

CG7

Festuca ovina-*Hieracium pilosella*-*Thymus praecox*/ *pulegioides* grassland

Synonymy

Herbland Tansley & Adamson 1925; Primitive Chalk grassland Tansley & Adamson 1925 *p.p.*; Rabbit-grazed Chalk grassland Tansley & Adamson 1925 *p.p.*; Breckland Grasslands A and B Watt 1940; Old ex-arable grassland Cornish 1954; *Hornungia petraea* stands Ratcliffe 1959 *p.p.*; Annual community Ratcliffe 1961 *p.p.*; Pulpit Hill Field vegetation Lloyd 1964; *Catapodium rigidum* stands Clark 1974 *p.p.*; *Festuca ovina*/*Hieracium pilosella*/*Cladonia* spp. lichen-rich grassland Wells *et al.* 1976; Ant-hill vegetation King 1977a *p.p.*; Breckland grasslands Ratcliffe 1977 *p.p.*; *Helictotrichon pratense*-*Koeleria cristata*-*Phleum phleoides* grassland Smith 1980; Lichen grasslands Smith 1980 *p.p.*

Constant species

Festuca ovina, *Hieracium pilosella*, *Leontodon hispidus*, *Thymus praecox*/*pulegioides*, *Hypnum cupressiforme*.

Rare species

Artemisia campestris, *Astragalus danicus*, *Carex ericetorum*, *Galium parisiense*, *Himantoglossum hircinum*, *Hornungia petraea*, *Medicago lupulina* ssp. *minima*, *M. sativa* ssp. *falcata*, *M. × varia*, *Minuartia hybrida*, *Phleum phleoides*, *Potentilla tabernaemontani*, *Silene conica*, *S. otites*, *Thymus serpyllum*, *Veronica spicata*, *V. verna*, *Pleurochaeta squarrosa*, *Bacidia muscorum*, *Buellia epigaea*, *Diploschistes scruposus* var. *bryophilus*, *Fulgensia fulgens*, *Lecidea decipiens*, *Squamaria lentigera*, *Toximia caerulea* var. *nigricans*, *T. lobulata*.

Physiognomy

The swards of the *Festuca*-*Hieracium*-*Thymus* grassland can be open or closed but, even where there is a continuous cover of vegetation, this usually lacks the dense, plush quality of the *Festuca*-*Avenula* swards. *Festuca ovina* (only on rare occasions replaced by *F. rubra*) is constant and frequently abundant, but it generally occurs as small isolated tussocks or an open

network of somewhat attenuated, procumbent shoots. *Koeleria macrantha* is the only other grass that is at all common throughout, other important Mesobromion species being markedly patchy or scarce. *Avenula pratensis*, for example, is frequent only in certain sub-communities and, even then, may be sparse in heavily-grazed swards. *Dactylis glomerata* and *Briza media*, two other major *Festuca*-*Avenula* grasses, are here strikingly uncommon.

In general, it is herbaceous dicotyledons, and especially chamaephytes and therophytes, which give the vegetation its distinctive character. Among the former, *Hieracium pilosella* is usually the most frequent and abundant: more than 1000 rosettes m⁻² have been recorded in this kind of vegetation (e.g. Bishop *et al.* 1978). *Thymus praecox* is also constant and it, too, can be locally prominent. *T. pulegioides*, though inadequately distinguished from *T. praecox* in the bulk of the data, is very characteristic of this community (Pigott 1955). In marked contrast to most kinds of *Festuca*-*Avenula* grassland, *Helianthemum nummularium* is scarce here, except in certain rather particular circumstances: it occurs, for example, in this vegetation on ant-hills, though only where there are plants nearby in the surrounding Mesobromion sward (King 1977a, b, c). *Sedum acre* is occasional and it can be locally abundant.

Mesobromion rosette species are few in number; indeed, hemicryptophytes in general are not very numerous and often rather unevenly represented between the different sub-communities. *Carex flacca* and *Scabiosa columbaria*, for example, are here at most occasional. More frequent are *Leontodon hispidus*, *Prunella vulgaris*, *Taraxacum officinale* agg. (often including plants of the *Erythrosperma* section), *Cirsium acaule*, *Sanguisorba minor* and *Lotus corniculatus*. This last, together with the more uncommon and patchily distributed *Anthyllis vulneraria* and *Galium verum* (and *Sedum acre*), can give stands a splash of yellow as their flowers appear in mid-summer after the purple of the thymes.

The open texture of this turf provides patches of bare ground which are exploited by coarse weeds and therophytes. Among the former, *Senecio jacobaea* (sometimes biennial) is the most frequent and characteristic of the whole community but there is occasionally some *Potentilla reptans* and, in some sub-communities, *Fragaria vesca* or *Rumex acetosa*. Though rarely abundant in individual stands, these species can give the swards a coarseness that is generally absent from the *Festuca-Avenula* grassland. Certain of the pauciennials, too, are large and conspicuous: *Crepis capillaris*, *Medicago lupulina*, *Erigeron acer* and *Blackstonia perfoliata*. Much more easily missed, especially when sampling is undertaken in summer, but nonetheless very typical of certain of these swards, are more diminutive therophytes, many of which behave as winter annuals, disappearing after flowering or persisting as shrivelled stems. *Linum catharticum* and *Gentianella amarella* occur occasionally throughout; less widely distributed are *Centaureum erythraea*, *Arenaria serpyllifolia*, *Aphanes arvensis*, *Myosotis ramosissima* and *Veronica arvensis* and, of much more restricted occurrence, a variety of national rarities (see below).

Bryophytes are very often an important component of the vegetation. *Hypnum cupressiforme* (usually var. *lacunosum* where different forms have been distinguished) is especially striking, being much more consistently frequent and abundant here than in the *Festuca-Avenula* grassland. *Pseudoscleropodium purum*, *Homalothecium lutescens* and *Fissidens cristatus* are also common with, rather more unevenly present in different sub-communities, *Dicranum scoparium* and *Weissia* cf. *microstoma*. Lichens, especially *Cladonia* spp., are particularly prominent in some kinds of sward.

Sub-communities

***Koeleria macrantha* sub-community:** Primitive Chalk grassland Tansley & Adamson 1925 p.p.; *Hornungia petraea* stands Ratcliffe 1959 p.p.; Annual community Ratcliffe 1961 p.p.; *Catapodium rigidum* stands Clark 1974 p.p.; Ant-hill vegetation King 1977a. Mesobromion species, such as *Avenula pratensis* and *Sanguisorba minor* and, less markedly, *Carex flacca*, *Briza media* and *Scabiosa columbaria*, are a little more frequent here than in some other sub-communities and *Galium verum* and *Plantago lanceolata* also occur commonly. The basic floristics of the community are, however, preserved: *F. ovina*, *H. pilosella* and *Thymus* spp. make up the bulk of the vascular cover and within the usually rather open sward there are scattered hemicryptophytes, patches of pleurocarpous mosses and bare ground. On the latter, coarser weeds and pauciennials, apart from *Senecio jacobaea*, are rather infrequent but there are commonly some smaller therophytes. *Linum catharticum*, *Gentia-*

nella amarella and *Arenaria serpyllifolia* are the commonest species but mixtures of the following can also occur: *Myosotis ramosissima*, *Aphanes arvensis*, *Veronica arvensis*, *Erophila verna*, *Acinos arvensis*, *Desmazeria rigida*, *Cerastium semidecandrum*, *Saxifraga tri-dactylites*, *Cardamine hirsuta* and *Arabidopsis thaliana*. The national rarities *Hornungia petraea* and *Draba muralis* and the perennial *Potentilla tabernaemontani* have been recorded in this vegetation in Derbyshire (Ratcliffe 1959, 1961).

The prominence of these different components and their disposition within the sward vary somewhat with the physiography of the habitat. Over flat limestone surfaces and rounded knolls, for example, the vegetation occurs as a loose-textured turf with its elements closely intermingled. On fine talus, the vascular species are confined to crevices with the bryophytes spreading between. Around exposures of harder limestones, where this vegetation can occur as distinctive 'eye-brows', the vascular plants thin out over the shallower soil and the therophytes become more prominent on loose detritus. On ant-hills, some striking patterns can be encountered as this vegetation develops from those perennials in the disrupted sward which are able to respond to burial or the exposure of bare soil and therophytes which, though largely absent from the surrounding vegetation, seed in on to the heaps. Such patterns also change with the ageing of the hills and their abandonment (King 1977a, b, c: see below).

***Cladonia* spp. sub-community:** Breckland Grassland B Watt 1940; *Festuca ovina*/*Hieracium pilosella*/*Cladonia* spp. lichen-rich grassland Wells et al. 1976; Breckland grasslands Ratcliffe 1977 p.p.; *Helictotrichon pratense*-*Koeleria cristata*-*Phleum phleoides* grassland Smith 1980. In its classic localities in the Breckland of the Norfolk/Suffolk borders, this sub-community occurs as a more or less continuous, though often rather sparse and wiry, turf in which *F. ovina*, together with complementary proportions of *K. macrantha*, *H. pilosella* and *Astragalus danicus* (different here), generally make up the bulk of the vascular component of the vegetation. At Porton Down, its only other known locality, *K. macrantha* is less frequent and prominent and *A. danicus* is absent though the general appearance of the vegetation remains the same. *Thymus praecox* and *T. pulegioides* (with very occasional *T. serpyllum*, essentially a plant of more calcifugous swards on sandier substrates) are now much less widespread than formerly, though they may be locally abundant and, with *A. danicus*, provide a flush of purple with their early summer flowers.

Most of the other associates are also decidedly patchy and the floristics and physiognomy of the vegetation are much less consistent than in the early descriptions of

heavily-grazed swards (e.g. Watt 1940, 1957). Among the most frequent associates under those conditions, *Lotus corniculatus*, *Taraxacum officinale* agg. and *Senecio jacobaea* (typical of the whole community) and *Avenula pratensis* and *Galium verum* (characteristic, too, of the *Koeleria* sub-community) remain common, though rather uneven in their occurrence and abundance. Likewise, *Cerastium fontanum* and *Luzula campestris* (both good preferentials for this sub-community) are still frequent as scattered individuals. *Carex flacca*, *Leontodon hispidus*, *Cirsium acaule* and *Sanguisorba minor* remain distinctively sparse, the last three being much less frequent here (at least in Breckland) than in most other kinds of *Festuca-Hieracium-Thymus* grassland.

Apart from these species, however, different stands show some general and some peculiar variations which reflect the kinds of gains and losses which Watt (1957, 1974) noted in ungrazed stands. In the first place, the vegetation is now generally grassier and, in places, decidedly rank. *Avenula pratensis*, in particular, though not much more frequent than in the early accounts, is now often more abundant and *Holcus lanatus* and *Trisetum flavescens* can also be locally prominent. *Achillea millefolium*, *Plantago lanceolata* and *Trifolium repens* sometimes accentuate the mesophytic look of the sward. Coarse grasses (such as *Avenula pubescens* and *Bromus erectus*), though sometimes encountered by Watt, are, however, absent in these data and some other species which held their frequency, increased or appeared with a lack of grazing, are very sparse here. Among the former, for example, *Phleum phleoides* and *Silene otites* were only rarely encountered and, among Watt's newcomers, *Ononis repens* and *Anthyllis vulneraria* were uncommon in Breckland samples (though the latter can be conspicuous at Porton) and *Medicago sativa* ssp. *falcata* was absent.

Second, as with Watt, there are some striking absences from the data. Finer grasses, for example, like *Agrostis capillaris*, *A. canina* ssp. *montana* and *Anthoxanthum odoratum*, are no more than occasional and both *Carex caryophyllaea* and *C. ericetorum* (the latter much more so than in Watt's ungrazed grasslands) are scarce. The present patchiness of *Thymus* spp. has already been noted and *Sedum acre*, another chamaephyte, is also now uncommon. But it is among the therophytes that the omissions are especially obvious. Although some caution is necessary before drawing too general conclusions from samples taken within a single season, especially a very dry one like 1976, all of the following, characteristic to varying degrees of grazed swards of this kind, are now apparently much rarer: *Aira praecox*, *Aphanes arvensis*, *Myosotis ramosissima*, *Rumex acetosella*, *Veronica arvensis* (also present in the more calcifugous grasslands), *Sagina apetala* spp. *apetala*, *Teesdalia nudicaulis* (more typical of the calcifugous swards but

occasionally present in grazed 'Grassland B'), *Aira caryophyllaea*, *Centaureum erythraea*, *Crepis capillaris*, *Desmazeria rigida*, *Erophila verna*, *Sagina apetala* ssp. *erecta*, *S. nodosa*, *Trifolium dubium* and the rarities *Minuartia hybrida* and *Veronica verna* (particularly characteristic of the more calcicolous grazed Breckland grasslands). Even *Arenaria serpyllifolia*, *Linum catharticum*, *Arabis hirsuta* and *Medicago lupulina*, which held up somewhat without grazing in Watt's studies, were uncommon in our samples.

There are marked reductions, too, in the frequency and variety of bryophytes and lichens, though this sub-community still preserves some preferential features in these elements of the vegetation. Of the rich and chequered pattern of bryophytes typical of the grazed swards of 'Grassland B', *Hypnum cupressiforme*, *Pseudoscleropodium purum* and *Homalothecium lutescens* (typical of this whole community) and *Dicranum scoparium* (a good preferential species here) are the most frequent. Less common, though still distinctive of this sub-community are *Brachythecium albicans*, *Ceratodon purpureus*, *Bryum capillare* and, in its southern outpost in Britain, *Rhytidium rugosum*. Most of the distinctive acrocarpous mosses of the grazed Breckland grasslands (e.g. *Encalypta vulgaris*, *Tortula ruralis* ssp. *ruraliformis*, *Ditrichum flexicaule*, *Weissia* spp., *Fissidens cristatus*, *Plagiomnium rostratum* and *Rhodobryum roseum*) and even some of the more robust pleurocarps which persisted without grazing in Watt's samples (e.g. *Pleurozium schreberi*, *Hylocomium splendens*, *Rhytidiadelphus triquetrus*, *Thuidium abietinum*) seem, however, to have declined, together with the more delicate hepatics (*Ptilidium ciliare*, *Frullania tamarisci*, *Lophozia excisa*, *Lophocolea bidentata* s.l.).

Although, in grazed 'Grassland B', lichens typically occurred as individuals rather than as pure patches or extensive sheets (Watt 1940), they were, nonetheless, a striking element in the vegetation. They remain, as a group, a good diagnostic feature of this sub-community, but their frequency and abundance have declined such that now usually just two or three species (sometimes even fewer) are present together in a stand. The most frequent are *Cornicularia aculeata*, *Cladonia rangiformis*, *C. impexa*, *C. arbuscula*, *C. pyxidata* and *C. foliacea* and the thallose *Peltigera canina*. *P. rufescens* and *P. polydactyla*, which Watt noted as declining more markedly than *P. canina* without grazing, were not recorded in our Breckland samples, though they were common at Porton in the survey of Wells *et al.* (1976). Indeed, the Porton swards of this kind seem to be much more like grazed 'Grassland B' in their variety and abundance of lichens than do surviving Breckland stands. Some of the vegetation at Porton even attained the very open character of 'Grassland A' with its flint- and Chalk-strewn surface and encrusting lichens were, likewise, common there. On balance, however, even these swards

seem to be better located here than in the next sub-community.

***Ditrichum flexicaule*-*Diploschistes scruposus* var. *bryophilus* sub-community:** Breckland Grassland A Watt 1940; Breckland grasslands Ratcliffe 1977 *p.p.*; Lichen grasslands Smith 1980 *p.p.* Only three samples were taken of this vegetation which is of very restricted distribution (see below), but they are distinctive in relation to the other sub-communities and show some of the important features noted in the original account (Watt 1940) and in the more recent descriptions of later changes (Watt 1981a, b). First, the cover is here generally open with small raised tussocks of *F. ovina* occurring within a ground of *H. pilosella* and scattered patches of *T. praecox*. *T. pulegioides* and *T. serpyllum* were not recorded though they apparently occur here in small amounts. Second, other perennials, especially hemicryptophytes, are sparse: there are sometimes scattered plants of *Avenula pratensis*, *Koeleria macrantha*, *Astragalus danicus*, *Leontodon hispidus*, *Lotus corniculatus*, *Taraxacum officinale* agg., *Senecio jacobaea*, *Plantago lanceolata* and *Cerastium fontanum*. The fern *Botrychium lunaria*, the abundance of which was a very diagnostic feature of 'Grassland A', was rare but, as its shoots are avidly eaten by rabbits, it may remain commoner than our data imply. Third, pauciennials occur in the more open areas. The most frequent species were *Carlina vulgaris*, *Centaureum erythraea*, *Linum catharticum*, *Sagina nodosa* and *Arabis hirsuta* but, as in the previous sub-community, many once-common species are now apparently sparse, even those of wide distribution such as *Desmazeria rigida*, *Myosotis ramosissima* and *Veronica arvensis* as well as the rarities *Minuartia hybrida* and *Galium parisiense*. Fourth, bryophytes and lichens remain a prominent feature of the sub-community. Among the former, *Hypnum cupressiforme*, *Campylium chrysophyllum*, *Encalypta vulgaris* and, especially typical of this kind of grassland, *Ditrichum flexicaule*, were abundant in the samples. The most frequent lichens were *Cornicularia aculeata*, *Peltigera canina*, *Cladonia foliacea*, *C. papillaria* (restricted to this sub-community), *C. furcata*, *C. impexa* and *C. rangiformis*. Particularly distinctive here is a further suite of lichens encrusting the soil surface and the abundant exposed flints and Chalk rubble: *Diploschistes scruposus* var. *bryophilus*, *Squamaria lentigera* and *Buellia epigaea* were recorded in the samples but other species known from this vegetation are *Bacidia muscorum*, *Dermatocarpon hepaticum*, *Fulgensia fulgens*, *Lecidea decipiens*, *Toximia caerulea* var. *nigricans* and *T. lobulata* (James *et al.* 1977, Ratcliffe 1977).

***Fragaria vesca*-*Erigeron acer* sub-community:** Herbland Tansley & Adamson 1925 *p.p.*; Old ex-arable grassland Cornish 1954 *p.p.*; Pulpit Hill Field vegetation Lloyd

& Pigott 1967. Although both *H. pilosella* and *Thymus* spp. remain constant here, they are generally less prominent in the swards and hemicryptophytes are more frequent and varied than in the preceding sub-communities. *F. ovina* (sometimes totally replaced by *F. rubra*) remains very much the most frequent and abundant grass but, though *Koeleria macrantha* is only occasional, there is often some *Trisetum flavescens* in the sward, less commonly a little *Agrostis stolonifera* and, more locally, *Holcus lanatus*, *Avenula pubescens* and *Phleum pratense* ssp. *bertolonii*. Typically, however, this grass cover remains sparse and the vegetation is usually short and somewhat open.

Among the herbaceous dicotyledons, the most frequent perennials are *Leontodon hispidus*, *Taraxacum officinale* agg., *Senecio jacobaea*, *Prunella vulgaris*, *Cirsium acaule* and, especially distinctive here, *Fragaria vesca*. *Potentilla reptans*, *Clinopodium vulgare* and *Inula conyzia* are much scarcer but can be locally prominent. Pauciennials are always an important component of the vegetation with coarser weed species, such as *Daucus carota*, *Erigeron acer* and *Crepis capillaris*, and less commonly *Pastinaca sativa* and *Arctium minus* agg., particularly noticeable. Smaller therophytes, such as *Linum catharticum*, *Gentianella amarella* and, preferential here, *Centaureum erythraea*, are also frequent. The rare species *Iberis amara*, *Teucrium botrys* and *Ajuga chamaepitys* have all been recorded in this vegetation. Occasional saplings of *Sambucus nigra* or *Cornus sanguinea* may add to the scruffy appearance of the vegetation but it never has a lush, rank character.

As usual in the community, bryophytes are frequent and sometimes abundant, though the species involved are few. *Hypnum cupressiforme*, *Homalothecium lutescens* and *Campylium chrysophyllum* form patches over the soil surface, but *Pseudoscleropodium purum* is noticeably scarce here. *Fissidens cristatus* and *Weissia* spp. are the most frequent acrocarps. Lichens are rare, though there may be occasional tufts of *Cladonia rangiformis* or *C. furcata*.

***Medicago lupulina*-*Rumex acetosa* sub-community.** In its general features, the somewhat grassier character of the sward, the greater prominence of hemicryptophytes and the presence of a conspicuous weed element, this vegetation is similar to that of the previous sub-community, though some of the species involved are different. *F. ovina* tends to be more abundant here and it commonly makes up the bulk of the vegetation, often with small amounts of *Phleum pratense* ssp. *bertolonii* and *Koeleria macrantha* and, less commonly, with a little *Avenula pubescens*.

Scattered in this ground which, though a little more extensive than in the *Fragaria*-*Erigeron* sub-community, is again not tall or luxurious, are small patches of the chamaephytes *H. pilosella* and *Thymus* spp., and

scattered rosettes of the same hemicryptophyte perennials with the addition, here, of *Sanguisorba minor*. Also preferential to this sub-community are *Rumex acetosa* and *Leontodon autumnalis* and, less commonly, *Ranunculus bulbosus* and *Viola hirta*. Ranker weeds are somewhat less conspicuous here (*Fragaria vesca* and *Potentilla reptans* occur occasionally) but, among the smaller pauciennials, *Medicago lupulina* and *Euphrasia officinalis* agg. are preferential and there are frequent records, too, for *Linum catharticum* and *Gentianella amarella*. *Iberis amara* and *Seseli libanotis* have been recorded in this vegetation.

The bryophytes are predominantly the more robust pleurocarpous mosses of the community with *Pseudoscleropodium purum* resuming its usually high frequency. Indeed, here it is the commonest species and often has extensive cover.

Habitat

The *Festuca-Hieracium-Thymus* grassland is characteristically a vegetation type of thin, stony, very free-draining and highly oligotrophic calcareous soils developed under more continental climatic conditions, with heavy rabbit-grazing and, sometimes, a history of past disturbance. It occurs, mainly over the Chalk, but also on some more southerly exposures of Carboniferous Limestone, on flat or gently-sloping sites, over knolls and around bedrock exposures, on some abandoned arable land and on spoil heaps. It can also be found where the typical edaphic, climatic and biotic factors coincide on the hills produced by mound-building ants.

The dry and impoverished nature of the soils is probably of prime importance in influencing both the floristics and the physiognomy of the community, perhaps of as much consequence as their generally calcareous and base-rich nature. In some habitats, the skeletal character of the soil cover is obvious: this vegetation can be found, for example, on those natural or man-made raw soils which develop in the crevices of certain rock exposures, between talus fragments or amongst disturbed rock waste where there is little more than an accumulation of wind-blown organic matter and mineral detritus (Tansley & Adamson 1925, Hope-Simpson 1940b, Ratcliffe 1959). More commonly, it occurs over more intact, extensive and somewhat deeper rendzinas but, wherever these have been analysed, they are strikingly poor in major nutrients. In the shallow, chalky soils at Lloyd's Pulpit Hill Field site in the Chilterns, for example (Lloyd 1964, Lloyd & Pigott 1967), and in the rendzinas under this kind of vegetation at Porton Down (Wells *et al.* 1976), nitrogen and phosphorus values were very low. In Breckland, the soils are of complex composition and provenance, being developed over Chalk with varying amounts of boulder clay and sand, disrupted by periglacial solifluction and

overlain to different degrees by aeolian material but here, too, the Newmarket brown rendzinas which typically underlie the community can be very oligotrophic (Watt 1936, 1940, Corbett 1973, Duffey 1976, Curtiss *et al.* 1976, *Soil Survey* 1983).

The effects of this can be seen throughout the vegetation in the generally low cover and poor vigour of the grasses and the prominence of herbaceous dicotyledons, especially those composites and labiates which can survive at low nutrient levels and those legumes which can obviate the need for soil nitrogen by having root-nodule bacteria. Though the large amounts of light reaching the sward surface enable low-growing species to persist, they are rarely able to produce lush growth and the consequent abundance of open ground leaves ample opportunity for the appearance of ephemerals and the spread of bryophytes and lichens. The importance of a poor nutrient supply in maintaining the balance between these components in this kind of vegetation was early confirmed by Farrow (1917), who applied farmyard manure to a Breckland sward and produced a more luxuriant herbage in which the balance of dominance was shifted towards the grasses. At Pulpit Hill, Lloyd (1964, Lloyd & Pigott 1967) demonstrated a similar response in *Festuca ovina*, *F. rubra* and *Koeleria macrantha*, suggesting that the normally poor availability of nitrogen in particular was a controlling factor in limiting their growth in the ungrazed swards there. *F. ovina* and *K. macrantha* were also the main species which responded to the addition of major nutrients in a series of fertiliser experiments on Breckland grasslands of this type carried out by Davy & Bishop (1984). An increase in their biomass and litter, especially marked in ungrazed plots, was accompanied by a catastrophic decline in *Hieracium pilosella* and a reduction in the cover of bryophytes and lichens. Much of the response of *H. pilosella* was attributed to the indirect effect of the more vigorous growth of its competitors but the addition of nutrients also greatly stimulated inflorescence production and accelerated the population decline in this species which, in Breckland, behaves as a monocarpic perennial (Bishop & Davy 1984). *Astragalus danicus*, a nationally rare and important species within the Breckland swards of this community, appeared to maintain itself in the fertilised plots, provided they were grazed.

Climatic conditions maintain and accentuate the harsh nature of the soil environment. The community is most characteristic of those eastern lowland limestones where the regional climate tends towards that of the Continental European mainland and outside this area generally occurs only where the local topoclimate brings conditions close to this, as on some south-facing slopes towards the upland margins (e.g. Ratcliffe 1961) or on the southern faces of ant-hills (e.g. King 1977a). In

Breckland, to which the *Cladonia* and *Ditrichum-Diploschistes* sub-communities are largely or wholly confined, there is the nearest approach in Britain to the extreme conditions of the European steppes and it is in these kinds of *Festuca-Hieracium-Thymus* grassland (and especially the latter sub-community) that the influence of climate is most strikingly seen.

The first feature of note about the climate is that it is dry. Over much of the range of the community, there are fewer than 120 wet days yr^{-1} (Ratcliffe 1968) and in Breckland the mean annual rainfall is generally less than 600 mm, with at least a 30% probability of it falling below 500 mm in any given year (Gregory 1957, Chandler & Gregory 1976). Second, there is a tendency for the bulk of such little rain as there is to fall in summer or, more precisely, in late summer to early autumn (Watt 1936, Chandler & Gregory 1976). The potential for a soil moisture deficit in spring and early summer is therefore very considerable over the typically shallow and free-draining profiles, especially when air temperatures begin to rise, late but fairly quickly, to high levels and humidity falls under the clear and sunny summer skies (Watt 1936, Smith 1976, Chandler & Gregory 1976). In agricultural terms, this area has one of the highest 'grass drought factors' of the whole country and, for good crop growth, irrigation is theoretically necessary in nine years out of ten (Smith 1976). Finally, the winters are comparatively dry and cold. Excess winter rain is the lowest of any British limestone region and minimum temperatures can be lower than any other area on the southern Chalk with up to 145 winter degree-days below freezing (Smith 1976). Morning snow-lie is rare (Salisbury 1932, Ratcliffe 1968).

Three effects of climate can be discerned in the vegetation. First, it plays a part in maintaining the generally open character of the sward, primarily perhaps through its influence on soil moisture. Shortage of water during much of the growing season may exclude or restrict the growth of certain perennial grasses and dicotyledons, acting directly or through inter-relationships with nutrient availability (e.g. Lloyd 1964, Lloyd & Pigott 1967, Davy & Taylor 1974a). The low frequencies here of certain mainstream Mesobromion species, such as *Dactylis glomerata*, *Briza media*, *Carex flacca* and *Scabiosa columbaria*, could be related to such effects, and low levels of *Festuca rubra* in this kind of vegetation on ant-hills have been attributed to water shortage (King 1977a). Even the constant perennials of the community may be markedly affected by seasonal variations in rainfall and especially by severe or prolonged drought. Patches of this vegetation among *Festuca-Avenula* swards, for example, often become tinged with brown as their shallow soils parch in mid-summer and, in 1975–6, *Hieracium pilosella* in Breckland swards of this kind showed a very marked (though

temporary) decline as rainfall dropped to its lowest level in this region for two centuries (Bishop *et al.* 1978, Bishop & Davy 1984). Watt (1981a) attributed some of the changes in relative abundance of the dominants in the *Ditrichum-Diploschistes* sub-community over a period of almost 40 years to variation in temperature and especially rainfall. In this particular kind of *Festuca-Hieracium-Thymus* grassland and perhaps also in more exposed stands of the *Koeleria* sub-community, other climatic factors, such as frost-heaving and wind-erosion in winter, are also likely to contribute to keeping the sward open.

Second, on the positive side, the more extreme climatic conditions approached in the habitats of the *Cladonia* and *Ditrichum-Diploschistes* sub-communities clearly help maintain an environment suitable for the survival in this country of a number of perennials with a Continental or steppe distribution through Europe. For the most part, these are not the same Continental species as are characteristic of the *Festuca-Avenula* grassland, which seem to prefer conditions not quite so harsh as here and which are typically rare in the community. Some do, however, also occur in the *Festuca-Carlina* grassland and in the *Helianthemum-Asperula* sub-community of the *Sesleria-Galium* grassland, e.g. *Veronica spicata*, *Carex ericetorum*, *Potentilla tabernaemontani*. For these species, the prime need seems to be for an open, calcareous habitat which can be produced under a fair variety of climatic regimes (e.g. Pigott & Walters 1954). With other species, climate seems to have a more precise role in determining the range. *Phleum phleoides*, *Silene otites*, and *Medicago sativa* ssp. *falcata*, for example, are much more strictly confined to this community in the more extreme Continental parts of East Anglia where they flourish even in ranker, ungrazed swards. Exactly what it is about the climate here that limits their distribution is, however, uncertain. Salisbury (1932) suggested that it may have something to do with the need for cold, dry winters to prevent rotting of overwintering parts as well as with a need for hot, dry early summers to allow seed-ripening. Among the non-vascular perennials, the distinctive suite of soil lichens typical of the *Ditrichum-Diploschistes* sub-community is also very characteristic of more Continental regions in Europe (James *et al.* 1977).

The third influence of climate is seen among the more diminutive and short-lived pauciennials of the community. These species, especially typical of the *Koeleria*, *Cladonia* and *Ditrichum-Diploschistes* sub-communities, are well adapted to take advantage of the network of bare patches which the climatic conditions help maintain, but most of them are also specifically geared to the distinctive annual patterns of temperature and rainfall variation associated with the continental climate. Some of these winter annuals, such as *Arabidopsis*

thaliana, *Arenaria serpyllifolia*, *Cardamine hirsuta*, *Erophila verna* and *Veronica arvensis*, are by no means restricted to calcareous habitats in Britain; others, such as *Cerastium semidecandrum*, *Myosotis ramosissima* and *Saxifraga tridactylites*, though perhaps more calcicolous, also occur in other communities than this. Even the nationally rare *Draba muralis* and *Hornungia petraea*, which are strict calcicoles, can be found in other vegetation types. But what these species have in common is a life-cycle which is finely tuned to climatic needs that are met in the more extreme habitats of this community (Ratcliffe 1961). This life-cycle involves often simultaneous germination in the autumn rains with the fairly rapid development of a root system, a period of overwintering as leaf-rosettes which seem not to be damaged by either moderate cold or water shortage, flower-initiation (in some species in winter, in others in spring) favoured by low temperatures, spring or early summer flowering, death of the parent and after-ripening of the seeds in the hot summer sun. Other annuals, more strictly confined to this community or occurring also on bare ground within more calcifugous Breckland swards and in arable fields there (e.g. *Veronica verna*, *Medicago lupulina* ssp. *minima*, *Silene conica*) have not been so closely investigated but it is possible that they, too, show this kind of specific adaptation.

In some kinds of *Festuca-Hieracium-Thymus* grassland it is combinations of such edaphic and climatic conditions that seem to exert the major control on the nature of the vegetation. This is probably true of certain stands of the *Koeleria* sub-community, such as those on exposed natural cliff tops (e.g. Ratcliffe 1961), but it has been most clearly shown for the *Ditrichum-Diploschistes* sub-community, Watt's 'Grassland A', a vegetation type strictly confined to the most shallow, calcareous and base-rich soils over the most exposed sites in Breckland. Although continuous comparisons with heavily-grazed swards of this kind have been complicated by the general reduction in the rabbit population following local extermination and myxomatosis, meticulous monitoring of an enclosure experiment over almost 40 years has demonstrated relatively minor qualitative changes in the floristics and physiognomy of this vegetation, compared with those which ensued on enclosure of the *Cladonia* sub-community, Watt's 'Grassland B' (Watt 1940, 1962, 1971a, 1981a, b). If anything, the early changes (Watt 1962) tended to strengthen the similarity between this vegetation and its Continental counterparts, newcomers being grazing-sensitive species but not those more mesophytic plants typical of ungrazed 'Grassland B'. Over the longer term (Watt 1981a), some of these latter have appeared and there have been some losses among the therophytes, but there is still none of the rank grass-dominance so characteristic of ungrazed 'Grassland B'. Rather, there is a discontinuous and still

very short carpet of vegetation with more, and more extensive, chamaephytes than before but still with *F. ovina* and *K. macrantha* playing a subordinate role and with hemicryptophytes, though more varied and numerous, often very stunted and flowering rarely. Manifestly, the *Ditrichum-Diploschistes* sub-community as originally described was not simply a very heavily grazed form of the *Cladonia* sub-community but was, and remains even in the absence of grazing, a distinctive vegetation in its own right related to impoverished and somewhat unstable soil conditions and an extremely harsh climate. What release from grazing did allow in this sub-community was the clear emergence of phasic quantitative changes in the sward, and especially among the major species of the community, *F. ovina*, *H. pilosella* and *T. praecox/pulegioides*, whose populations seemed to vary in relation to climatic differences from year to year and to competition among themselves (Watt 1962, 1981b).

With some of the other sub-communities, however, it is clear that grazing, and especially grazing by rabbits with the particular kinds of disturbance that this involves, has played a central role, with soil and climate, in maintaining the vegetation. With the demise of the rabbit population in the 1954/5 myxomatosis epidemic, their influence is now much less obvious and stands of the community have declined in number and extent but, in many areas, rabbits are increasing again and it is possible that some stands, though little affected at the present time, still bear the enduring signs of intensive grazing and disturbance in the past. The effect of rabbits can be seen in some stands of the *Koeleria* sub-community which includes vegetation from beyond the most grossly disturbed zone immediately around burrows (e.g. Tansley & Adamson 1925) and from ant-hills which, when they occur within rank grasslands, often suffer heavy preferential grazing (e.g. King 1977a). It is of some importance, too, in the *Fragaria-Erigeron* and *Medicago-Rumex* sub-communities though, here, other forms of disturbance often seem to have played a part in the development of the vegetation (see below). But it is in the *Cladonia* sub-community that the impact of rabbits is (or has been) most obvious. This vegetation type now survives in areas renowned for their very high rabbit populations, in Breckland and at Porton Down, often being associated with sites where the animals were encouraged in artificial warrens. Again, we are indebted primarily to Watt (1940, 1957, 1974) for a detailed understanding of their effects on this sub-community and some clue as to their likely general importance in *Festuca-Hieracium-Thymus* swards. That influence seems to comprise the following elements.

First, rabbits help keep the vegetation open and short by their assiduous grazing and by their burrowing and scuffing which can uproot plants and increase the extent

of bare ground. These are important, too, in maintaining the balance, in swards which remain generally sparse, between perennial grasses which can stand repeated defoliation, chamaephytes which benefit indirectly from the lack of competition for light, therophytes which can take quick advantage of patches of exposed soil and bryophytes and lichens which can spread between. Enclosure of this kind of vegetation (as with exclusion of rabbits from closely-related communities: e.g. Farrow 1917, Tansley 1922, Tansley & Adamson 1925, Hope-Simpson 1941*b*) results in the fairly rapid development of a more extensive and taller, though uneven, sward in which, with the passage of time, there is a shift towards the grasses and away from the chamaephytes, therophytes, bryophytes and lichens (Watt 1957, 1974), a striking contrast to the open and short turf which persists with the enclosure of the *Ditrichum-Diploschistes* sub-community (Watt 1962, 1981*a, b*; see above). Watt's studies have shown just how intricate the quantitative changes involved in this kind of shift can be and how complex are the interactions with variables other than grazing: how the grasses expand into ranker tussocks and coalesce; how chamaephytes and therophytes become increasingly confined to lower patches of herbage or to mole-hills; how some taller annuals may persist longer than the more diminutive; how those perennials which are lost or reduced tend to be smaller species, reproducing largely by sexual means, while survivors can either scramble or produce large rosettes; how some bryophytes rather than others are benefited by the damper, litter-choked vegetation and how the resulting mosaic of species may show fluxes related to their cyclical or uni-directional patterns of reproduction and growth. These latter rhythms have been further illuminated for *Hieracium pilosella* by the studies of Bishop *et al.* (1978; see also Bishop & Davy 1984, Davy & Bishop 1984) who showed how, superimposed upon the changes induced by shading in the ranker surrounding sward, there were alterations in the annual pattern of natality and mortality directly related to the influence of rabbits which removed inflorescences and thus perhaps freed more resources for the growth of stolons produced after floral initiation. Ungrazed populations thus turned over more slowly as well as being subject to greater competition for light.

Intensive defoliation and moderate disturbance by rabbits tend to produce the same results as the typically harsh soil and climatic conditions endured by this vegetation. When swards of the *Cladonia* sub-community have been fertilised with major nutrients (Davy & Bishop 1984), continued grazing offsets the enrichment somewhat such that, though the vegetation grows greener, the expansion of grasses and the demise of chamaephytes, bryophytes and lichens occur more slowly. In the normally already impoverished con-

ditions, rabbit-grazing may strongly accentuate the effects of nutrient and water shortage. Moreover, and here we may recognise a second influence of these animals, because rabbits deposit their re-ingested dung in special latrines, there is no distributed return of faecal nutrients to the sward. Over the long term, the continued shunting of nutrients, perhaps quite considerable amounts of nitrogen and phosphorus (e.g. Watt 1981*a*), out of the system, could be expected to have an effect, contributing to the run-down of fertility that characterises such areas as Breckland.

The third feature of rabbit-grazing is that it is preferential and, in general, this selectivity works in the same direction as the simple defoliation, in that grasses tend to be grazed hard and chamaephytes, therophytes, bryophytes and lichens avoided. Some particular choices and avoidances are well documented (e.g. Tansley 1939, Thompson & Worden 1956, Watt 1957). *Arenaria serpyllifolia*, for example, and many other annuals, as well as some of the coarser weeds of the community such as *Senecio jacobaea* and *Erigeron acer*, are commonly ignored. Among the chamaephytes, the *Thymus* spp. are sometimes nibbled, though generally avoided (Pigott 1955) and *H. pilosella* likewise seems relatively unpalatable (Meylaender *et al.* 1968, Bishop & Davy 1984). *Sedum acre*, too, is avoided. The very low frequencies here of *Helianthemum nummularium* are worth special comment because it is also reckoned to be rabbit-resistant (Tansley 1939): its poor performance in this vegetation may be related to its drought-susceptibility, when it cannot put down deep roots (Proctor 1956), or to its apparently inefficient dispersal (Proctor 1956, King 1977*a*). The abundance of bryophytes and, in the *Cladonia* and *Ditrichum-Diploschistes* sub-communities, of lichens is also certainly attributable in part to the fact that these are usually avoided (Allorge 1921–2, Tansley & Adamson 1925, Hope-Simpson 1941*a*, Wells *et al.* 1976). Such normal preferences may be upset in severe drought when rabbit-grazing becomes more frantic and indiscriminating. Even under normal conditions rabbits may restrict sexual reproduction of generally unpalatable species by eating their flowers, as in *Thymus* spp. (Pigott 1955) or *H. pilosella* (Bishop *et al.* 1978, Bishop & Davy 1984); in the latter species, this may play a key role in controlling the relative importance of clonal or sexual spread.

Only those palatable species which are especially well adapted to the harsh soil and climatic conditions of the habitat can survive this selective, heavy grazing. Hemipterophytes seem to be especially hard hit in this respect and, of all the life-form groups, it is they which increase in diversity and extent upon enclosure, though they have also to be capable of tall or sprawling growth in the increasingly rank sward (Watt 1957, 1974). Some important Mesobromion grasses and dicotyledons may

be absent from or restricted in this community because of their palatability or an inability to survive both heavy grazing and shortages of water and nutrients. As Watt (1974) has shown, which particular species enter on the cessation of grazing depends very much on the nature of the surrounding vegetation, the dispersal mechanisms of the available seed-parents and the presence of agents of dispersal including, it must be said, human visitors monitoring the vegetation changes.

Two further kinds of biotic influence have been of obvious importance in certain kinds of *Festuca-Hieracium-Thymus* grassland. The first is the effect of ploughing and abandonment of shallow rendzinas which has been a common phenomenon at various times in the past as increased cereal prices have encouraged farmers to exploit marginal land on limestones, especially around knolls and scarp tops on the Chalk (e.g. Smith 1980). The general natural infertility of the soils in such situations, poor not only in major nutrients but also in such micro-nutrients as copper, shortage of which seems to be involved in certain cereal diseases, often meant that the fields were quickly abandoned, sometimes even with the failed crop left to rot. It was early noticed (e.g. Hudson 1900, 1910) that such sites often failed to grass over, even with the passage of many years, and subsequent studies (e.g. Cornish 1954, Lloyd 1964, Lloyd & Pigott 1967, Wells *et al.* 1976) have clearly demonstrated the persistence of vegetation which is here largely included in the *Fragaria-Erigeron* sub-community. Once the pre-existing swards in these situations were disrupted by ploughing, there seems to have been a leaching of whatever nitrogen was present (or added with the seed), the exposed soil being too dry and infertile for colonisation by all but the more oligotrophic species, even when other potential invaders were close at hand. This kind of *Fragaria-Erigeron* vegetation has persisted for 25 years (Lloyd 1964), up to 70 years (Cornish 1954) or 100 years (Wells *et al.* 1976) and can provide a valuable habitat for rare arable weeds such as *Iberis amara*, *Ajuga chamaepitys* and *Seseli libanotis*. Similar disturbance may also have been involved in the development of the *Medicago-lupulina* sub-community which, though still weedy, tends to be somewhat grassier and may represent a later stage in colonisation, though we have no documentary evidence to test this view.

Lichens can clearly invade such abandoned ploughland, though their persistence may depend on heavy rabbit-grazing (not always present in the sub-communities dealt with above). At Porton Down, stands of the *Cladonia* sub-community were found by Wells *et al.* (1976) to overlie land which had, in some cases, been ploughed in the preceding century and recent brecks in East Anglia can carry vegetation which approximates to this (Ratcliffe 1977). However, stands are never so rich as those in the more ancient swards of Breckland proper,

though this is not to say that prehistoric shifting cultivation was unimportant there in the development of the impoverished soils and distinctive open vegetation.

The second biotic effect is related to the mound-building activities of ants, notably *Lasius flavus*. Their continued heaping of sorted soils, not necessarily infertile though, on the southern faces of the hills, often hot and dry in summer, and the frequent grazing and disturbance of these hills by rabbits, creates conditions very similar to those encountered in natural expanses of shallow rendzinas in more continental areas. Vegetation of the *Koeleria* sub-community can develop on these ant-hills and apparently persist for many years provided the ants remain in residence (King 1977a, c), but it is subject to its own rather specialised internal patterning and to successional change when the hills are abandoned (King 1977b, c).

Zonation and succession

Zonations between the *Festuca-Hieracium-Thymus* grassland and other vegetation types generally reflect edaphic gradients or seral changes mediated by grazing.

Most frequently, in soil-related sequences, the community represents the most oligotrophic extreme of a range of calcicolous communities, giving way, with varying degrees of abruptness, to more closed and mesophytic swards, over deeper, moister and richer soils. The *Koeleria* sub-community is the usual kind of *Festuca-Hieracium-Thymus* grassland encountered in such zonations and, in moving away from the rocky knolls, cliff tops, fine talus or rock waste on which it typically occurs, it thickens up, generally to some type of *Festuca-Avenula* grassland or, where grazing has been relaxed, to ranker swards dominated by coarse calcicolous grasses. At Porton Down, the *Cladonia* sub-community occurs in comparable mosaics with the *Festuca-Avenula* grassland, picking out patches of the poorest and most chalky and flint-strewn soils (Wells *et al.* 1976). Such zonations can be gradual, the deepening of the soil being reflected in a hazy shift from chamaephytes, therophytes and bryophytes (and lichens in the *Cladonia* sub-community) to grasses and hemicryptophytes. However, where soil impoverishment has been produced by gross disturbance, such as ploughing, vegetation boundaries are characteristically sharp: stands of the *Fragaria-Erigeron* sub-community, for example, can pick out the shape of an arable field long after its abandonment, passing abruptly at its margins to the usually rank swards of adjacent neglected pastures (e.g. Cornish 1954, Lloyd 1964, Lloyd & Pigott 1967). Similarly stark patterns characterise the occurrence of *Festuca-Hieracium-Thymus* grassland (usually the *Koeleria* sub-community) on the continually-disturbed soils of occupied ant-hills (King 1977a, b).

More unusually, though much more famously, the

community represents the most calcicolous extreme of a spectrum of oligotrophic communities, passing, over deeper and more acidic soils, to calcifugous grasslands and heaths. This is the kind of sequence first fully described by Watt (1936, 1940) from Breckland where both the *Ditrichum-Diploschistes* and *Cladonia* sub-communities occur as part of the range of his 'grass-heaths'. The former type of *Festuca-Hieracium-Thymus* grassland is very much confined to the most exposed and inhospitable, flinty rendzinas, being replaced over slightly deeper and less calcareous, though still base-rich, soils by the latter sub-community. This, in turn, gives way, over sandy brown earths, to *Festuca-Agrostis-Rumex* grassland as calcicoles are eclipsed by calcifuges and the grass cover thickens up somewhat but, in the harsh continental climate and with (at the time of Watt's survey) continued heavy rabbit-grazing and mole-disturbance, the general contribution made to the vegetation by therophytes, bryophytes and lichens remains important. As Watt stressed, the actual manifestations of this sequence, and its continuation into very calcifuge vegetation over podzols, are complex and often incomplete at a single site. Moreover, even the most intact of these zonation are now much altered because of the reduction in rabbit-grazing.

However, it is clear that the various kinds of *Festuca-Hieracium-Thymus* grassland respond rather differently to the cessation of grazing. In the more extreme types of sward, such as those of the *Ditrichum-Diploschistes* sub-community, edaphic and climatic conditions are so harsh as to prevent the speedy development of a more intact and mesotrophic vegetation upon enclosure (Watt 1962, 1981a, b). Some stands of the *Koeleria* sub-community, such as those over very rocky cliff tops, are probably similarly uncongenial to the spread of grasses and the appearance of hemicryptophytes. In other cases, as with the *Fragaria-Erigeron* sub-community, artificially enhanced oligotrophy seems to be so severe as to impede the formation of a more grassy sward (Lloyd 1964, Lloyd & Pigott 1967). With these vegetation types, the stabilisation of the soil surface and the accumulation of fertility is likely to be a very slow process (Watt 1981b).

The *Cladonia* sub-community, on the other hand, shows much more pronounced and rapid changes with enclosure, so that the vegetation comes to resemble something akin to a *Festuca-Avenula* sward (Watt 1957, 1962). At Porton, too, Wells *et al.* (1976) suggested that this might be the fate of ungrazed stands of the *Cladonia* sub-community. But such resemblances are likely to be temporary, because the *Festuca-Avenula* grassland is also dependent on grazing for its maintenance and, among herbaceous species, it is perhaps the ranker grasses which are the likelier candidates as eventual dominants after long enclosure or abandonment. Here,

too, though, there may be complexities: *Bromus erectus*, for example, in many ways eminently suited to these more oligotrophic, calcareous soils, seems strikingly slow to invade them, perhaps because of its poor dispersal (Watt 1957, 1962, Lloyd 1964, Lloyd & Pigott 1967). *Avenula pratensis* may likewise be inhibited from spreading for a number of reasons not directly related to the poor nutrient content of the soils (Wells *et al.* 1976). Other possible colonisers, such as *Avenula pubescens* and *Festuca rubra*, though they can gain an initial hold on abandoned ant-hills, may need a considerable accumulation of fertility before they can spread extensively (Wells *et al.* 1976, King 1977a, c).

Even where changes in the herbaceous vegetation are fairly rapid and considerable, evidence suggests that, in some cases, they are likely to be overtaken by the invasion of those woody species which can establish themselves directly in the open and inhospitable conditions. At Lloyd's Pulpit Hill Field site, for example, *Cornus sanguinea* was noticeably common among the *Fragaria-Erigeron* vegetation and he suggested that a number of features gave it an advantage over *Crataegus monogyna*, a very abundant early invader of *Festuca-Avenula* swards: high percentage viability and quick germination of the seed, indeterminate shoot growth and the ability to sucker and spread vegetatively once established (Lloyd 1964, Lloyd & Pigott 1967). *C. sanguinea* also occurred at Porton though, here, *Juniperus communis* ssp. *communis* was an important coloniser of swards of the *Cladonia* sub-community after myxomatosis, forming open scrub (Wells *et al.* 1976). In Breckland, *Pinus sylvestris* is the most prominent woody species, seeding in from the extensive plantations nearby, and even the *Ditrichum-Diploschistes* vegetation would seem to be progressing to open pinewood (Watt 1957, 1962, 1974, 1981a).

Distribution

The community occurs in scattered localities over the Chalk of south-east England with outliers on south-facing slopes on the Yorkshire Wolds Chalk and the Carboniferous Limestone of Derbyshire and the Mendips. Breckland still retains the greatest concentration and extent of this kind of vegetation but, though the *Ditrichum-Diploschistes* sub-community is wholly, and the *Cladonia* sub-community largely, confined there, their cover and composition have altered since the days of the early accounts. The former vegetation type has shrunk and changed less, though its extent in living memory was always very small: it still occurs as patches within a matrix of the latter sub-community over a few hectares of the most exposed ground at Lakenheath Warren, Suffolk. Several hectares of vegetation over flint-strewn soil at Deadman's Grave on the Icklingham Heaths, also in Suffolk, approach it in composition and

physiognomy (Ratcliffe 1977). The *Cladonia* sub-community itself is, for the most part, much more restricted than formerly and surviving stands are often rank and encroached upon by scrub. Even where grazing continues, as at Eriswell Warrens near Lakenheath, cattle are sometimes pastured when the ground can become poached or strewn with fodder in winter (Ratcliffe 1977). Stands of the typically open and more species-rich vegetation of this sub-community remain at Lakenheath and, over the Norfolk border, at Weeting Heath and within the Stanford Practical Training Area where sheep are still pastured. The other locality for the *Cladonia* sub-community, at Porton Down, was not revisited for this survey.

Affinities

In its more extreme forms, the vegetation of the *Festuca-Hieracium-Thymus* grassland can be seen as the Continental counterpart of the *Festuca-Carlina* grassland and its possible relationships to the Xerobromion swards of the European mainland were noted by Watt (1962). With its poor representation of Mesobromion species, it clearly belongs among the more arid grasslands of the Festuco-Brometea and, like the *Festuca-Carlina* grassland, its open swards provide a congenial location in Britain for a number of species which are rare here but which, in Europe, are more common and widespread in dry, calcareous situations. In this community, however, the Oceanic Southern element of the *Festuca-Carlina* grassland is replaced by a more strictly Continental component and this seems to argue for a link with either the *Stipa*-dominated vegetation of the Festucion valesiacae or the grasslands of the Koelerio-Phleion phleoidis (e.g. Ellenberg 1978, Oberdorfer 1978). Certainly,

with its distinctive mixture of calcicolous perennials, therophytes, bryophytes and lichens, the *Festuca-Hieracium-Thymus* grassland represents one of the nearest approaches among British vegetation types to the steppe-grasslands of eastern Europe.

The prominent therophyte element in the community provides floristic links with a variety of other vegetation types in which these species, mostly characteristic of the Sedo-Scleranthetea, are able to exploit gaps in the sward produced by a variety of processes. Here, their prominence reflects edaphic and climatic features, such as the extent of sand-blow and the incidence of summer drought or winter frost-heave, and the activities of rabbits, ants and moles (Watt 1981b). Some calcareous maritime habitats, such as the tops of limestone cliffs and deposits of consolidated shell-sand, are characterised by a similar coincidence of factors and they may carry vegetation which is physiognomically and floristically close to the *Festuca-Hieracium-Thymus* grassland. For example, the *Arenaria serpyllifolia* sub-community of the *Armeria maritima-Cerastium diffusum* ssp. *diffusum* maritime therophyte vegetation, typical of the crumbling tops of limestone sea-cliffs, shares many species with the *Koeleria* sub-community here. Likewise, there is a considerable overlap between this sub-community and the assemblages of smaller annuals found on moderately stable dunes.

With other habitats, it is more a combination of biotic disturbance and calcareous soils which provides a link with the conditions here and, in this case, the floristic transitions involve the more weedy vegetation of the *Fragaria-Erigeron* and *Medicago-Rumex* sub-communities which show overlaps with more ephemeral communities of arable fields on limestone-derived soils.

Floristic table CG7

	a	b
<i>Festuca ovina</i>	V (2–9)	V (4–8)
<i>Hieracium pilosella</i>	V (1–4)	IV (3–8)
<i>Hypnum cupressiforme</i>	IV (1–6)	IV (2–6)
<i>Leontodon hispidus</i>	IV (2–7)	II (2–5)
<i>Thymus praecox/pulegioides</i>	V (1–6)	II (2–5)
<i>Koeleria macrantha</i>	IV (1–7)	V (3–7)
<i>Avenula pratensis</i>	III (1–4)	III (2–6)
<i>Galium verum</i>	III (1–6)	III (2–5)
<i>Plantago lanceolata</i>	III (1–4)	III (1–4)
<i>Sedum acre</i>	II (1–3)	II (3)
<i>Arenaria serpyllifolia</i>	II (1–3)	II (2–3)
<i>Myosotis ramosissima</i>	I (1–2)	I (2–4)
<i>Aphanes arvensis</i>	I (1–4)	I (3)
<i>Erophila verna</i>	I (1–2)	I (2–4)
<i>Veronica arvensis</i>	I (1–2)	I (1–2)
<i>Acinos arvensis</i>	I (1–2)	I (1)
<i>Desmazeria rigida</i>	I (1–2)	I (1)
<i>Carex flacca</i>	II (1–5)	I (4)
<i>Briza media</i>	II (1–6)	I (3–4)
<i>Scabiosa columbaria</i>	II (1–3)	
<i>Plantago media</i>	I (1–4)	I (2–3)
<i>Dicranum scoparium</i>	I (2–6)	III (3–6)
<i>Cerastium fontanum</i>	I (1–3)	III (1–4)
<i>Astragalus danicus</i>		III (2–5)
<i>Luzula campestris</i>		III (2–5)
<i>Trifolium repens</i>	I (1–3)	II (2–6)
<i>Holcus lanatus</i>	I (3)	II (1–4)
<i>Achillea millefolium</i>	I (1–3)	II (2–4)
<i>Rumex acetosella</i>		II (2–4)
<i>Agrostis capillaris</i>		II (1–5)
<i>Anthoxanthum odoratum</i>		II (3–4)

d	e	7
V (1-8)	V (2-8)	V (1-9)
V (1-8)	V (1-7)	V (1-8)
IV (1-8)	III (1-8)	IV (1-8)
V (1-7)	V (2-8)	IV (1-8)
IV (1-6)	IV (1-7)	IV (1-6)
II (1-4)	III (1-4)	III (1-7)
I (1-2)	II (1-4)	II (1-6)
I (1-3)	II (1-4)	II (1-6)
I (1-4)	II (1-4)	II (1-4)
I (1-3)	I (1-3)	I (1-3)
		I (1-3)
		I (1-4)
		I (1-4)
		I (1-4)
		I (1-2)
		I (1-2)
		I (1-2)
I (1-4)	I (1-5)	I (1-5)
I (2-4)		I (1-6)
	I (1-2)	I (1-3)
		I (1-4)
I (1-4)	I (1-3)	I (1-6)
I (1-3)	I (1)	I (1-4)
		I (2-5)
		I (2-5)
I (2-3)	I (1-3)	I (1-6)
I (1-3)	I (1-5)	I (1-5)
	I (1-2)	I (1-4)
		I (2-4)
		I (1-5)
		I (3-4)

Floristic table CG7 (cont.)

	a	b
<i>Cladonia rangiformis</i>		II (1–6)
<i>Cladonia impexa</i>		II (2–6)
<i>Cornicularia aculeata</i>		II (3–4)
<i>Cladonia arbuscula</i>		II (2–8)
<i>Cladonia pyxidata</i>		II (1–3)
<i>Cladonia foliacea</i>		II (3)
<i>Ceratodon purpureus</i>		II (2–4)
<i>Bryum capillare</i>		II (1–4)
<i>Rhytidium rugosum</i>		II (1–6)
<i>Brachythecium albicans</i>		II (3–5)
<i>Erodium cicutarium</i>		II (1–4)
<i>Peltigera canina</i>		II (3–4)
<i>Galium saxatile</i>		I (2–4)
<i>Cladonia fimbriata</i>		I (2–3)
<i>Ptilidium ciliare</i>		I (3–4)
<i>Cladonia gracilis</i>		I (2–4)
<i>Sagina nodosa</i>		I (3)
<i>Teesdalia nudicaulis</i>		I (3–4)
<i>Cladonia tenuis</i>		I (2–5)
<i>Polytrichum juniperinum</i>		I (2–4)
<i>Cladonia squamosa</i>		I (2–3)
<i>Barbula unguiculata</i>		I (2–3)
<i>Sedum album</i>		I (3)
<i>Carex ericetorum</i>		I (2–3)
<i>Fragaria vesca</i>	I (1–4)	I (1–3)
<i>Erigeron acer</i>	I (1–3)	I (1–3)
<i>Crepis capillaris</i>	II (1–3)	I (1–2)
<i>Daucus carota</i>	I (1–3)	I (1–2)
<i>Centaurium erythraea</i>		I (1–3)
<i>Agrostis stolonifera</i>	I (1–2)	I (4)
<i>Campylidium chrysophyllum</i>	I (1–2)	I (1–3)
<i>Sambucus nigra</i> sapling		

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

<i>Medicago lupulina</i>	II (1–6)	I (2)	II (1–6)	IV (1–7)	II (1–7)
<i>Rumex acetosa</i>	I (1–3)	I (2–3)	I (1)	IV (1–3)	II (1–3)
<i>Phleum pratense bertolonii</i>	I (1–3)		I (1–3)	III (1–3)	I (1–3)
<i>Leontodon autumnalis</i>	I (1–3)		I (1–3)	III (1–3)	I (1–3)
<i>Euphrasia officinalis</i> agg.	I (1–4)		I (1–2)	III (1–5)	I (1–5)
<i>Ranunculus bulbosus</i>	I (1–4)	I (3)	I (1)	II (1–2)	I (1–4)
<i>Viola hirta</i>	I (1–5)		I (1–3)	II (1–5)	I (1–5)
<i>Avenula pubescens</i>	I (1–4)		I (2–3)	II (1–4)	I (1–4)
<i>Lotus corniculatus</i>	IV (2–8)	III (3–4)	II (1–5)	IV (1–7)	III (1–8)
<i>Taraxacum officinale</i> agg.	III (1–3)	III (1–4)	III (1–3)	IV (1–3)	III (1–4)
<i>Senecio jacobaea</i>	III (1–3)	III (1–4)	III (1–3)	III (1–3)	III (1–4)
<i>Pseudoscleropodium purum</i>	III (1–8)	III (2–5)	I (1–5)	IV (1–7)	III (1–8)
<i>Prunella vulgaris</i>	III (1–4)	I (2)	IV (1–4)	IV (1–3)	III (1–4)
<i>Cirsium acaule</i>	III (1–6)	I (1–2)	IV (1–6)	IV (1–4)	III (1–6)
<i>Linum catharticum</i>	III (1–4)	I (3)	III (1–3)	III (1–3)	III (1–4)
<i>Homalothecium lutescens</i>	III (1–6)	II (1–5)	III (1–6)	III (1–4)	III (1–6)
<i>Sanguisorba minor</i>	III (2–7)		I (1–8)	IV (1–7)	II (1–8)
<i>Campanula rotundifolia</i>	III (1–3)	I (2–3)	II (1–4)	II (1–2)	II (1–4)
<i>Gentianella amarella</i>	II (1–3)	II (1–3)	II (1–3)	III (1–4)	II (1–4)
<i>Fissidens cristatus</i>	II (1–3)	II (1–3)	II (1–3)	I (1–2)	II (1–3)
<i>Trisetum flavescens</i>	II (1–3)	II (1–3)	III (1–5)	III (1–4)	II (1–5)
<i>Asperula cynanchica</i>	II (1–4)	II (1–3)	I (1–3)	II (1–4)	II (1–4)
<i>Potentilla reptans</i>	II (1–3)	I (1–3)	I (1–3)	II (1–3)	I (1–3)
<i>Helianthemum nummularium</i>	II (1–6)	I (1)	I (2–5)	I (1–4)	I (1–6)
<i>Arrhenatherum elatius</i>	I (1–3)	I (3)	I (2)	I (1–2)	I (1–3)
<i>Dactylis glomerata</i>	I (1–4)	I (3)	I (1–3)	I (1–3)	I (1–4)
<i>Polygala vulgaris</i>	I (1)	I (3)	I (1–2)	I (1–2)	I (1–3)
<i>Anthyllis vulneraria</i>	I (1–5)	I (3–4)	I (2–4)	I (1–4)	I (1–5)
<i>Cirsium palustre</i>	I (1)	I (3)	I (1)	I (1)	I (1–3)
<i>Pastinaca sativa</i>	I (2–3)	I (1)	I (1–3)	I (1–2)	I (1–3)
<i>Weissia</i> cf. <i>microstoma</i>	I (1–3)		II (1–3)	I (1)	I (1–3)
<i>Festuca rubra</i>	I (3–8)		I (2–7)	I (2–8)	I (2–8)
<i>Coeloglossum viride</i>	I (1–3)		I (1)	I (1–3)	I (1–3)
<i>Blackstonia perfoliata</i>	I (1–3)		I (1–3)	I (1)	I (1–3)
<i>Ctenidium molluscum</i>	I (1–3)		I (1–3)	I (1–2)	I (1–3)
<i>Arctium minus</i> agg.	I (1–3)		I (1–3)	I (1)	I (1–3)

Floristic table CG7 (cont.)

	a	b
<i>Bellis perennis</i>	I (1–4)	
<i>Rhytiadelphus triquetrus</i>	I (1–2)	
<i>Poa pratensis</i>	I (1)	
<i>Vicia cracca</i>	I (1–3)	
<i>Hypericum perforatum</i>	I (1)	
<i>Centaurea scabiosa</i>	I (2–4)	I (3)
<i>Carlina vulgaris</i>	I (1–2)	I (1–4)
<i>Cirsium vulgare</i>	I (1–3)	I (3)
<i>Carex caryophyllea</i>	I (2–4)	I (2–5)
<i>Inula conyza</i>	I (1–3)	
<i>Knautia arvensis</i>		
<i>Clinopodium vulgare</i>		
<i>Agrimonia eupatoria</i>		
<i>Juniperus communis communis</i>		
Number of samples	81	30
Number of species/sample	19 (6–27)	21 (9–31)

a *Koeleria macrantha* sub-community

b *Cladonia* spp. sub-community

d *Fragaria vesca*-*Erigeron acer* sub-community

e *Medicago lupulina*-*Rumex acetosa* sub-community

7 *Festuca ovina*-*Hieracium pilosella*-*Thymus praecox/pulegioides* grassland (total)

d	e	7
I (1–3)	I (1)	I (1–4)
I (1–2)	I (1)	I (1–2)
I (1)	I (1)	I (1)
I (1)	I (1–3)	I (1–3)
I (2)	I (1–3)	I (1–3)
	I (2)	I (2–4)
I (1–3)		I (1–4)
I (1)		I (1–3)
I (1)		I (1–5)
I (1–3)		I (1–3)
I (1)	I (1)	I (1)
I (1–3)	I (1–4)	I (1–4)
I (1)	I (1)	I (1)
I (1)	I (2)	I (1–2)
79	60	260
18 (5–30)	22 (6–31)	19 (5–31)

Floristic table CG7c

<i>Festuca ovina</i>	3 (4–6)
<i>Hieracium pilosella</i>	3 (3–4)
<i>Thymus praecox</i> / <i>pulegioides</i>	3 (4–5)
<i>Hypnum cupressiforme</i>	3 (2–4)
<i>Centaureum erythraea</i>	3 (3–4)
<i>Linum catharticum</i>	3 (3)
<i>Carlina vulgaris</i>	3 (1–3)
<i>Cladonia foliacea</i>	3 (2–5)
<i>Cornicularia aculeata</i>	3 (2–4)
<i>Peltigera canina</i>	3 (2–3)
<i>Sagina nodosa</i>	3 (2–4)
<i>Cladonia papillaria</i>	3 (2–4)
<i>Diploschistes scruposus</i>	2 (3–4)
<i>Ditrichum flexicaule</i>	2 (4)
<i>Squamaria lentigera</i>	2 (3–4)
<i>Cladonia impexa</i>	2 (3–5)
<i>Cladonia rangiformis</i>	2 (1–4)
<i>Encalypta vulgaris</i>	2 (3–5)
<i>Campylidium chrysophyllum</i>	2 (2–4)
<i>Astragalus danicus</i>	2 (1–4)
<i>Avenula pratensis</i>	2 (3)
<i>Leontodon hispidus</i>	1 (4)
<i>Lotus corniculatus</i>	1 (3)
<i>Cladonia pyxidata</i>	1 (2)
<i>Rhytidium rugosum</i>	1 (2)
<i>Bryum capillare</i>	1 (3)
<i>Cladonia squamosa</i>	1 (2)
<i>Carex ericetorum</i>	1 (3)
<i>Buellia epigaea</i>	1 (3)
<i>Collema tenax</i>	1 (1)
<i>Botrychium lunaria</i>	1 (1)
<i>Barbula unguiculata</i>	1 (2)
<i>Koeleria macrantha</i>	1 (1)
<i>Taraxacum officinale</i> agg.	1 (2)
<i>Senecio jacobaea</i>	1 (3)
<i>Plantago lanceolata</i>	1 (3)
<i>Cerastium fontanum</i>	1 (3)
Number of samples	3
Number of species/sample	28 (21–31)



