon. Apart from *Koeleria macrantha*, fine-leaved grasses retain their frequency and cover throughout but they are often joined here by a variety of other grasses, many of which are more bulky or coarse-leaved. Most notable among these are *Holcus lanatus*, *Dactylis glomerata*, *Agrostis stolonifera*, *Cynosurus cristatus* and *Trisetum flavescens* with, less frequently, *Agrostis capillaris*, *Phleum pratense* ssp. *bertolonii*, *Arrhenatherum elatius* and *Brachypodium sylvaticum*. Though none of these is ever consistently abundant or clearly dominant,

each may be present in some quantity in the sward and together they give the turf a distinctly coarse quality and, in less heavily grazed stands, a marked tussocky look. Some dicotyledons, too, are preferential: *Trifolium repens* joins *T. pratense* as a constant and there are occasionally scattered plants of *Achillea millefolium*, *Medicago lupulina*, *Crepis capillaris* and *Senecio jacobaea*. For the most part, the Continental rarities typical of the two previous sub-communities are noticeably rare here, although *Pulsatilla vulgaris* survives, within the *Festuca*-*Avenula* grassland, more frequently in this sub-community than any other. Bryophytes, apart from the robust pleurocarp *Pseudoscleropodium purum*, are infrequent and rarely abundant.

***Dicranum scoparium* sub-community:** Natural pasture Moss 1907, 1913 p.p.; *Festucetum ovinae* Moss 1911 p.p.; Open *Festucetum* Balme 1953; Carboniferous Limestone grassland Hope-Simpson & Willis 1955 p.p., Gittins 1965a p.p.; *Thymo*-*Festucetum* A Williams & Varley 1967; *Festuca ovina*-*Helictotrichon pratense* community Lloyd 1968; *Helictotricho*-*Caricetum flacca* typicum Shimwell 1968a; Species-rich *Festuca ovina* grassland Lloyd 1972; Species-rich Carboniferous Limestone grassland Lloyd 1972. Two floristic features, one strongly negative, the other weakly positive, characterise this sub-community. First, as in the *Holcus*-*Trifolium* sub-community, Continental species, both those which are common and those which are rare through the south-east part of the range of the community, are virtually absent here. Second, along with the community constants, which mostly retain their very high frequencies, there is a group of weak preferentials. Some of these are species which become a much more consistent feature of calcicolous swards in the northern and western uplands: *Festuca rubra*, for example, sometimes rivals or exceeds *F. ovina* in this sub-community and *Agrostis capillaris* and *Anthoxanthum odoratum* become occasional components of the sward. *Galium sternerii* also occurs in this vegetation at the southern limit of its English distribution in Derbyshire. Among the bryophytes, which are frequent and sometimes abundant, *Dicranum scoparium* is especially distinctive and there are also somewhat increased frequencies for *Ctenidium molluscum* and *Fissidens cristatus*. These last two species sometimes find a niche in rock crevices within stands of this sub-community which, in contrast to much *Festuca*-*Avenula* grassland, is frequently disposed over the stabilised talus and around exposures of harder limestones. Thus, though the vegetation is usually close-grazed and presents the characteristic appearance of a short sward, it may be somewhat uneven and open. The partial replacement of *Leontodon hispidus* by *L. taraxacoides* here is perhaps also related to the quality of the substrate. Two other features

deserve mention. First, *Brachypodium sylvaticum* is sometimes locally abundant, lending a distinctive look to the vegetation with its usually ungrazed tussocks which often assume a rather lurid green colour in the full sun. Second, two Continental Northern rarities, *Astragalus danicus* and *Linum perenne* ssp. *anglicum*, occur in this sub-community at some of their northern English localities. *Silene nutans*, too, is also found in some stands which, around more rocky situations, are transitional to a distinctively rich kind of ungrazed *Arrhenatheretum*.

Habitat

The *Festuca-Avenula* grassland is most characteristic of free-draining, calcareous lithomorphous soils developed from native limestone parent materials in a relatively warm and dry, lowland temperate climate. It occurs on a variety of these calcareous bedrocks, mostly over steeper natural slopes but also in some artificial habitats, such as on ancient earthworks, abandoned quarry workings and road verges. The community is always dependent for its maintenance on a certain balance of grazing, traditionally by sheep and rabbits, and is now much reduced in extent because of changes in pastoral practice and the conversion of land to arable.

The most important natural variables controlling the national distribution of the community and influencing floristic variation within it are climate, especially precipitation and temperature, and geology. These exert their effect both indirectly through the soils and directly on the growth and reproductive ability of the plants themselves. The *Festuca-Avenula* grassland as a whole occurs on most of those drift-free exposures of limestone which experience a mean annual rainfall of less than 1000 mm (*Climatological Atlas* 1952, Chandler & Gregory 1976), with under 160 wet days yr^{-1} (Ratcliffe 1968), and have a mean annual summer maximum temperature in excess of 26 °C (Conolly & Dahl 1970). Under such conditions, soils derived entirely from the native calcareous bedrocks can be maintained in a permanently immature state because, though the limestones are always porous, precipitation/evaporation ratios are usually insufficient to leach even the superficial layers of the profile of calcium carbonate. The characteristic soils encountered beneath this vegetation are thus various kinds of free-draining rendzina (*sensu* Avery 1980) which have a usually azonal profile, with bedrock or talus (or, in artificial habitats, disturbed rock waste), near, sometimes very near, the surface (Tansley & Rankin 1911, Tansley & Adamson 1926, Anderson 1927, Tansley 1939, Balme 1953, Gittins 1965a). Such soils are typically rich in free calcium carbonate and of high pH (generally between 7 and 8), features reflected in the community by the preponderance of stricter calcicoles. The soils are also, generally speaking, oligotrophic, being deficient especially in the major nutrients nitrogen and phosphorus, a natural edaphic condition often

reinforced by a long history of traditional sheep-pasturing with its continual close cropping of the herbage and little manuring apart from the dropping of dung and urine by the grazing stock. The general importance in the vegetation of herbaceous dicotyledons as against grasses is partly related to this feature. Though not always as dry as is sometimes assumed, the soils also have a tendency to parching in dry summer weather (e.g. Anderson 1927, Locket 1946b, Salisbury 1952, Smith 1980) and some of the species show various morphological and physiological adaptations to this: xerophytic aerial organs, an ability to recover from wilting (e.g. Anderson 1927, Fenner 1975) or the possession of very long roots which can tap sources of moisture deep in the profile or in bedrock crevices (as in *Thymus praecox* (Pigott 1955), *Helianthemum nummularium* (Proctor 1956), *Cirsium acaule* (Pigott 1968) and *Hippocrepis comosa* (Fearn 1973); see also Anderson 1927). The persistent verdure of *Festuca-Avenula* swards in even very dry summers has long attracted attention (e.g. Cobbett 1830, Hudson 1900) but the intricacies of this quality are still little understood (Smith 1980).

In Britain, the limestones which occur within the region of temperate climate are largely the younger strata and, over much of its range, the community therefore occurs on the Chalk. Here, native rendzinas of the kind described have been mapped along the North and South Downs, through the western chalklands, up through the Chilterns to the Lincolnshire and Yorkshire Wolds, largely as the Upton and (where there is a humose topsoil) the Icknield Series (see *Soil Survey* 1983; also, for example, Avery 1964, Hodgson 1967, R.A. Jarvis 1968, M.G. Jarvis 1973, Green & Fordham 1973, Cope 1976). Essentially similar rendzinas also carry *Festuca-Avenula* grassland on the Corallian Limestone of the North York Moors, the Magnesian Limestone of Durham and the Carboniferous Limestone of the Mendips, north and south Wales and the Derbyshire Dales. The community is markedly uncommon on the soft Lower Oolite of the Cotswolds and Northamptonshire, but *Bromus erectus* and *Brachypodium pinnatum* grasslands with a strong calcicolous element are frequent there and regional peculiarities of treatment history may play some part in this replacement. In artificial habitats, the community occurs over rendziniform man-made soils and, very rarely, it is encountered on coastal sand pararendzinas.

Over the various limestone bedrocks, the more calcareous of these rendzina soils develop only where there is an absence of contamination with heavier superficial deposits and the associated *Festuca-Avenula* grassland is therefore typically confined to those drift-free plateaus which have not been put under arable cultivation or improved grassland and to steeper natural slopes. On the latter, the immaturity of the soils may be accentuated by slow downslope movement of material within the

profile and, on cooler, north-facing slopes, by some slight solifluctional churning. Such disturbance may be further enhanced by the trampling of stock and the activities of rabbits. Terracing of the surface, with the development of small-scale mosaics within the turf, is common in *Festuca*-*Avenula* swards (e.g. Cornish 1954). Although bedrock exposures and screes are uncommon on the Chalk (but see Smith 1980), they occur widely on the older and harder limestones and fragmentation of the soil cover around these may introduce some heterogeneity into the vegetation. In general, however, this grassland is characterised by a closed sward and it gives way to other communities where the stability of the soil cover is markedly disrupted.

In a typical valley-side topography, stands of the community are usually limited above by often more poorly draining and less calcareous superficial deposits (such as till within the limit of the Final Glaciation and, beyond this zone, periglacial material like Clay-with-Flints) and below by accumulations of colluvium. The soils developed from such materials tend, through brown rendzinas, towards calcareous or typical brown earths, generally deeper, moister and more mesotrophic and with some horizon differentiation which can involve the eluviation of any calcium carbonate from the upper layers with a slight fall in pH. Where such soils remain moderately calcareous, the *Festuca*-*Avenula* grassland may extend on to them in the form of the *Holcus-Trifolium* sub-community. Stands of this vegetation type often mark the upper, gently-sloping brows of limestone slopes where there is some plateau downwash, perhaps augmented by ploughing above. This kind of pattern has been well described from some Derbyshire Dales (e.g. Balme 1953, Pigott 1962, Grime 1963a, b, Bryan 1967) and from the Mendips (Shimwell 1968a, 1971b) and it can also be discerned in data from the Pewsey Vale scarp (Thomas *et al.* 1957: see also Figure 21). Deeper, mesotrophic but still moderately base-rich soils over flat limestone surfaces can also carry this sub-community (e.g. Gittins 1965a).

Within these general limits, climatic variation plays a very considerable part in influencing the floristic differences between the various sub-communities and its effects are visible at a variety of levels: over whole regions, between one local area and another and even within individual stands of the vegetation. Geology is important here because of the coincidental way in which the different limestones are disposed over the country and because the physiography of the exposures modifies the impact of climate, most notably through aspect and slope.

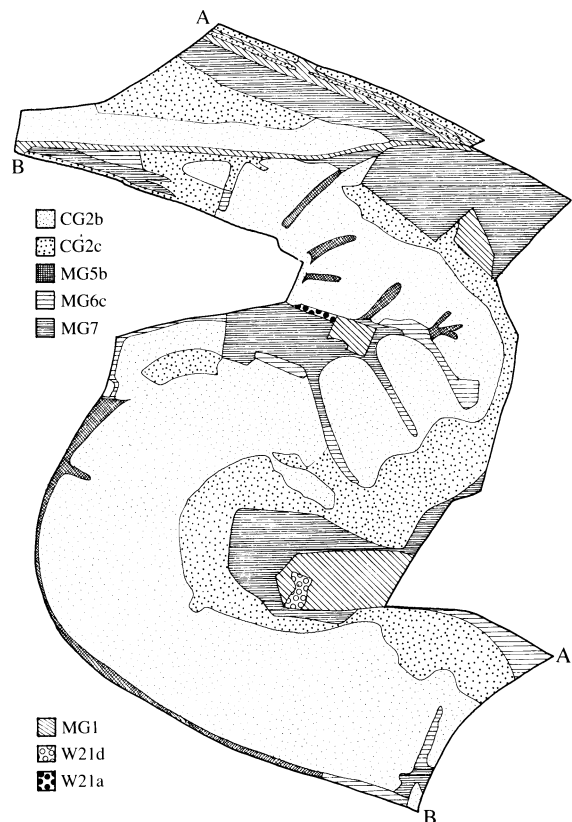
The most obvious regional climatic trend reflected in the community is that from the lowland south and east (where the major limestone is the Chalk) to the upland fringes of the north and west (where older limestones occur with the northern Chalk and the Corallian). The

former area is, generally speaking, drier, warmer and sunnier, especially in the growing season. Over much of this region, the annual rainfall is less than 800 mm with usually under 250 mm falling between May and August (Climatological Atlas 1952, Chandler & Gregory 1976). Average means of daily maximum August temperatures exceed 20 °C and, throughout the summer, there is much bright sunshine, generally more than 5½ hours daily in August (Pigott 1970b). Towards the more elevated northern and western limits of the community, beyond

Figure 21. Simplified vegetation map of Pewsey Down in Wiltshire (after NCC reports).

- CG2b *Festuca*-*Avenula* grassland, *Succisa-Leucanthemum* sub-community
- CG2c *Festuca*-*Avenula* grassland, *Holcus-Trifolium* sub-community
- MG1 *Arrhenatheretum elatioris*
- MG5b *Centaureo-Cynosuretum*, *Galium* sub-community
- MG6c *Lolio-Cynosuretum*, *Trisetum* sub-community
- MG7 *Lolium perenne* ley
- W21a *Crataegus-Hedera* scrub, *Hedera-Urtica* sub-community
- W21d *Crataegus-Hedera* scrub, *Viburnum* sub-community

A-A indicates scarp top, B-B scarp bottom.



the Humber–Severn line, the annual rainfall is generally higher, often approaching and sometimes exceeding 1000 mm, with up to 350 mm falling in the summer months which are also markedly cooler and cloudier (Pigott 1970b, Chandler & Gregory 1976). Among the different kinds of *Festuca-Avenula* grassland, the *Cirsium-Asperula* and *Succisa-Leucanthemum* sub-communities are almost entirely confined to the former region, the *Dicranum* sub-community to the latter. Two components can be discerned in this floristic response.

The most obvious is the restriction of the Continental element largely to the former sub-communities. This is unlikely to be a simple matter but, for some species at least, it is known to be related to the need for a drier, warmer and sunnier climate to maintain their reproductive capacity. In *Cirsium acaule*, for example, both fruit production and the occurrence of established seedlings decline towards the north-western limit of distribution (Pigott 1968, 1970b). The former is dependent on long daylight hours for the initiation of capitula and on high temperatures for their continuing development and embryo growth after pollination. The stigmas are receptive for but a short period, which must coincide with fine clear weather to maximise the possibility of visits by flying insects, in this case mostly bees. Furthermore, wet weather may allow the capitula to become infected with the fungus *Botrytis cinerea*, which can severely limit fruit production or cause entire heads to rot. Such mature fruits as do survive and disperse do not germinate or grow well in moister conditions, perhaps because of damping-off. Thus, where a late spring gives way to generally cooler, damper and cloudier summers, with a greater unpredictability in the weather, as to the north and west, this species is less able to consolidate its position and more vulnerable to environmental change. Similar climatic influences, perhaps equally complex, have been suggested as playing a role in limiting the distribution of *Thymus pulegioides* (Pigott 1955), *Pulsatilla vulgaris* (Wells & Barling 1971), *Hippocrepis comosa* (Fearn 1973) and *Senecio integrifolius* ssp. *integrifolius* (Smith 1979). Close investigation of other members of the Continental element in this respect would clearly be worthwhile.

The other component in the response works through soil differences. To the north and west, there is a greater tendency for even drift-free soils on gentle slopes to become leached of calcium carbonate in their superficial layers. This is reflected in the *Dicranum* sub-community by its more narrow restriction to steeper slopes than are occupied by the other sub-communities further south and by the occasional presence in the swards of some species indicative of slight surface leaching, species which are, in general, rare in southern *Festuca-Avenula* grasslands except where there is contamination with less lime-rich superficials.

This major floristic distinction among the sub-communities can be seen, writ small, where local topographic variation accentuates or ameliorates the effects of the large-scale climatic trend. This phenomenon was noted in some early studies (e.g. Tansley & Adamson 1925, 1926, Hope-Simpson 1940a, 1941b) but first given neat expression in Perring's (1958, 1959, 1960) attempts to produce a theoretical model to account for floristic variation in *Festuca-Avenula* grasslands over Chalk in relation to climate and topography.

The most obvious effects are felt through the influence of aspect though, as always with this variable, the frequent absence of a complete range of exposures within local areas may make it difficult to perceive its impact. Over the range of the community as a whole, however, two effects are quite clear. First, towards the north and west, the Continental species become increasingly confined to those south and south-west facing slopes where the topoclimate continues to approximate to the regional climate further south. There is thus a narrow zone of overlap between the *Dicranum* and *Cirsium-Asperula* sub-communities (mostly between the 20° and 20.5° August isotherms with an outlier in north Wales) where both vegetation types can be seen on opposed aspects. This is particularly striking in those few Derbyshire Dales which happen to run in an east–west direction and have identical pastoral regimes on both their northern and southern slopes (Pigott 1970b). Conversely, in the south-east of the country, it is on cooler and damper, north-facing slopes that the *Cirsium-Asperula* sub-community most closely approaches the *Dicranum* sub-community in its floristics, with a sometimes marked quantitative reduction in, though rarely a total loss of, various of the Continental species.

The other effect is seen on what are probably the very warmest and sunniest slopes occupied by the *Cirsium-Asperula* sub-community. On some south-west facing slopes through the range of this kind of *Festuca-Avenula* grassland, a good representation of Continental species is further augmented by unusually high frequencies of *Helianthemum nummularium*, *Filipendula vulgaris* and *Sanguisorba minor* in the *Filipendula-Helianthemum* variant, a floristic transition to the Xerobromion swards of the *Festuca-Carlina* grassland.

However, attempting to unravel the effects of climate in the southern part of the range of the community is very difficult because here there is a further climatic trend of major importance. This exerts its influence again partly through temperature but most obviously through precipitation, both its absolute values and its seasonality. Towards East Anglia, the annual rainfall may be as little as 600 mm but there is a slight tendency for a summer maximum which accentuates the continental quality of the climate with its warm summers and

cold winters (Chandler & Gregory 1976). Towards the south-west, on the other hand, annual rainfall is mostly in excess of 800 mm and locally (as in the western South Downs (Adamson 1921, Hope-Simpson 1941*b*) and on the western Chalk in Wiltshire and Dorset (Rodda *et al.* 1976, Smith 1980)) as high as 1000 mm. There is, moreover, a strong tendency for a winter maximum which, with the milder temperatures in that season, gives the local climate a distinctly oceanic character.

Many of the typical species of the southern *Festuca-Avenula* swards retain their frequency across this region, though some (e.g. *Polygala calcarea* and the Oceanic West European *Thesium humifusum*) are more abundant to the west. Among other associates, though, some clearer responses can be seen. First, within the *Cirsium-Asperula* sub-community, the *Pseudoscleropodium-Prunella* variant, with its distinctive abundance and variety of bryophytes, tends to be better represented in the wetter, western areas, the Typical variant being somewhat more widespread. As before, local topographic variation can enhance or reduce this effect. The former variant, for example, is especially prominent on north-facing slopes within the wetter areas, most notably in the western South Downs. The fact that most of those few accounts of 'Chalk grassland' bryophytes that we have (e.g. Tansley & Adamson 1925, 1926, Hope-Simpson 1940*a*, Watson 1960) have drawn many of their data from this area is of some importance. It should be remembered, too, that the bryophyte component in these swards is strongly influenced by grazing; and that particular kinds of pastoral treatment have sometimes been concentrated in areas with a distinctive regional climate or where certain aspects predominate, thus compounding these effects (see below). Outside the wetter areas, the Typical variant tends to occur even on the cooler, damper northern slopes, as on the Chiltern scarp, until, on the sand-smeared Chalk of Breckland, it gives way to the more obviously continental vegetation of the *Festuca-Hieracium-Thymus* grassland.

Second, the more oceanic climate of the western Chalk probably plays some part in influencing the distribution and floristics of the *Succisa-Leucanthemum* sub-community. This very distinctive kind of *Festuca-Avenula* grassland is almost entirely restricted to parts of Wiltshire and Dorset, where it is especially well developed (or, at least, now largely remains) over south- and west-facing slopes where higher amounts of rainfall, especially winter rainfall, coincide with a warm and sunny summer topoclimate. Substantial amounts of periglacial and post-glacial loess seem to have been deposited in this area (e.g. Catt *et al.* 1971, Perrin *et al.* 1974, Cope 1976) and incorporated into the soils which, generally, are humic rendzinas, often quite poor in calcium carbonate in their superficial layers. Moreover, both soils and vegetation appear to have remained

largely undisturbed for very considerable periods of time, being on the more intractable topographies or responding poorly to earlier forms of arable cultivation, the soils turning to dust when exposed (Cope 1976). There has also been a longer tradition of cattle-, rather than sheep-, grazing in some parts of this region (e.g. Smith 1980: see below). Rewarding work could be done on elucidating how much of this combination of variables is coincidental and which components of it influence the different elements of the peculiar mixture of calcicoles, more mesotrophic pasture species, plants like *Stachys betonica* and *Succisa pratensis*, often indicative of a pH hovering between high and low, and the rarities. Among the last, *Carex humilis* has already attracted particular attention (e.g. Coombe in Pigott & Walters 1954, Wells 1975). It does not occur in all stands, being more strictly confined to south-west facing slopes than the sub-community as a whole, a strong association with aspect that is also seen in the *Festuca-Carlina* grassland (Figure 20).

Under whatever climatic conditions the *Festuca-Avenula* grassland occurs, permanent stands of the community are always plagioclimax vegetation maintained by grazing. Repeated defoliation by stock and wild herbivores is responsible for the characteristic close, tight structure of the sward with its preponderance of perennials, especially hemicryptophytes, which can escape permanent damage by having buds very close to the ground, and chamaephytes, such as *Thymus praecox*, *Helianthemum nummularium* and *Hippocrepis comosa*, which benefit indirectly through the maintenance of high light in the short turf. The most important grazers have traditionally been sheep (with some cattle and, rarely, horses) and rabbits (less commonly, hares). Any pronounced relaxation of grazing by one or more of these components in the herbivore population results in alterations in the sward and, if maintained, can lead to successional change (detailed below). The balance between the different components also influences floristic variation in the community.

Wells (1969, 1971) has warned of the dangers of making facile assumptions about the past uniformity of pastoral practice over the Chalk and, in assessing the impact of grazing on the *Festuca-Avenula* grassland throughout its range, account should always be taken of the possibility of fine variation in factors like the breeds of animals used, stocking rates and grazing regimes, which might lie behind general regional patterns and apparently stable traditions prevailing in particular periods of agricultural history. Close observation on the effects of grazing on individual species which are especially characteristic of the community also indicates the complexity of responses among its components (e.g. Pigott 1955 on *Thymus praecox* and *T. pulegioides*, Proctor 1956 on *Helianthemum nummularium*, Wells

1967 on *Spiranthes spiralis*, Wells & Barling 1971 on *Pulsatilla vulgaris*, Fearn 1973 on *Hippocrepis comosa*, Smith 1979 on *Senecio integrifolius* ssp. *integrifolius*). Unfortunately, apart from the early enclosure studies (Tansley & Adamson 1925, Hope-Simpson 1941b), almost all experimental work on the influence of variations in grazing on lowland calcareous grasslands has been on swards which are not mainstream types of *Festuca-Avenula* grassland (e.g. the Hurley grassland, which seems to be a rough approximation to the *Holcus-Trifolium* sub-community developed over ploughed and re-sown land: Norman 1957, Norman & Green 1958, Kydd 1964) or which already have substantial amounts of *Bromus erectus* (e.g. Morris 1967, 1971b, Wells 1971) or *Arrhenatherum elatius* (e.g. Wells 1969). (The work of Farrow (1917) and Watt (1962 *et seq.*) on the Breckland grasslands of Norfolk is considered under the *Festuca-Hieracium-Thymus* community.) The following generalisations should, therefore, be treated with caution.

Until recent decades, the most characteristic grazing stock pastured on *Festuca-Avenula* grasslands have been sheep and, over the Chalk, the traditional style of folding management was an integral part of an extensive, artificial ecosystem which, with its vast expanses of rolling downland, combined the aesthetic delights of small-scale variegation (the 'fairy flora' of Hudson 1900) and airy exhalation (especially in Wiltshire: e.g. Aubrey 1685, Hudson 1910). With the demise of this kind of low-cost, labour-intensive agriculture, much of this landscape and the larger stands of the community have been lost but, where *Festuca-Avenula* grassland remains, it still often owes its distinctive physiognomy and its attractive floristic diversity to the very close, even grazing that sheep provide. This is especially true of the *Cirsium-Asperula* sub-community which comprises the bulk of the community in many parts of the southern Chalk but it is also true of the *Dicranum* sub-community, even though most of its stands lie in areas like Derbyshire and the Mendips, which have long had a more mixed regional grassland economy with different breeds of sheep and also dairy cattle and which have probably never known the kind of folding pastoralism characteristic of the Chalk.

In moderate numbers, rabbits produce a sward which seems to be physiognomically and floristically very similar to that developing under sheep (e.g. Tansley & Adamson 1925) and they probably often simply supplemented the effect of stock or, as when their increasing numbers compensated for the decline in sheep between the First and Second World Wars, replaced it. Even when relatively sparse, however, they can contribute to sward heterogeneity in *Festuca-Avenula* grassland by avoiding species such as *Helianthemum nummularium* (Tansley 1939) or *Galium verum* (Smith 1980). The more dramatic zonal and successional impacts of heavy

rabbit pressure and the results of their decline after myxomatosis are dealt with below.

Even over the southern Chalk, with its traditional devotion to sheep-rearing, many parishes long had their 'cow down' and in some areas, such as parts of Wiltshire (Hosier & Hosier 1951, Cope 1976, Smith 1980), cattle-grazing seems to have been practised on *Festuca-Avenula* grasslands earlier and more systematically than in others. Furthermore, over the past few decades, there has been an increasing tendency to return to grazing these grasslands, after the neglect between the wars, not with sheep alone, but, at least partly and often wholly, with dairy and beef cattle (e.g. Smith 1980). There is a clear association within the community between cattle-grazing and the *Holcus-Trifolium* sub-community which can develop, under this kind of pastoralism, from both the southern *Cirsium-Asperula* and the northern *Dicranum* types. In general, cattle graze less closely and more selectively than sheep and their larger and more persistent faeces lead more readily to the development of avoidance-mosaics. The effects of these differences can be seen in the *Holcus-Trifolium* sub-community in the increase in coarser grasses and dicotyledons and in the development of an often tussocky sward with a fall in abundance, and sometimes a loss, of the more shade-sensitive vascular plants, acrocarpous mosses and less robust pleurocarps. Although there is not always a reduction in species-richness where this sub-community develops under light cattle-grazing, there is a shift from the more fine-textured turf with its range of bright-flowered calcicoles towards a ranker sward with duller mesophytes, and prolonged and/or heavy cattle-grazing may help mediate a transition to other grassland types (see below). In heavily-grazed swards, there is also an increased danger of poaching where turf becomes broken by the heavier hoof pressure of cattle. However, the likelihood is that it is the manurial effects of the stock that are of especial importance in the development of these *Holcus-Trifolium* swards. The same group of mesophytic species increases also where the *Festuca-Avenula* grassland extends on to naturally more mesotrophic soils (see above) or when it, or grasslands approximating to it (e.g. Norman 1956, Smith *et al.* 1971), are enriched by the addition of major nutrients in artificial fertilisers.

Some of the *Holcus-Trifolium* species are also characteristic of the *Succisa-Leucanthemum* sub-community and it is possible that cattle-grazing has also played a part in its development, typical as it is of areas of the Wiltshire Chalk. Interestingly, Wells (1969) noted that grazing by Ayrshires in this region produced a much more even sward than is usual with cattle and this may assist in maintaining the higher diversity of this vegetation.

The general importance of grazing in the maintenance

of the *Festuca-Avenula* grassland raises the question of the origin of these swards and their antiquity. The early view (Tansley & Rankin 1911) that much of this grassland occurs on ground incapable of supporting woody vegetation is unlikely to be true. Indeed, it is a general characteristic of the habitat of this community that it is much more amenable to a complete succession than is the open, rocky environment of the *Festuca-Carlina* grassland, although particularly warm, dry and steep slopes might be able to support little more than open scrub (e.g. Pigott & Walters 1954, Proctor 1956, Rose 1957, 1973). For the most part, therefore, the *Festuca-Avenula* grassland has probably been derived by the clearance of woody vegetation. Here, too, it is now generally accepted that we must conceive of a more gradual and patchy development of open grassland than earlier accounts, with their visions of enormous and uniform prehistoric expanses of unwooded limestone country, implied (e.g. Evans 1972, Pigott 1981, Smith *et al.* 1981, Tinsley & Grigson 1981, Turner 1981). What we can say is that through the Mesolithic and Bronze Ages and into the Iron Age, there seem to have been widespread clearances for pastoral and arable agriculture on the southern Chalk and, to a lesser extent, on other limestones (e.g. the Durham Magnesian Limestone: Bartley *et al.* 1976) and, in some areas at least, no marked resurgence of a woodland cover (Godwin & Tallantire 1951, Evans 1972). It is conceivable that some stands of the *Festuca-Avenula* grassland represent a survival of these swards, although it is difficult, even where there is an abundance of documentary and other archaeological evidence, to prove a continuity from then to now. It is certainly impossible to make unequivocal assertions of great age about any of the *Festuca-Avenula* sub-communities and we know that combinations of the constants of the community can develop relatively rapidly, given the right climatic and treatment conditions, from bare limestones (e.g. Tansley & Adamson 1925, Hope-Simpson 1940b). Nonetheless, certain stands of this grassland, especially within the *Cirsium-Asperula* and *Succisa-Leucanthemum* sub-communities, have an especially good representation of those rarer species whose persistence is generally taken to imply a continuance of open conditions. The fact that such stands often occur on ancient monuments, such as hill-fort banks and tumuli, or on steep slopes not amenable to ploughing, and perhaps less susceptible to shrub and tree invasion, tends to confirm that these may be of unusual antiquity. It is also possible that the different patterns of regional distribution of some of these species within the *Festuca-Avenula* grassland may be related to the timing of the major prehistoric clearances (e.g. Pigott & Walters 1954, Rose 1957, 1973).

Zonation and succession

Most of the zonations within stands of the *Festuca-Avenula* grassland or between the community and other vegetation types are related to topographic and soil variation or represent stages in successions mediated by treatment.

Gradations between different sub-communities related to topographic modifications of climate are relatively uncommon. In some areas, the local physiography is such that even quite extensive stretches of the community are predominantly of one aspect, as along the scarps of the North and South Downs. Elsewhere, the effect of exposition is confused by variations in treatment or stands are so fragmented that they do not encompass the range of possible aspects within a single site. However, in some places, uniform treatment prevails over rounded hills, scarp tops, circular or hemispherical ancient monuments or along the slopes of sharply-twisting valleys, and here transitions may be seen. In wetter regions, as on a very few localities on the South Downs, the *Pseudoscleropodium-Prunella* variant of the *Cirsium-Asperula* sub-community gives way, on south-facing slopes, to the Typical variant; in drier areas, such as parts of the Chiltern scarp, the Typical variant occupies north-facing slopes, passing to the *Filipendula-Helianthemum* variant on southerly exposures. To the west, as on hills and hill forts on the Dorset Chalk, or in the steep and narrow valleys of south-west Wiltshire, the *Succisa-Leucanthemum* sub-community is very characteristic of south-west aspects, grading to the *Cirsium-Asperula* sub-community (often the *Pseudoscleropodium-Prunella* variant) on north-facing slopes. Further north, there are a very few sites in the regional overlap of the *Cirsium-Asperula* and *Dicranum* sub-communities where these two vegetation types pass one into the other with a change in aspect, e.g. parts of Dovedale in Derbyshire and on the Great Orme in Gwynedd. Very often, however, in all these cases, a number of discrete stands of the *Festuca-Avenula* grassland are needed to include this kind of variation.

Some edaphic differences are probably involved in these topoclimatic patterns (e.g. Perring 1958, 1959), but the effect of soil variation on zonations is much more clearly seen where sequences of profiles have developed over limestones partly overlain by different amounts and various kinds of superficial deposits. Strictly speaking, these soil sequences should not be described as catenas, because of the hybrid origin of some of the profiles (e.g. Balme 1953, Pigott 1962, Grime 1963b, Bryan 1967): the sharpness of the edaphic transitions and the related vegetation patterns depend very much on the disposition of the superficals which is, in turn, related to topography. In general, however, the sequences are marked by an increase in the extent of the

soil cover and its depth, and a decline in the influence of the underlying calcareous bedrock on the development and character of the soils. In such situations, the *Festuca-Avenula* grassland can occur in suites of vegetation types which may run from very open calcicolous chasomphyte communities on exposed bedrock right through to heath over brown earths.

As with aspect-related zonation, many such sequences have now been disturbed or disrupted by agricultural activity leaving modified remnants in disjunct array, but two kinds of intact sequences can still be seen. The first occurs where flatter limestone surfaces have an uneven cover of superfcials which thins in places to shallow native rendzinas or rock exposures. Such patterns are best seen on the characteristic benches which develop on Carboniferous Limestone where the *Festuca-Avenula* grassland often forms a narrow zone towards their outer edges, giving way to heath further back and to some kind of open calcicolous vegetation over the rocky bench edge (rarely with pavement outside the limits of the Final Glaciation where the community is mostly found). On the western coastal exposures of the Carboniferous Limestone in the Mendips and Wales, where these rocky cliff tops are often very hot and dry, some very distinctive zonation of this kind occur with various types of *Festuca-Carlina* grassland grading to *Festuca-Avenula* grassland (often through the *Filipendula-Helianthemum* variant of the *Cirsium-Asperula* sub-community), then to Nardo-Galion grasslands and heath (e.g. Proctor 1956, 1958, Shimwell 1968a, Rodwell 1974, South Gower Coast Report 1981). Sometimes, a more discontinuous cover of drift is reflected in complex mosaics of *Festuca-Avenula* grassland and heath (e.g. Gittins 1965a).

Such patterns are rarer on the Chalk where the dip-slope plateaus have been more systematically exploited for agriculture but fragments were described from Porton Down on the Hampshire/Wiltshire border by Wells *et al.* (1976) where rendzinas carrying some *Festuca-Avenula* grassland were replaced locally by brown earths over Tertiary cappings with Nardo-Galion grasslands. At Lullington Heath in Sussex, Grubb *et al.* (1969) found some transitions from heath to *Festuca-Avenula* grassland where practice blast-bombing had blown away a cover of loess from the Chalk surface leaving a man-made rendziniform soil. (The much more complete sequences described by Watt (1940 *et seq.*) from the Breckland Chalk are considered under the *Festuca-Hieracium-Thymus* grassland.)

The second and much more widespread situation occurs where soil sequences develop over the graded slopes of valley sides and the more rounded scarps of softer limestones. Here, slope rendzinas with *Festuca-Avenula* grassland pass, with varying degrees of abruptness at the brow-top, to drift-derived soils with Nardo-Galion grasslands and heath. The zonation described

from the Derbyshire Dales (Balme 1953, Pigott 1962, Grime 1963b, Shimwell 1968a, b) are of this kind and here, on the harder Carboniferous Limestone, the sequence may run on to scree and cliffs with a fragmentation of the *Festuca-Avenula* sward and its replacement by open fern-dominated or Thero-Airion vegetation on crevice protorendzinas. This element is usually lacking on the softer Chalk, although open communities do occur in those few places, as on river cliffs and in the gaps along the North and South Downs (e.g. Lousley 1950, Rose 1973), where bedrock is exposed. The basic sequence is, however, widespread in the south, although it is often truncated or fragmented by cultivation right to the scarp top and the conversion of the bulk of the dip slopes to arable (e.g. Hodgson 1967, Jarvis 1973, Cope 1976, Ratcliffe 1977, Jarvis *et al.* 1979).

The particular sub-communities and variants of the *Festuca-Avenula* grassland involved in these zonation vary (largely in relation to regional and local climate) but especial interest attaches to the fact that the *Holcus-Trifolium* sub-community often forms a transition zone between the more calcicolous kind of *Festuca-Avenula* swards on the shallow rendzinas and the Nardo-Galion grasslands on the deeper brown earths. The soils under this sub-community are often contaminated with superfcials as, for example, around deep drift deposits on plateaus or where, towards the upper parts of slopes, there is some downwash (Pigott 1962, Grime 1963b) but, in general, they approximate to the calcareous brown earth type ('mull rendzina' in the older terminology). They are deeper, moister and somewhat more mesotrophic than rendzinas and, at least towards their surface, less calcareous and of lower pH. Not only does this combination of features promote a lush and more mesophytic kind of *Festuca-Avenula* grassland but it also creates conditions which allow the invasion of certain calcifuges and the development of mixed vegetation which gives way to calcifugous swards and heath over the deeper drift (e.g. Pigott 1962, Grime 1963a, b, Grubb *et al.* 1969, Rodwell 1974). There is some evidence that certain of the calcifugous invaders can acidify the soils in their rhizospheres (Grubb *et al.* 1969, Pigott 1970a) and this may allow a progressive advance of the Nardo-Galion grassland into the *Festuca-Avenula* swards, though some species of the *Holcus-Trifolium* sub-community can persist to provide the calcicolous element in what has become known as 'Chalk heath' or 'limestone heath'. Grazing also affects such changes because, if it is relaxed, such competitive power as the surviving calcicoles retain may be lost as the sward grows rank. Many areas showing the more subtle zonation between the *Festuca-Avenula* grassland and heaths, especially those on the Chalk, have been lost since the demise of rabbits in the myxomatosis epidemic (e.g. Grubb *et al.* 1969, Ratcliffe 1977).

There is one further kind of zonation related to

interactions between soil and climate and that is the type of pattern which develops where *Festuca-Avenula* grasslands come under the influence of salt-spray on coastal limestone exposures. Maritime influence is relatively low within the community itself, partly because some limestones, like the Chalk along the Channel coast, typically form very high cliffs whose tops are out of reach of spray. Even where stands are close to the sea, the influence of high calcium levels can overwhelm the impact of small amounts of salt-deposition such that there are just very occasional records for species such as *Plantago maritima* and *Armeria maritima* in what is essentially a typical *Festuca-Avenula* sward. In some places, however, the community grades to more maritime vegetation with increasing salt-spray influence, as on low Chalk cliffs and on the Carboniferous Limestone of the Gower coast. The usual pattern is for the community to give way down the cliff to the *Sanguisorba* sub-community of the *Festuca-Daucus* grassland or, on ledges and slumped chunks of cliff, to the *Brassica* community. Both these vegetation types preserve a calcicolous element though, with the decreased accessibility to grazing stock on such sites, these transitions are often marked by a striking increase in taller herbs and tussocks of *Brachypodium pinnatum*.

Although some small measure of seral change in the *Festuca-Avenula* grassland may occur in response to pedogenesis (see above), it is variation in grazing pressure that, above all, controls successions to and from the community. Whenever grazing is increased or relaxed to any marked degree, or when there are substantial shifts in the proportions of the different grazing animals, physiognomic and floristic changes ensue. These are easy to describe in general terms, though there are relatively few detailed studies on the subject.

It is the effects of grazing relaxation that are nowadays the more obvious. With the general decline in sheep pastoralism since the First World War (Shrub 1973, Smith 1980) and the catastrophic reduction in the rabbit population in the 1954/5 myxomatosis epidemic (Lockley 1964, Sheail 1971), extensive areas of *Festuca-Avenula* grassland have become rank and overgrown by scrubby woodland (e.g. Ratcliffe 1977). The early enclosure experiment on a stand of the community at Downley Bottom A (Tansley 1922, Tansley & Adamson 1925, Hope-Simpson 1941b) and later observations (e.g. Hope-Simpson 1940b, Thomas 1960, 1963, Wells 1967a, 1969, 1973) give some indication of the processes involved.

The first general change is that the sward grows taller and more uneven. Although there is often a flush of profuse flowering among the dicotyledons in the season after grazing ceases, it is the grasses which, in the longer term, make the most pronounced vegetative response. They produce more and lusher foliage which can accumulate, after death, as a layer of resistant litter and

some develop a pronounced tussock habit. The increased competition for nutrients, water and, especially perhaps, for light, then begins to induce a second kind of general alteration in the sward, this time in its floristic composition.

Some of the characteristic dicotyledons of the *Festuca-Avenula* grassland are quickly overwhelmed, e.g. *Hieracium pilosella*, *Asperula cynanchica*, *Polygala* spp. and the therophytes and more delicate bryophytes of patches of bare ground. Others can maintain their position for some time in the ranker herbage by producing larger rosettes which depress or grow through the grasses (e.g. *Cirsium acaule*, *Sanguisorba minor*, *Plantago lanceolata*) or adopting a bushier habit and sprawling over them (e.g. *Thymus praecox*, *T. pulegioides*, *Hippocrepis comosa*, *Helianthemum nummularium*, *Lotus corniculatus*). Even here, however, there may be some reduction in flowering and seed production. Surviving plants may become very attenuated and eventually die and they cannot easily be replaced because there is little well-illuminated ground where seedlings can become established. As a result of these changes, the sward begins to assume the composition and structure of a different vegetation type.

Where there is no rapid invasion into the ungrazed sward of shrubs and trees, the nature of the derived vegetation depends partly on which grasses gain eventual ascendancy and partly on which particular kind of *Festuca-Avenula* grassland is involved. The two are not unrelated because certain grasses are especially characteristic of different sub-communities or variants or appear particularly suited to invade one type of sward rather than another. Floristic variation in the original sward also determines which range of dicotyledonous associates is available to respond to the abandonment of grazing and the expansion of the grasses. Of those grasses which are frequent throughout the community, *Avenula pratensis* and *Dactylis glomerata* often become prominent in these circumstances and, in the more mesophytic vegetation of the *Holcus-Trifolium* sub-community, *Holcus lanatus* can increase (e.g. Norman 1957, Kydd 1964). Even the more diminutive species such as *Festuca ovina*, *Briza media* and *Koeleria macrantha* can remain very frequent and locally abundant in ungrazed swards. For the most part, however, it is the coarser and much more aggressive tussock grasses that now begin to make their mark and become overwhelming dominants.

The most important of these, at least over the southern part of the range of the community, are *Bromus erectus* and *Brachypodium pinnatum*. Both are present in small amounts as low-frequency occasionals in the *Festuca-Avenula* grassland, though they are less common, especially the former, in the northern *Dicranum* sub-community. They can also invade recently ungrazed swards, provided there is a seed source nearby,

although they may not be able to gain new entry into grasslands which have already grown rank. Once established, they respond strikingly to relaxation of grazing, expanding to overwhelm the neighbouring turf and converting the vegetation to communities in which each or both are dominant. The development of *Bromus erectus* grassland is reversible with a resumption of hard grazing and, even where this species continues to increase, the death and decay of the centres of its expanding clones may allow the reappearance of something resembling a *Festuca-Avenula* sward (Austin 1968a). *Brachypodium pinnatum* is different. It is much less palatable and, once established, it can be extremely difficult to reduce, let alone eradicate. Even at the time of the earliest surveys (Tansley & Adamson 1925, Hope-Simpson 1940b, 1941b), grasslands dominated by these species were very widespread on the southern Chalk and they have continued to increase in extent since then.

It is possible that some of the floristic variation within them is inherited from the original swards which they invaded. Both *Bromus* and *Brachypodium* grasslands exhibit a contrast between more calcicolous and more mesophytic types which reflects the distinction between the *Cirsium-Asperula* and *Holcus-Trifolium* sub-communities of the *Festuca-Avenula* grassland.

There is a third coarse and aggressive tussock grass which may be especially able to take advantage of the more mesotrophic conditions of which the *Holcus-Trifolium* sub-community is characteristic. This is *Arrhenatherum elatius*, an occasional in these swards and a ready invader. Lack of grazing is a key factor in its expansion and it can quickly assume dominance to form an *Arrhenatheretum*, perhaps, in this case, of the kind included in the *Centaurea nigra* sub-community. It is, however, very palatable and resumption of grazing can reduce it to virtual insignificance in the sward (e.g. Thomas 1960, 1963, Wells 1969).

Two further species are of importance here. *Avenula pubescens* is frequent in some kinds of *Festuca-Avenula* grassland, again more conspicuously in the more mesophytic *Holcus-Trifolium* sub-community but also in the *Succisa-Leucanthemum* sub-community, the floristics and environmental relationships of which are more complex. It, too, can increase very markedly when grazing is relaxed and some stands of grassland in which it is dominant may have developed from ungrazed *Festuca-Avenula* swards. *Festuca rubra* is a more complex case. It is, in these data, much more uneven in its occurrence than *F. ovina*, though it is invariably *F. rubra* which is reported as becoming the more prominent of the two with lack of grazing. It is certainly very characteristic of some kinds of ungrazed calcicolous grassland, often in association with *A. pubescens*, though at some localities, like Swyncombe Down in Oxfordshire (Smith *et al.* 1971) and Porton Down on the Hampshire/

Wiltshire border (Wells *et al.* 1976), as an uncompromising dominant.

Finally, and much more local in its importance, there is *Brachypodium sylvaticum*. This is a generally uncommon grass in *Festuca-Avenula* swards, assuming but patchy prominence under grazing and especially associated with stands over harder limestones (like many in the *Dicranum* sub-community) where, incidentally, it is by no means always an indicator of former woodland. It can expand when grazing is relaxed and, being relatively unpalatable (e.g. Wells 1969), is less easily eradicated than, say, *A. elatius*, but it rarely forms a major component of closed, ungrazed swards over intact soils.

The relationships between each of these species and the ungrazed environment, including its edaphic and climatic characteristics, are complex and little understood. Moreover, these grasses can often expand or invade together, producing a further element of complexity in the derived communities.

Also, many of the stands in which they are now dominant, either alone or in various combinations, originate not from ungrazed *Festuca-Avenula* swards but from much more grossly disturbed situations, as, for example, where calcicolous grassland has been ploughed and abandoned. Some of the intricacies of these relationships are examined under the descriptions of the various communities in which these species are dominant.

Shrubs and trees can invade ungrazed *Festuca-Avenula* grassland rapidly if there are nearby seed sources, and the expansion and closure of a woody canopy may then proceed alongside or overtake changes in the herbaceous component of the vegetation (as in the Downley enclosure which was adjacent to a woodland). The most widespread early invaders seem to be *Crataegus monogyna*, *Prunus spinosa*, *Rubus fruticosus* agg., *Rosa* spp. and *Ligustrum vulgare* with, thinning northwards, *Rhamnus catharticus* and *Cornus sanguinea* and, around disturbed and enriched sites, *Sambucus nigra*. These can thicken up quite quickly to form stands of various kinds of *Crataegus-Hedera* scrub, the edges of which often become clothed in tangles of *Clematis vitalba*. A number of orchids, notably *Aceras anthropophorum*, *Himantoglossum hircinum* and the very rare *Orchis militaris*, are particularly associated with the ranker ungrazed *Festuca-Avenula* swards found around the margins of such scrub. Two much more local invaders which can form distinctive kinds of scrub are *Juniperus communis* ssp. *communis* and *Buxus sempervirens*. The further development of these communities to mixed deciduous, *Fagus* and *Taxus* woodlands is considered in the volume on Woodlands and Scrub.

The consequences of very heavy grazing of *Festuca-Avenula* grasslands are now much more rarely seen than in the days of rabbit infestation between the World Wars

and into the 1950s when their impact became especially obvious with the decline in numbers of sheep. Then, their vociferous nibbling and scraping, their dunging and urinating on the sward and their excavations in the softer strata and superficial deposits, produced striking and very widespread effects (see, for example, plates 2 and 3 in Tansley 1939 and figure 5 in Hope-Simpson 1940b). In some areas, their numbers have risen again as less virulent strains of myxomatosis have stabilised within the population. Their general effect on the *Festuca-Avenula* grassland seems to be to convert it to the kind of vegetation that is included in the *Festuca-Hieracium-Thymus* grassland, the community on which most of the classic studies of the effects of rabbits have been carried out (Farrow 1917, Watt 1940 *et seq.*). Here, there is a marked reduction in the numbers and cover of more palatable grasses, sedges and dicotyledons and a rise to prominence of certain bryophytes, notably *Hypnum cupressiforme*, *Homalothecium lutescens* and *Pseudoscleropodium purum*, in the more open sward. Also, with the greater disturbance, there is an increase in weedy species, not only those therophytes which are characteristic of open areas within the *Festuca-Avenula* grassland, but also grosser species such as *Senecio jacobaea*, *Erigeron acer* and *Fragaria vesca*. It was the local abundance of these, together with patches of, for example, *Urtica dioica*, *Arctium* spp., *Verbascum thapsus*, *Hyoscyamus niger*, *Atropa belladonna* and *Solanum dulcamara*, often attaining a grand stature on the rich burrow spoil, that gave the old rabbit warrens their distinctive, and often highly peculiar, appearance (e.g. Tansley & Adamson 1925, Thomas 1960, 1963).

Variations in grazing intensity in the *Festuca-Avenula* grassland have a very considerable impact, not only on the vegetation itself, but also on its often very characteristic invertebrate populations (e.g. Duffey 1962a, b, Duffey *et al.* 1974, Morris 1967, 1968, 1969, 1971a, b, 1973). The complex relationships between the numerous and varied species and the plants are an essential part of the *Festuca-Avenula* grassland environment and make themselves felt through inter-dependencies such as those involved in pollination. Many of these effects are subtle and hidden. One often very obvious impact of the invertebrate fauna on the vegetation, however, is that produced by the mound-building activities of ants, especially *Lasius flavus* (Thomas 1962, Grubb *et al.* 1969, Wells *et al.* 1976, King 1977a, b, c). The hills produced by this species are large and roughly hemispherical and they introduce an element of structural complexity into stands of the *Festuca-Avenula* grassland, especially on the southern Chalk, which long outlasts their occupation; indeed, the ant-hills may even outlast the grassland, persisting after the abandonment of grazing and beyond the development of a woodland cover.

The soil of the ant-hills is structurally finer and less dense than that of the surrounding intact profiles, though it does not seem to be significantly different in its chemical properties. It is also more free-draining and subject to greater fluctuations of temperature, the drying and heating being especially marked on the southern face. The mounds are also subject to various kinds of disturbance by rabbits, which use them as latrines, and various ant-eating or dust-bathing birds. Both sheep and rabbits may graze them preferentially, especially where the surrounding vegetation has grown rank.

These effects combine to produce a complex floristic mosaic within *Festuca-Avenula* swards which is subject to its own distinctive successional changes. In King's studies, the most characteristic species of the ant-hills were of two kinds: those within the immediately surrounding sward which were more readily able to grow through or on to the accumulating soil (notably the chamaephytes *Thymus praecox*, *Helianthemum nummularium*, *Cerastium fontanum* and, to a lesser extent, *Asperula cynanchica*) and therophytes, virtually absent from the intact grassland but able to find a very congenial germination ground on the mounds (*Arenaria serpyllifolia*, *Veronica arvensis*). With ageing, but continued occupation, the vegetation seemed to stabilise with large amounts of *T. praecox* and *H. nummularium* but, on abandonment, other species, especially *Hieracium pilosella*, became conspicuous to form vegetation which appears to resemble that of the *Festuca-Hieracium-Thymus* grassland.

Although hills produced by moles (*Talpa europaea*) are frequent in *Festuca-Avenula* grassland and may be confused with ant-hills (see King 1977a), they present a somewhat different disruption of the surface and show a less peculiar flora. Mole-holes are rapidly excavated in a single operation and are quickly eroded by rain and trampling by stock to ground-level. Their soil is not structurally sorted, being simply a disturbed pile of material, and it may contain seeds and vegetative fragments which can readily regenerate (King 1977a). Though there may be a temporary flush of therophytes on the mound, the vegetation seems quickly to return to that of the surrounding grassland.

The aesthetic appeal of *Festuca-Avenula* swards has long made them popular for recreation which can entail heavy trampling and sometimes the driving or parking of vehicles on the vegetation. Around picnic spots, there may also be particular kinds of cultural eutrophication. In recent years, a declining number of stands has come under increasing pressure from a growing and more mobile population and some sites, as on the North Downs (Streeter 1971, Dixon 1973) or along the north Wales coast (Rodwell 1974), have become especially vulnerable.

The distinctive springy turf of the community seems

resilient to a certain amount of trampling but, where this is concentrated, as along paths and around viewing-points, clear changes occur in the vegetation. In such places, there is often a local increase in resistant grasses, notably *Cynosurus cristatus*, but in some cases also *Dactylis glomerata*, *Agrostis stolonifera* and *Holcus lanatus*, and in some of the rosette species, such as *Plantago lanceolata*, *Bellis perennis* and *Taraxacum officinale* agg., at the expense of more sensitive plants like the chamaephytes. This gives such swards a somewhat similar composition to the *Holcus-Trifolium* sub-community and recreational trampling may play a part in the development of some stands of this kind of *Festuca-Avenula* grassland. Typically, however, the sward lacks the tussocky physiognomy of this vegetation, being extremely short. Also, the further appearance in the turf of *Lolium perenne*, especially where there is some eutrophication, often presages a rapid move towards Lolio-Plantaginion vegetation. Very similar changes to these were observed by Perring (1967) with an increase in horse-galloping pressure on stretches of Newmarket Heath, Suffolk, used for race-horse exercising. Most unusually among *Festuca-Avenula* species, the rarity *Pulsatilla vulgaris* is actually benefited by heavy trampling, which stimulates the formation of new rosettes from deep adventitious root-buds (Wells & Barling 1971). Even where this species is present, however, very heavy pressure may eventually disrupt the sward, allow soil erosion and expose the bedrock.

Distribution

The *Festuca-Avenula* grassland is widely distributed over southern lowland limestones. The *Cirsium-Asperula* sub-community characteristically occurs south of the Humber-Severn line where it is largely confined to the Chalk, though it has outliers on the Carboniferous Limestone of south and north Wales and Derbyshire. The *Succisa-Leucanthemum* sub-community is virtually restricted to parts of the Wiltshire and Dorset Chalk. The *Dicranum* sub-community is the northern counterpart of the *Cirsium-Asperula* type and it occurs over Carboniferous Limestone in north Wales, the Mendips and Derbyshire (with a very few samples further north on the Isle of Man, Craven and around Morecambe Bay), on the northern Chalk of the Yorkshire Wolds, the Corallian of the North York Moors and the Magnesian Limestone of Durham. The *Holcus-Trifolium* sub-community occurs in both the north and south, being especially frequent in Wiltshire, Derbyshire, the Yorkshire Wolds and the North York Moors.

Some idea of the remaining extent of the community over the Chalk was provided by Blackwood & Tubbs (1970), although, in that survey, 'Chalk grassland' also included swards dominated by rank grasses and some small areas of abandoned arable and more mixed vegetation over superficials.

Affinities

This community is the central kind of stable plagio-climax Mesobromion grassland in Britain. It takes in much of the vegetation included as 'Chalk grassland' in some descriptive accounts (e.g. Tansley & Adamson 1925, 1926, Tansley 1939, Ratcliffe 1977) as well as essentially similar swards from other limestones (notably those included in the *Helictotricho-Caricetum flacca* of Shimwell 1968a). It thus returns to the early concept of a *Festucetum* enunciated by Tansley & Rankin (1911) and recently resurrected by Smith (1980) and cuts across schemes which rely on bedrock type as the basis of classification. It also includes a variety of vegetation types erected around individual species, often rare ones. Similar *Halbtrockenrasen* have been widely described from limestones in north-west Europe (e.g. LeBrun *et al.* 1949, Bornkamm 1960, Westhoff & den Held 1969, Stott 1970, Oberdorfer 1978), though it should be noted that, in moving from the Continent to Britain, there is a shift in the fidelity of species regarded there as characteristic of the different kinds of Brometalia grasslands (e.g. Shimwell 1968a, 1971a, b).

The *Festuca-Avenula* grassland is very closely related to both the rank grasslands dominated by such species as *Bromus erectus*, *Brachypodium pinnatum* and *Avenula pubescens* and also the *Festuca-Hieracium-Thymus* grassland. These communities, too, are of the Mesobromion type and show floristic transitions to the *Festuca-Avenula* grassland which are mediated largely by grazing.

In Britain, these kinds of grasslands are intermediate between the sub-Mediterranean Xerobromion swards of the *Festuca-Carlina* grassland and the sub-montane and montane grasslands in which Mesobromion plants are eclipsed by calcicoles of cooler, damper climates and Nardo-Galion species. The *Festuca-Avenula* grassland grades to the former through the *Filipendula-Helianthemum* variant of the *Cirsium-Asperula* sub-community and to the latter through the *Dicranum* sub-community.

More diffuse relationships can also be seen within the community, through the *Holcus-Trifolium* sub-community, to the more mesophytic swards, both grazed and ungrazed, of the Arrhenatheretalia.

Floristic table CG2

	a	b	c	d	2
<i>Festuca ovina</i>	V (1–9)	V (2–9)	V (2–9)	V (3–8)	V (1–9)
<i>Carex flacca</i>	V (1–8)	V (2–8)	V (1–8)	V (1–9)	V (1–9)
<i>Sanguisorba minor</i>	V (1–8)	V (1–7)	IV (1–8)	IV (1–6)	V (1–8)
<i>Koeleria macrantha</i>	V (1–6)	IV (1–5)	V (1–4)	IV (1–6)	V (1–6)
<i>Plantago lanceolata</i>	IV (1–7)	V (1–7)	V (1–6)	IV (1–5)	IV (1–7)
<i>Briza media</i>	IV (1–9)	V (1–6)	V (1–5)	IV (1–5)	IV (1–9)
<i>Lotus corniculatus</i>	IV (1–6)	V (1–7)	V (1–6)	IV (1–5)	IV (1–7)
<i>Avenula pratensis</i>	IV (1–7)	V (1–6)	IV (1–7)	IV (1–8)	IV (1–8)
<i>Leontodon hispidus</i>	IV (1–7)	V (1–7)	IV (1–5)	III (1–5)	IV (1–7)
<i>Linum catharticum</i>	III (1–4)	IV (1–4)	IV (1–3)	IV (1–5)	IV (1–5)
<i>Hieracium pilosella</i>	IV (1–7)	III (1–4)	III (1–5)	IV (1–7)	IV (1–7)
<i>Scabiosa columbaria</i>	III (1–5)	V (1–5)	IV (1–5)	III (1–6)	IV (1–6)
<i>Thymus praecox</i>	IV (1–7)	III (1–4)	III (1–7)	V (1–6)	IV (1–7)
<i>Cirsium acaule</i>	IV (1–7)	V (1–6)	II (1–7)	I (1–7)	III (1–7)
<i>Asperula cynanchica</i>	III (1–7)	IV (1–4)	I (1–3)	I (1)	II (1–7)
<i>Hippocrepis comosa</i>	II (1–6)	III (1–8)	I (3)	I (1)	II (1–8)
<i>Polygala calcarea</i>	I (1–4)	II (1–4)	I (1–2)		I (1–4)
<i>Onobrychis viciifolia</i>	I (1–4)	I (2–4)	I (3)		I (1–4)
<i>Thesium humifusum</i>	I (1–4)	I (1–4)	I (1)		I (1–4)
<i>Senecio integrifolius integrifolius</i>	I (1–3)	I (1)	I (1)		I (1–3)
<i>Thymus pulegioides</i>	I (1–5)	I (1)	I (1)		I (1–5)
<i>Hypochoeris maculata</i>	I (1–3)	I (1–2)			I (1–3)
<i>Gentianella anglica</i>	I (1–2)	I (1)			I (1–2)
<i>Astragalus danicus</i>	I (1–3)			I (1)	I (1–3)
<i>Phyteuma tenerum</i>	I (1–5)				I (1–5)
<i>Trifolium pratense</i>	I (1–5)	IV (1–6)	IV (1–6)	I (1–4)	III (1–6)
<i>Carex caryophylla</i>	III (1–7)	IV (1–5)	III (1–4)	III (1–5)	III (1–7)
<i>Prunella vulgaris</i>	III (1–4)	IV (1–4)	III (1–4)	II (1–3)	III (1–4)
<i>Dactylis glomerata</i>	II (1–5)	V (1–6)	III (1–6)	III (1–4)	III (1–6)
<i>Plantago media</i>	II (1–4)	V (1–5)	III (1–5)	I (1–5)	III (1–5)
<i>Succisa pratensis</i>	I (1–6)	IV (1–6)	II (1–5)	I (1–3)	II (1–6)
<i>Centaurea nigra</i>	I (1–5)	III (1–4)	II (1–4)	II (1–6)	II (1–6)
<i>Avenula pubescens</i>	II (1–6)	III (1–5)	II (1–8)	I (1–4)	II (1–8)
<i>Leucanthemum vulgare</i>	I (1–3)	III (1–3)	I (1–3)	I (1–3)	I (1–3)

Floristic table CG2 (cont.)

	a	b	c	d	2
<i>Campanula glomerata</i>	I (1–4)	II (1–3)	I (1–2)	I (1)	I (1–4)
<i>Serratula tinctoria</i>	I (1–5)	II (1–5)	I (1–2)	I (2)	I (1–5)
<i>Stachys betonica</i>	I (1–3)	II (1–5)	I (1–7)	I (1–4)	I (1–7)
<i>Carex humilis</i>	I (3–8)	II (1–8)	I (5)		I (1–8)
<i>Holcus lanatus</i>	I (1–5)	I (1–7)	IV (1–6)	II (1–6)	II (1–7)
<i>Trifolium repens</i>	I (1–4)	I (1–4)	IV (1–7)	I (1–5)	II (1–7)
<i>Medicago lupulina</i>	I (1–5)	III (1–5)	III (1–5)	II (1–5)	II (1–5)
<i>Agrostis stolonifera</i>	I (1–3)	II (1–4)	III (1–5)	I (2–3)	I (1–5)
<i>Cynosurus cristatus</i>	I (1–5)	II (1–5)	III (1–6)	I (1–4)	I (1–6)
<i>Trisetum flavescens</i>	I (1–5)	I (1–2)	III (1–5)	II (1–6)	I (1–6)
<i>Achillea millefolium</i>	I (1–5)	I (1–3)	II (1–4)	II (1–5)	I (1–5)
<i>Crepis capillaris</i>	I (1–5)	I (1–2)	II (1–3)	I (1–5)	I (1–5)
<i>Phleum pratense bertolonii</i>	I (1–2)	I (1–3)	II (1–4)	I (1–2)	I (1–4)
<i>Arrhenatherum elatius</i>	I (1–6)	I (1–4)	II (1–7)	I (1–5)	I (1–7)
<i>Pulsatilla vulgaris</i>	I (1–4)		II (1–3)	I (1–3)	I (1–4)
<i>Dicranum scoparium</i>	I (1–4)		I (1–3)	III (1–4)	I (1–4)
<i>Leontodon taraxacoides</i>	I (1–4)	I (1–5)	I (1–5)	II (1–4)	I (1–5)
<i>Agrostis capillaris</i>	I (2–4)	I (1)	II (1–7)	II (1–5)	I (1–7)
<i>Brachypodium sylvaticum</i>	I (1–5)	I (1–2)	I (1–7)	II (1–9)	I (1–9)
<i>Anthoxanthum odoratum</i>	I (1–5)	I (1)	I (1–3)	II (1–5)	I (1–5)
<i>Ctenidium molluscum</i>	I (1–8)	I (1–4)	I (1)	II (1–4)	I (1–8)
<i>Fissidens cristatus</i>	I (1–5)	I (1–4)	I (1–2)	II (1–2)	I (1–5)
<i>Galium sternerii</i>				I (1–5)	I (1–5)
<i>Campanula rotundifolia</i>	III (1–5)	III (1–4)	III (1–4)	III (1–4)	III (1–5)
<i>Helianthemum nummularium</i>	III (1–8)	III (1–6)	II (1–7)	IV (1–7)	III (1–8)
<i>Pseudoscleropodium purum</i>	III (1–8)	III (1–8)	III (1–4)	II (1–3)	III (1–8)
<i>Euphrasia officinalis</i> agg.	II (1–6)	III (1–4)	II (1–3)	II (1–5)	II (1–6)
<i>Ranunculus bulbosus</i>	II (1–4)	III (1–4)	II (1–3)	II (1–3)	II (1–4)
<i>Pimpinella saxifraga</i>	II (1–4)	III (1–4)	III (1–4)	II (1–4)	II (1–4)
<i>Galium verum</i>	II (1–4)	III (1–7)	III (1–5)	III (1–5)	III (1–7)
<i>Bromus erectus</i>	II (1–4)	II (1–3)	II (1–4)	I (1–3)	II (1–4)
<i>Gentianella amarella</i>	II (1–4)	II (1–3)	I (1–3)	II (1–4)	II (1–4)
<i>Filipendula vulgaris</i>	II (1–6)	II (1–4)	II (1–5)	I (1–5)	II (1–6)
<i>Homalothecium lutescens</i>	II (1–8)	II (1–4)	I (1–3)	II (1–5)	II (1–8)

<i>Primula veris</i>	I (1–4)	II (1–3)	II (1–4)	II (1–5)	II (1–5)
<i>Viola hirta</i>	II (1–5)	I (1–4)	I (1–3)	II (1–3)	I (1–5)
<i>Polygala vulgaris</i>	II (1–4)	I (1–3)	I (1)	II (1–3)	I (1–4)
<i>Senecio jacobaea</i>	I (1–3)	I (1–2)	II (1–3)	II (1–3)	I (1–3)
<i>Anthyllis vulneraria</i>	I (1–7)	I (1–7)	I (1–5)	I (1–7)	I (1–7)
<i>Festuca rubra</i>	I (2–9)	I (2–7)	I (1–5)	II (1–5)	I (1–9)
<i>Bellis perennis</i>	I (1–4)	I (1)	I (1–3)	I (1–5)	I (1–5)
<i>Taraxacum officinale</i> agg.	I (1–3)	I (1–3)	I (1–3)	I (1–3)	I (1–3)
<i>Calliergon cuspidatum</i>	I (1–7)	I (1–6)	I (1–3)	I (1–4)	I (1–7)
<i>Centaurea scabiosa</i>	I (1–4)	I (1–4)	I (1–5)	I (1–5)	I (1–5)
<i>Blackstonia perfoliata</i>	I (1–5)	I (1)	I (1–3)	I (1–3)	I (1–5)
<i>Galium mollugo</i>	I (1–4)	I (1–4)	I (1–5)	I (1–2)	I (1–5)
<i>Weissia</i> cf. <i>microstoma</i>	I (1–3)	I (1)	I (1)	I (1–3)	I (1–3)
<i>Danthonia decumbens</i>	I (1–6)	I (1–5)	I (1–7)	I (1–7)	I (1–7)
<i>Campyllum chrysophyllum</i>	I (1–4)	I (1–4)	I (2)	I (1–3)	I (1–4)
<i>Picris hieracioides</i>	I (1–2)	I (1–4)	I (1–4)	I (1–2)	I (1–4)
<i>Rhytidiadelphus squarrosus</i>	I (1–3)	I (1–4)	I (1–4)	I (1–3)	I (1–4)
<i>Daucus carota</i>	I (1–4)	I (1–3)	I (1–2)	I (1)	I (1–4)
<i>Festuca arundinacea</i>	I (1–6)	I (1–4)	I (1–5)	I (1–4)	I (1–6)
<i>Carlina vulgaris</i>	I (1–5)	I (1–2)	I (1–5)	I (1–3)	I (1–5)
<i>Poa pratensis</i>	I (1–3)	I (1)	I (1–3)	I (1–3)	I (1–3)
<i>Cerastium fontanum</i>	I (2–3)	I (1)	I (1)	I (1–3)	I (1–3)
<i>Luzula campestris</i>	I (1–2)	I (1)	I (1–3)	I (1–3)	I (1–3)
<i>Brachypodium pinnatum</i>	I (1–4)	I (3)	I (3)	I (3)	I (1–4)
<i>Cirsium vulgare</i>	I (1)	I (1)	I (1)	I (1–3)	I (1–3)
<i>Leontodon autumnalis</i>	I (1–3)	I (1)	I (1–3)	I (1)	I (1–3)
<i>Rhinanthus minor</i>	I (1–5)	I (1–3)	I (2–3)	I (1)	I (1–5)
<i>Agrimonia eupatoria</i>	I (1–2)	I (1)	I (1–3)	I (3)	I (1–3)
<i>Crataegus monogyna</i> sapling	I (1–3)	I (1)	I (1)	I (1–3)	I (1–3)
<i>Ulex europaeus</i>	I (1–4)	I (1)	I (1)	I (1)	I (1–4)
<i>Ophrys apifera</i>	I (1–3)	I (1)	I (1)	I (1)	I (1–3)
<i>Dactylorhiza fuchsii</i>	I (1–3)	I (1)	I (1)	I (1–2)	I (1–3)
<i>Cirsium arvense</i>	I (1–6)	I (2)	I (1–3)	I (1–3)	I (1–6)
<i>Carduus nutans</i>	I (1)	I (1)	I (1)	I (1–2)	I (1–2)
<i>Veronica chamaedrys</i>	I (1–3)	I (1–2)	I (1–3)	I (1–3)	I (1–3)
<i>Lolium perenne</i>	I (1)	I (1)	I (1–3)	I (1)	I (1–3)
<i>Rhytidiadelphus triquetrus</i>	I (1–5)	I (1–6)	I (1–3)	I (1–2)	I (1–6)
<i>Ononis repens</i>	I (1–4)	I (1–6)	I (1–7)		I (1–7)
<i>Tragopogon pratensis</i>	I (1–3)	I (1)	I (1)		I (1–3)

Floristic table CG2 (cont.)

	a	b
<i>Urtica dioica</i>	I (1)	I (1)
<i>Coeloglossum viride</i>	I (1–3)	I (1)
<i>Centaureum erythraea</i>	I (1–4)	
<i>Hypochoeris radicata</i>	I (2–4)	
<i>Sedum acre</i>	I (1–3)	
<i>Fragaria vesca</i>	I (1–4)	
<i>Teucrium scorodonia</i>	I (2–3)	
<i>Arenaria serpyllifolia</i>	I (2–3)	
<i>Rumex acetosa</i>	I (1)	
<i>Hylocomium splendens</i>	I (1)	
<i>Deschampsia cespitosa</i>	I (2)	
<i>Lathyrus pratensis</i>	I (1)	
<i>Hypnum cupressiforme</i>	I (1–7)	I (1–2)
<i>Vicia cracca</i>	I (1–3)	I (1)
<i>Neckera complanata</i>	I (1–3)	I (1)
<i>Gymnadenia conopsea</i>	I (1–2)	I (1–3)
<i>Cirsium palustre</i>		I (1)
<i>Inula conyza</i>	I (1–3)	
<i>Geranium sanguineum</i>	I (1)	
<i>Phleum pratense pratense</i>	I (3)	
<i>Viola riviniana</i>		
<i>Cladonia rangiformis</i>		
<i>Hypericum montanum</i>		
<i>Potentilla erecta</i>		
<i>Cirsium eriophorum</i>		
Number of samples	343	177
Number of species/sample	25 (7–45)	30 (18–45)

- a *Cirsium acaule*-*Asperula cynanchica* sub-community
- b *Succisa pratensis*-*Leucanthemum vulgare* sub-community
- c *Holcus lanatus*-*Trifolium repens* sub-community
- d *Dicranum scoparium* sub-community
- 2 *Festuca ovina*-*Avenula pratensis* grassland (total)

c	d	2
I (1)		I (1)
I (1-3)		I (1-3)
I (1-3)	I (1-3)	I (1-4)
I (1-3)	I (1)	I (1-4)
I (1)	I (1)	I (1-3)
I (1-3)	I (1-4)	I (1-4)
I (1)	I (1-3)	I (1-3)
I (1)	I (1-3)	I (1-3)
I (1)	I (3)	I (1-3)
I (1)	I (1)	I (1)
I (1)	I (1-3)	I (1-3)
I (1)	I (1)	I (1)
	I (1-3)	I (1-7)
	I (3)	I (1-3)
	I (1)	I (1-3)
	I (1-4)	I (1-4)
I (1)	I (1-3)	I (1-3)
	I (1)	I (1-3)
	I (1-3)	I (1-3)
I (1-3)		I (1-3)
I (1-4)	I (1-5)	I (1-5)
I (1)	I (1-5)	I (1-5)
I (1-3)	I (3)	I (1-3)
I (1-5)	I (1-5)	I (1-5)
I (1-3)	I (1)	I (1-3)
167	169	856
30 (16-44)	26 (5-47)	27 (5-47)

Floristic table CG2a, variants

	ai	aII	aIII
<i>Festuca ovina</i>	IV (3–9)	V (2–9)	V (1–9)
<i>Carex flacca</i>	V (1–5)	V (2–8)	V (1–8)
<i>Sanguisorba minor</i>	V (1–8)	V (2–8)	IV (1–7)
<i>Koeleria macrantha</i>	V (1–6)	IV (1–5)	V (1–6)
<i>Plantago lanceolata</i>	IV (1–7)	IV (1–5)	V (1–5)
<i>Briza media</i>	IV (1–6)	IV (1–7)	V (1–9)
<i>Lotus corniculatus</i>	IV (1–5)	IV (1–6)	V (1–6)
<i>Avenula pratensis</i>	IV (1–6)	IV (1–6)	V (1–7)
<i>Leontodon hispidus</i>	IV (1–4)	IV (1–5)	IV (1–7)
<i>Linum catharticum</i>	II (1–4)	III (1–3)	IV (1–4)
<i>Hieracium pilosella</i>	IV (1–7)	III (1–5)	V (1–6)
<i>Scabiosa columbaria</i>	III (1–4)	IV (1–5)	III (1–5)
<i>Thymus praecox</i>	III (1–5)	III (1–6)	IV (1–6)
<i>Cirsium acaule</i>	III (1–6)	IV (1–7)	IV (1–7)
<i>Asperula cynanchica</i>	III (1–5)	III (1–4)	IV (1–7)
<i>Hippocrepis comosa</i>	II (1–4)	II (1–6)	II (1–6)
<i>Helianthemum nummularium</i>	IV (1–6)	III (2–8)	II (1–6)
<i>Filipendula vulgaris</i>	V (1–6)	I (1–4)	I (1–6)
<i>Festuca rubra</i>	III (2–9)	I (3–8)	I (1–9)
<i>Pseudoscleropodium purum</i>	III (1–8)	III (1–7)	IV (1–8)
<i>Prunella vulgaris</i>	III (1–4)	I (1–3)	IV (1–4)
<i>Homalothecium lutescens</i>	II (1–6)	I (1–5)	III (1–8)
<i>Ranunculus bulbosus</i>	I (1–2)	I (1–3)	III (1–4)
<i>Bellis perennis</i>	I (2–3)	I (1)	II (2–4)
<i>Senecio jacobaea</i>	I (1–3)	I (1–3)	II (1–3)
<i>Ctenidium molluscum</i>	I (1–4)	I (1–8)	II (1–6)
<i>Fissidens cristatus</i>	I (1–4)	I (1–5)	II (1–3)
<i>Trifolium pratense</i>	I (1–4)	I (1–5)	II (1–4)
<i>Medicago lupulina</i>	I (1–4)	I (1–3)	II (1–5)
<i>Rhynchospora triquetra</i>	I (5)		I (1–4)
<i>Neckera complanata</i>			I (1–3)
<i>Hylocomium splendens</i>			I (1–3)
<i>Deschampsia cespitosa</i>			I (2)
<i>Ulex europaeus</i>			I (1–4)
<i>Campanula rotundifolia</i>	III (1–5)	III (1–3)	III (1–3)
<i>Carex caryophylla</i>	III (1–7)	II (1–4)	III (1–5)
<i>Galium verum</i>	III (1–4)	II (1–4)	II (1–4)
<i>Pimpinella saxifraga</i>	II (1–4)	III (1–4)	II (1–3)
<i>Plantago media</i>	II (1–4)	II (1–4)	II (1–4)
<i>Euphrasia officinalis</i> agg.	II (1–3)	II (1–5)	II (1–6)
<i>Avenula pubescens</i>	II (1–6)	II (1–4)	II (1–4)
<i>Bromus erectus</i>	II (2–4)	II (1–4)	I (1–4)
<i>Polygala vulgaris</i>	II (1–4)	I (2–4)	II (1–3)
<i>Gentianella amarella</i>	I (1–3)	II (1–3)	II (1–4)

Floristic table CG2a, variants (*cont.*)

	ai	aii	aiii
<i>Viola hirta</i>	II (1–4)	I (1–4)	II (1–5)
<i>Dactylis glomerata</i>	I (1–3)	II (1–3)	II (1–5)
<i>Centaurea nigra</i>	I (2–4)	II (1–5)	I (1–4)
<i>Anthyllis vulneraria</i>	I (1–5)	II (1–4)	I (1–7)
<i>Succisa pratensis</i>	I (1–4)	I (1–6)	I (1–5)
<i>Cynosurus cristatus</i>	I (2–3)	I (1–2)	I (1–5)
<i>Trisetum flavescens</i>	I (1–4)	I (1–5)	I (1–5)
<i>Achillea millefolium</i>	I (2–3)	I (1–5)	I (1–3)
<i>Primula veris</i>	I (1–3)	I (1–4)	I (1–4)
<i>Campanula glomerata</i>	I (1–3)	I (1–4)	I (1–3)
<i>Calliergon cuspidatum</i>	I (1–2)	I (2–5)	I (1–7)
<i>Daucus carota</i>	I (1–3)	I (1–4)	I (1–3)
<i>Campylium chrysophyllum</i>	I (1–3)	I (1–3)	I (2–4)
<i>Danthonia decumbens</i>	I (1–4)	I (1–6)	I (1–5)
<i>Leucanthemum vulgare</i>	I (1–2)	I (1–3)	I (1–3)
<i>Leontodon taraxacoides</i>	I (1–3)	I (3–4)	I (1–4)
<i>Galium mollugo</i>	I (1–3)	I (1–3)	I (1–4)
<i>Crataegus monogyna</i> sapling	I (1–3)	I (1–3)	I (1–2)
<i>Thesium humifusum</i>	I (1–3)	I (3–4)	I (1–2)
<i>Hypnum cupressiforme</i>	I (1–7)	I (3–7)	I (1–4)
<i>Centaurea scabiosa</i>	I (1–4)	I (1–4)	I (1–4)
<i>Polygala calcarea</i>	I (1–4)	I (1–4)	I (1–4)
<i>Thymus pulegioides</i>	I (1–5)	I (1–4)	I (2–5)
<i>Onobrychis viciifolia</i>	I (3–4)	I (1–4)	I (4)
<i>Blackstonia perfoliata</i>	I (2)	I (1–5)	I (1–3)
<i>Carex humilis</i>	I (5)	I (3–7)	I (3–8)
<i>Arrhenatherum elatius</i>	I (3)	I (1–4)	I (1–6)
<i>Taraxacum officinale</i> agg.	I (1–2)	I (1)	I (1–3)
<i>Fragaria vesca</i>	I (1–3)	I (2–4)	I (1–4)
<i>Anacamptis pyramidalis</i>	I (1–3)	I (1–3)	I (1–3)
<i>Phyteuma tenerum</i>	I (3–5)	I (1–3)	I (2–4)
<i>Carlina vulgaris</i>	I (1–3)	I (1–5)	I (1–4)
<i>Weissia</i> cf. <i>microstoma</i>	I (1–2)	I (1–3)	I (1–3)
<i>Crepis capillaris</i>	I (1–5)	I (2)	I (1–2)
<i>Brachypodium sylvaticum</i>	I (1)	I (1–5)	I (2–5)
<i>Hypochoeris radicata</i>	I (2–3)	I (3–4)	I (3)
<i>Cerastium fontanum</i>	I (2–3)	I (2)	I (2–3)
<i>Senecio integrifolius integrifolius</i>	I (1–2)	I (1)	I (1–3)
<i>Centaureum erythraea</i>	I (2–3)	I (3)	I (1–4)
<i>Agrostis stolonifera</i>	I (2)	I (1–2)	I (1–3)
<i>Astragalus danicus</i>	I (1)	I (1–3)	I (1–4)
<i>Agrostis capillaris</i>	I (3–4)	I (3)	I (2–4)
<i>Anthoxanthum odoratum</i>	I (1–2)	I (3)	I (1–5)
<i>Picris hieracioides</i>	I (2)	I (1–2)	I (1–2)
<i>Trifolium repens</i>	I (1)	I (2)	I (1–4)
<i>Phleum pratense bertolonii</i>	I (1)	I (1)	I (1–2)

<i>Ononis repens</i>	I (2)	I (1–3)	I (4)
<i>Vicia cracca</i>	I (1–3)	I (1)	I (1)
<i>Coeloglossum viride</i>	I (1)	I (1–3)	I (1)
<i>Ophrys apifera</i>	I (1)	I (3)	I (1–3)
<i>Rosa canina</i> agg.	I (1)	I (1–3)	I (1)
<i>Agrimonia eupatoria</i>	I (1)	I (1)	I (2)
<i>Urtica dioica</i>	I (1)		I (1)
<i>Cirsium vulgare</i>	I (1)		I (1)
<i>Rhinanthus minor</i>	I (2–4)		I (1–5)
<i>Tragopogon pratensis</i>	I (1–3)	I (1)	
<i>Sedum acre</i>	I (1–3)	I (1)	
<i>Lathyrus pratensis</i>	I (1)	I (1)	
<i>Rumex acetosa</i>	I (1)	I (1)	
<i>Pulsatilla vulgaris</i>	I (1–3)	I (1–4)	
<i>Holcus lanatus</i>		I (1–2)	I (1–5)
<i>Serratula tinctoria</i>		I (3–5)	I (1–5)
<i>Dicranum scoparium</i>		I (2–3)	I (1–4)
<i>Brachypodium pinnatum</i>		I (4)	I (1–4)
<i>Leontodon autumnalis</i>		I (1)	I (1–3)
<i>Luzula campestris</i>		I (1)	I (1–2)
<i>Rhynchospora squarrosa</i>		I (1–3)	I (1–3)
<i>Festuca arundinacea</i>		I (2–6)	I (1–5)
<i>Poa pratensis</i>		I (1)	I (1–3)
<i>Dactylorhiza fuchsii</i>		I (1)	I (3)
<i>Cirsium arvense</i>		I (3–6)	I (1)
<i>Gymnadenia conopsea</i>		I (2)	I (1)
Number of samples	81	101	161
Number of species/sample	24 (9–45)	22 (9–39)	27 (7–42)

ai *Filipendula vulgaris*-*Helianthemum nummularium* variant

aii Typical variant

aiii *Pseudoscleropodium purum*-*Prunella vulgaris* variant

