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Festuca ovina-Agrostis capillaris-Rumex acetosella grassland

Synonymy

Graminetum arenosum Tansley 1911 p.p.; Grass heath association Tansley 1911, Farrow 1915; Festuco-Agrostidetum Watt 1936 p.p.; Grass-heath Tansley 1939 p.p.; Breckland Grasslands D-G Watt 1940; Aira praecox-Teesdalia nudicaulis vegetation Jarvis 1974.

Constant species

Agrostis capillaris, Festuca ovina, Rumex acetosella.

Rare species

Astragalus danicus, Crassula tillaea, Dianthus deltoides, Lychnis viscaria, Scleranthus perennis, Silene conica, S. otites, Thymus serpyllum ssp. serpyllum, Veronica spicata.

Physiognomy

The Festuca ovina-Agrostis capillaris-Rumex acetosella grassland is a very diverse but highly distinctive vegetation type, with an open sward of small tussocky grasses, among which there can be an abundance of dicotyledons, many of them diminutive ephemerals, and sometimes an extensive cover of lichens and/or mosses. Of the grasses, Festuca ovina (only very locally replaced by F. rubra) and Agrostis capillaris are the most frequently encountered and abundant overall, though their total cover and proportions in individual stands are very variable. A. capillaris is the more sporadic and it certainly seems less universally prominent now than in the days of long-continued and heavy grazing by rabbits, an influence of very great importance when the most renowned stands of the community were first described from Breckland (Farrow 1915, Watt 1940, 1960a). A. stolonifera and A. canina ssp. montana have also been recorded less often than seems to have been the case in some areas prior to myxomatosis: then they could be common and sometimes abundant, whereas now they are usually no more than occasional.

Other perennial grasses are generally of limited importance in the community. *Koeleria macrantha* is the most widely distributed overall, though it is never more

than moderately frequent and is always of low cover, its relative scarcity here contrasting with its common occurrence in the Festuca-Hieracium-Thymus grassland, the community which, in this scheme, includes the more calcicolous of the swards grouped together among the Breckland 'grass-heaths' of the classic accounts (Tansley 1911, Farrow 1915, Watt 1940). In other stands included here, where the Festuca-Agrostis-Rumex grassland extends a little way on to less parched soils, Anthoxanthum odoratum can be found, together with occasional *Holcus lanatus*, though neither of these plays the important role that they assume among Nardo-Galion swards in north-western Britain. Deschampsia flexuosa is likewise of restricted occurrence: it has become locally abundant even among some of the drier Breckland stands following myxomatosis (Ratcliffe 1977), but it only attains any frequency here where the rainfall is higher, as in the western Weald and towards the upland fringes, where vegetation transitional to the Deschampsia grassland can be found. Beyond the Weald, too, where the Festuca-Agrostis-Rumex grassland becomes much more local in the moist and equable climate of south-west England, Agrostis curtisii is sometimes seen in close association with stands of the community, but its absence from this vegetation itself provides a clear floristic boundary with more open patches of the Agrostis grassland.

The amount of ground between the grass tussocks, which rarely attain much more than 10 cm in height, is sometimes very extensive, particularly where parching, erosion or continued grazing hold their growth severely in check or cause die-back; and, even in swards that have grown a little more rank, where *F. ovina* is now the usual dominant, there is a pattern of death and decay among the tussocks that exposes a patchwork of bare and litterlined areas (Watt 1971a). Over this ground, a wide variety of associates can gain a hold, coming and going according to their own growth pattern and phenology. Among these, perennial vascular plants are usually in a minority, although a small number are distinctive, most notably *Rumex acetosella* agg., sometimes recorded as

R. tenuifolius (e.g. Watt 1960a). This is the only constant of the community apart from F. ovina and A. capillaris and, although it can sometimes be found among the Festuca-Hieracium-Thymus swards, it is much more diagnostic of this community and its small tufts of shoots, produced adventitiously from long horizontal roots, can be very numerous. Then, there is quite often some Hieracium pilosella, not so consistent an associate here as in the Festuca-Hieracium-Thymus grassland, but still sometimes prominent, on occasion even dominating among the grasses (e.g. Bishop et al. 1978) and adding a welcome touch of colour in mid-summer, by which time the vegetation often looks very shrivelled and brown. Stonecrops can also provide a bright splash at this time, though they are rather patchy in their occurrence. Sedum acre, for example, is more sporadic than in the Festuca-Hieracium-Thymus grassland, although it does occur in abundance on some of the more recently reverted arable land that can be included here, as around the Stanford Practical Training Area (Ratcliffe 1977), and the naturalised S. album appears to be spreading along track-side stands of the community in various parts of East Anglia. And, where the Festuca-Agrostis-Rumex grassland extends into dry, rocky situations at scattered localities through south-west Britain, the Oceanic West European S. anglicum can be found, occasionally with the Oceanic Southern Umbilicus rupestris, the two of them giving a rather different floristic stamp to the vegetation than is characteristic through the heart of its range. The other prominent chamaephytes of the Festuca-Hieracium-Thymus grassland, Thymus praecox and T. pulegioides are very scarce in this community, although around Breckland the Festuca-Agrostis-Rumex grassland provides the typical British locus for their rare relative, T. serpyllum ssp. serpyllum. Although recently refound on the Chalk in Cambridgeshire (Perring & Farrell 1977), this is generally not a plant of limestone soils with us (Pigott 1955).

Among hemicryptophytes, Plantago lanceolata is the most common overall, and its rosettes can be quite numerous, particularly along trackways and in closelygrazed stands, where P. media and P. coronopus are also occasionally found, this community providing an important inland locus for the latter species through south-east England. Taraxacum officinale agg., often identifiable as T. laevigatum, also occurs occasionally in most kinds of Festuca-Agrostis-Rumex grassland, with Hypochoeris radicata diagnostic of one particular subcommunity. Then, Lotus corniculatus, Galium verum and G. saxatile are quite frequent through some of the swards included here, although it should be noted that the last seems to be very much less common in this community now than when the vegetation was heavily rabbit-grazed.

Coarse weedy species sometimes make a prominent

show, too, rendered conspicuous by virtue of their unpalatability. Senecio jacobaea is the most frequent of these, but there can also be patches of Epilobium angustifolium and, around rabbit burrows, Urtica dioica. Small prostrate or decumbent herbs also occur occasionally as patches among the turf: Cerastium fontanum, Potentilla reptans, P. argentea, Glechoma hederacea and Veronica chamaedrys, with the more short-lived Spergularia rubra, Stellaria media, Filaginella uliginosa and Sagina apetala. Bilderdykia convolvulus can also be locally abundant, scrambling over the ground.

More easily missed when sampling is undertaken in summer are diminutive ephemerals, many of which behave as winter annuals, beginning growth in autumn when their rosettes can be found on the open ground among the grasses that have been freshened up in the late rains, but shrivelling after flowering in the following spring. Some annual grasses, notably Aira praecox and Poa annua, with Bromus hordeaceus ssp. hordeaceus much less common, make a contribution among this group, with Teesdalia nudicaulis, Aphanes arvensis, Erodium cicutarium, Erophila verna, Myosotis ramosissima and Veronica arvensis the most frequent among the dicotyledons, often occurring together and, with more local enrichment, in one particular sub-community. The rare Continental annual Silene conica occurs in this vegetation in East Anglia too, and both there and in the scattered stands around Poole Harbour, the Oceanic Southern Crassula tillaea is occasionally seen, characteristically marking out trampled areas where compaction impedes the draining away of rainwater (Watt 1971b, Crompton & Sheail 1975). Other Continental rarities occurring in the Festuca-Agrostis-Rumex grassland are the perennials Scleranthus perennis and Veronica spicata, for both of which this kind of open vegetation provides an important locus in Breckland (Pigott & Walters 1954), and Silene otites, a grazing-sensitive plant excluded from many East Anglian stands in the days of heavy rabbit-infestation, but increasing somewhat since myxomatosis (Watt 1971b). As with the Festuca-Hieracium-Thymus grassland, this community also quite commonly has some of the Continental Northern Astragalus danicus in East Anglia and, on the rocks of Craig Breidden in Powys, this vegetation and adjacent open heath have Lychnis viscaria, another Continental Northern plant but one much rarer and more disjunct in its distribution (Jarvis & Pigott 1973, Jarvis 1974).

A different kind of variety is provided by the scattered occurrence in the Festuca-Agrostis-Rumex grassland of sub-shrubs usually kept in check by grazing but now often spreading to form heathy mosaics with more open turf. Calluna vulgaris itself can be quite frequent in the community in small amounts, with Ulex minor appearing in the Weald and U. gallii beyond Poole Harbour. U.

europaeus also often spreads where stands have been disturbed and somewhat less impoverished soils may have some Rubus fruticosus agg. too. Infestation of surrounding soils by Pteridium aquilinum is also very common and scattered fronds are sometimes found in the community. Then, where this kind of grassland has developed over loose sand, erosion of the turf may precipitate a blow-out with Carex arenaria spreading on to the exposed material and invading the surrounding grassland, although this kind of pattern is now seen at only a very few inland localities.

The other important element in many of these swards is the cryptogams. In young stands, or in open areas exposed in established grasslands, it is small acrocarpous mosses like *Polytrichum piliferum* with, more occasionally, *P. juniperinum* and *Ceratodon purpureus*, that are important, often becoming locally abundant as colonisers and persisting patchily as the grasses get a hold. Later, larger species such as *Dicranum scoparium* and *Brachythecium albicans* can spread extensively, being better able to cope with the extensive deposition of wind-blown material, and there can also be occasional *Hypnum cupressiforme s.l.*, *Pseudoscleropodium purum* and *Rhytidiadelphus squarrosus*.

Then, in some stands, lichens are very prominent. Species such as *Cornicularia aculeata* and *Cladonia arbuscula* become established early on in colonisation and can remain very frequent and extensive in more closed swards, often with a variety of other species like *C. tenuis*, *C. impexa*, *C. foliacea* and *C. uncialis*. *Peltigera canina* also occurs occasionally.

Sub-communities

Cornicularia aculeata-Cladonia arbuscula sub-community. F. ovina tends to be very much the most common of the grasses here, with A. capillaris and K. macrantha making just an occasional contribution. And, though some stands have quite an extensive cover of their tussocks, the usual picture is of an open sward in which other vascular plants play but a very small part. R. acetosella is frequent but otherwise there is just a very occasional plant of Hieracium pilosella, Senecio jacobaea and Galium saxatile.

Mosses and lichens, on the other hand, are often varied and together they quite commonly make up the bulk of the cover. Recently-colonised ground often has patches of Polytrichum piliferum, P. juniperinum and Ceratodon purpureus with Cornicularia aculeata and Cladonia arbuscula, but Dicranum scoparium later becomes frequent with Cladonia impexa, C. tenuis, C. foliacea and C. uncialis very common, C. furcata, C. squamosa, C. gracilis, C. fimbriata and C. pyxidata occasional. Hypnum cupressiforme s.l., Pohlia nutans,

Ptilidium ciliare and the introduced moss Campylopus introflexus can also be seen in some stands.

Typical sub-community. Small acrocarps and lichens retain occasional representation in this sub-community but the cover of vascular plants is generally more extensive and somewhat more diverse than above. Both F. ovina and A. capillaris are very common, and each can be quite abundant, with Koeleria macrantha occasional, Anthoxanthum odoratum, Holcus lanatus and Deschampsia flexuosa scarce but sometimes showing local prominence. Aira praecox and Poa annua can also be found quite often and annual dicotyledons such as Teesdalia nudicaulis, Erodium cicutarium, Aphanes arvensis, Myosotis ramosissima and Ornithopus perpusillus also occur, but with nothing like the coincident frequency characteristic of the next sub-community. More typically, it is perennials such as Rumex acetosela, more occasionally Plantago lanceolata, Hieracium pilosella, Taraxacum officinale agg., Hypochoeris radicata, Senecio jacobaea, Cerastium fontanum and Achillea millefolium, that are the commonest associated plants. and even these are usually of low cover. Many stands have a rather coarse weedy look, while in others a little Calluna, Pteridium or Carex arenaria can give a distinctive appearance. In the data available, it is in this poorer kind of sward that Silene conica, S. otites and Scleranthus perennis have been recorded and some pathway stands have a local abundance of Crassula tillaea.

Apart from the acrocarpous mosses noted above, *Brachythecium albicans* is common here and sometimes quite extensive.

Erodium cicutarium-Teesdalia nudicaulis sub-community. This is the richest and most striking kind of Festuca-Agrostis-Rumex grassland in which there is generally a rather open cover of F. ovina, with somewhat less frequent A. capillaris and occasional Koeleria macrantha, Agrostis stolonifera and Holcus lanatus. Rumex acetosella, Senecio jacobaea, Hieracium pilosella, Cerastium fontanum and Plantago lanceolata are all very common, with P. coronopus, P. media, Cerastium arvense, Galium verum and Achillea millefolium occasional, but the sward is rarely rank and indeed often very short with just scattered individuals of these plants.

More distinctive here is the ephemeral flora among which Aira praecox, Erodium cicutarium, Teesdalia nudicaulis, Aphanes arvensis, Myosotis ramosissima, Erophila verna, Veronica arvensis, Trifolium dubium, Ornithopus perpusillus, Geranium molle and Logfia minima can all be found frequently and often in considerable abundance over the more open ground. Less commonly Viola tricolor ssp. curtisii, Veronica agrestis, V. polita, Filaginella uliginosa and Arenaria serpyllifolia occur, though

by summer it often becomes difficult to identify any of these plants as their remains shrivel up. By this time, the vegetation can look rather lifeless, although in June the flowers of Astragalus danicus add a touch of purple to many stands, with Thymus serpyllum ssp. serpyllum following on in its localities here in July and August, and Sedum acre and S. album providing patches of yellow and white through the summer.

As in the Typical sub-community, the cryptogam flora is usually somewhat restricted in variety and cover here although some stands preserve the pioneer acrocarp flora and others have a reasonably rich mixture of lichens. *Brachythecium albicans* is again the commonest moss, with occasional *Hypnum cupressiforme s.l.*, *Pseudoscleropodium purum* and *Dicranum scoparium*.

Anthoxanthum odoratum-Lotus corniculatus community. The cover of grasses in this sub-community is rather more varied, more extensive and a little ranker than in other kinds of Festuca-Agrostis-Rumex grassland, though it is never luxuriant and usually still somewhat open. In addition to F. ovina and A. capillaris which are both constant, Anthoxanthum is very common, Holcus lanatus less frequent though still preferential and Koeleria macrantha occasional. And among these are some rather distinctive dicotyledons, Lotus corniculatus, Galium verum, Achillea millefolium, Campanula rotundifolia and Plantago lanceolata, which can give the vegetation a rather mesophytic look. Also interesting is the occasional presence of oak seedlings in the sward.

However, Rumex acetosella, Hieracium pilosella and Senecio jacobaea all remain very common and there are sparse records in open areas of the turf for many of the ephemerals of the Erodium-Teesdalia sub-community. Apart from occasional Brachythecium albicans, Dicranum scoparium, Hypnum cupressiforme s.l. and Pseudoscleropodium purum, mosses are few, although their cover can be quite extensive. Lichens occur only very rarely and hardly ever show any abundance.

Galium saxatile-Potentilla erecta sub-community. In this sub-community, F. ovina and A. capillaris are often joined by small amounts of Deschampsia flexuosa and occasional Anthoxanthum, while K. macrantha is quite absent. Among the dicotyledons, Galium saxatile and Potentilla erecta are both very common here with occasional Hieracium pilosella, Senecio jacobaea, Lotus corniculatus and Cerastium fontanum. Although R. acetosella remains very frequent, the characteristic small ephemeral herbs of the community are very sparse indeed among the quite extensive cover of perennials. Cryptogams, too, play little part in the flora of this kind of Festuca-Agrostis-Rumex grassland. Small plants of

Calluna are sometimes to be seen and it is here that *Ulex* spp. occur most often as occasional scattered bushes.

Hypochoeris radicata sub-community: Aira praecox-Teesdalia nudicaulis vegetation Jarvis 1974. F. ovina is partly replaced in this sub-community by F. rubra and, with A. capillaris, these account for the bulk of the perennial grass cover. Generally, though, this is very open and, in the gaps between the tussocks, annual grasses such as Aira praecox, Poa annua, Bromus hordeaceus ssp. hordeaceus and B. mollis can be quite numerous. Among the dicotyledons, R. acetosella is less common than usual and H. pilosella and Senecio jacobaea are very scarce but rosette hemicryptophytes are very frequent with Hypochoeris radicata strongly preferential, Plantago lanceolata common and P. coronopus and Leontodon taraxacoides occasional. Ephemerals are not very numerous but Teesdalia occurs in some stands, Centaurium erythraea is weakly preferential and there are sparse records for a variety of other winter annuals. Other peculiarities include the occasional occurrence of Sedum anglicum and Umbilicus rupestris and, on Craig Breidden in Shrophsire, this kind of vegetation has the rarities Lychnis viscaria and Veronica spicata, as well as frequent Hieracium peleteranum and occasional Helianthum nummularium and Thymus praecox.

Polytrichum piliferum, P. juniperinum, Ceratodon purpureus and Hypnum cupressiforme s.l. all occur quite commonly and with locally high cover, but lichens are very scarce.

Habitat

The Festuca-Agrostis-Rumex grassland is characteristic of base-poor, oligotrophic and summer-parched soils in the warm and dry lowlands of southern Britain, with grazing and disturbance often very important contributory factors in maintaining the typical aspect of the vegetation. It is a community of open habitats, still most strikingly seen among the swards of Breckland, where the continental climate and a distinctive history of land use give it a special character, but locally congenial conditions extend its range into scattered localities far to the oceanic south-west and around the upland fringes. However, the decline of heath-grazing by stock and the demise of rabbits has led to the loss of many stands, such that this vegetation now often survives as fragments among sub-shrub vegetation, on pathways, along the edges of arable fields and around rock outcrops, with some artificial habitats providing new opportunities for establishment.

The Festuca-Agrostis-Rumex grassland is the most widespread calcifuge sward over southern Britain, being found throughout those parts of the country with less than 1000 mm rainfall annually (Climatological Atlas

1952) and under 140 wet days yr⁻¹ (Ratcliffe 1968) and with a mean annual maximum temperature above 26 °C (Conolly & Dahl 1970), climatic features which help give this vegetation a rather different character from its counterpart on permeable acidic soils in the cool and wet sub-montane zone of the north and west of the country, the Festuca-Agrostis-Galium grassland. The broad geographical division between the two vegetation types, and the floristic and physiognomic contrasts they show, reflect the influence which the climate has on the soil moisture regime and surface humidity. The range of the Festuca-Agrostis-Rumex grassland coincides closely with those parts of Britain where the warm and dry climate results in a marked potential water deficit (Climatological Atlas 1952), the impact of which is especially severe on the more sharply draining profiles of the region, such as are colonised by this community. In comparison with the Festuca-Agrostis-Galium grassland, then, Festuca rubra, Anthoxanthum odoratum and Potentilla erecta, which are constant through many north-western swards, have a restricted role here, and such plants as Viola riviniana, Carex pilulifera, Hylocomium splendens and Pleurozium schreberi, which are among their characteristic associates there, are hardly ever found in the community.

Water shortage tends to be especially severe in spring and early summer. Over much of the region, the bulk of such rain as there is falls in the second half of the year and, more particularly, between late summer and early autumn (Gregory 1957, Chandler & Gregory 1976) so that, as air temperatures rise, sometimes quite late, but fairly quickly, to relatively high levels, and humidity drops with the ensuing sunny and fairly cloudless skies of summer, the possibility of parching can become severe (Smith 1976, Chandler & Gregory 1976). Even for those perennials able to tolerate the generally dry conditions, therefore, shortage of water during much of the warmer part of the year can markedly restrict growth, acting either directly or by its influence on the availability of nutrients. This is one of the reasons why the grass cover in this vegetation is characteristically open and tussocky, in marked contrast to the often plush swards of the Festuca-Agrostis-Galium grassland, and why, by summer, the herbage often looks shrivelled and brown.

The poor competitive ability of the grasses allows for a bigger contribution here than among the north-western swards from low-growing light-demanding chamaephytes like *Hieracium pilosella* (Bishop et al. 1978) and the *Sedum* spp., these also well adapted to a xerophytic existence, and from *Rumex acetosella*, which behaves rather like a geophyte in its ability to spring up from underground organs in well-lit gaps. And the community is also one of those vegetation types which offers a locus for rarities such as *Thymus serpyllum* ssp. serpyllum (Pigott 1955), Scleranthus perennis and Vero-

nica spicata (Pigott & Walters 1954) which generally rely on the maintenance of open conditions for their survival.

More widely, the patchwork of bare spaces, periodically renewed by the death of the perennials in old age or because of exceptional drought (Watt 1971b, Bishop et al. 1978, Bishop & Davy 1984), offers ample opportunity for colonisation by more ephemeral species. Some of these, like Senecio jacobaea, are coarse weedy plants, biennial or sometimes longer-lived. But the most distinctive group comprises the diminutive annuals, many of which are specifically adapted to capitalise on the relatively short period very late in the growing season, when the autumn rains moisten the soil surface, but before there is a critical fall in air temperature (Ratcliffe 1961, Newman 1964). For these plants, germination is often of the simultaneous type, and the establishment of a root system quite rapid, with the plants over-wintering as leaf rosettes. In some cases, flower initiation is favoured by the low temperatures of winter and spring, and after-ripening facilitated by the hot summer sun. Among these plants, relatively few, Teesdalia and the rare Silene otites being the notable exceptions, are strictly Continental in their European range. Some such as Aira praecox, Aphanes arvensis, Erophila verna, Veronica arvensis and Geranium molle occur widely through the British lowlands; others are essentially southern lowland plants, extending beyond the range of this community largely in drier coastal habitats, for example, Erodium cicutarium, Myosotis ramosissima, Ornithopus perpusillus, Logfia minima and Cerastium arvense. But, for all of these, the Festuca-Agrostis-Rumex grassland provides a major locus within its range, so that the vegetation often looks more like a Thero-Airion community than a Nardo-Galion grassland.

Within its characteristic climatic zone, the distribution of the Festuca-Agrostis-Rumex grassland is strictly limited by the occurrence of acidic, free-draining soils, which are of but local occurrence through much of the southern lowlands, and the extremely impoverished nature of these soils accentuates the influence of water shortage on the general floristics and physiognomy of the sward (Watt 1936, 1940, 1971a). Pre-eminent among parent materials giving rise to such soils through this part of Britain are various sands and fine gravels, and arenaceous sedimentaries. In the heart of its range, in Breckland, the profiles are of complex make-up and provenance, but the Festuca-Agrostis-Rumex grassland typically occupies the more base-poor of the range of soils derived from mixtures of boulder clay and sand, variously disturbed by periglacial solifluction and overlain by aeolian deposits. These are now classified as Worlington argillic brown sands and, more frequently, Redlodge humo-ferric podzols, though such soils are often found in quite complex mosaics, sometimes with less decalcified profiles (Watt 1940, Hodge & Seale 1966, Corbett 1973, Hodge et al. 1984). To the north, on the Norfolk Commons near The Wash, typical brown sands of the Newport Series developed from glacial sands and Greensand can carry the community, with very similar soils over coastal dune sands near Cromer and Sheringham and on Pliocene and Pleistocene Crag through the Suffolk Sandlings (Soil Survey 1983). Further afield, Newport soils also occur on the cover sands of the Scunthorpe Commons, and locally over more pervious Triassic rocks and overlying coarse-grained superficials right through the Midland Plain. Then, to the south, the Festuca-Agrostis-Rumex grassland is found on Frilford argillic brown sands and Shirrell Heath humo-ferric podzols over the arenaceous strata of the Lower Greensand running around The Weald, particularly at its western end, and more locally, over the sands of the Hastings Beds in the High Weald.

With the shift westwards into a zone of more oceanic climate, and up around the upland fringes, the community becomes increasingly local, being dependent on the occurrence of often fragmentary sandy rankers and podzols kept in a summer-parched condition by sharp drainage and strong insolation over south-facing rocky slopes. This is the characteristic habitat of the Festuca-Agrostis-Rumex grassland on the Scillies, around the South-West Peninsula and at scattered localities up the Welsh coast, where granites, other igneous rocks and Devonian Old Red Sandstone provide suitable soils. Further inland, along the Welsh Marches, the community occurs in topographically very similar situations over Pre-Cambrian, Cambrian and Ordovician rocks which make up the sharply-defined ridges of the Malvern Hills, Wenlock Edge, The Wrekin, Long Mynd and The Stiperstones, with some of the dolerites on Titterstone Clee and Craig Breidden providing rather unusual basepoor, but quite calcium-rich, soils (Jarvis & Pigott 1973, Jarvis 1974, Sinker et al. 1985). Far to the north, towards the geographical limit of the community, compacted andesite gravels comprise another peculiar substrate along some of the rivers draining from the Cheviots through the Northumbrian lowlands, while down through Durham and around the southern Pennines, some of the more low-lying Carboniferous gritstone edges support stands of the community. Finally, throughout its range, a variety of man-made raw soils provide sharply-drained, acid substrates over such varied materials as compacted quarry soil, cinders and disintegrating airfield runways.

In more extreme situations, it is possible that harsh climatic and edaphic conditions are largely responsible for maintaining the characteristic composition and structure of the *Festuca-Agrostis-Rumex* grassland but, in many stands, grazing, with its attendant trampling and surface disturbance, is, or has been, a third general

influence of great consequence. Prior to the 1954/5 myxomatosis epidemic, rabbits were a very noticeable feature over larger tracts of this vegetation, especially in areas like Breckland, where many of the stands were associated with artificial warrens, some dating back to late medieval times (Tidmarsh 1939, Crompton & Sheail 1975). But sheep have also very often been pastured on poor-quality grazings supported by impoverished acid soils in southern Britain, sometimes in vast numbers, and in the long term have probably played a more crucial role, from the Neolithic period on, in maintaining the kind of open pastoral landscape of which this community is such a distinctive element (Yates 1972, Crompton & Sheail 1975, Chadwick 1982, Webb 1986). Locally, cattle and horses have also been grazed.

The more assiduous among these herbivores help keep this vegetation short and open by their close cropping, and maintain a balance between the resistant perennial grasses and rosette plants, the light-demanding chamaephytes and the ephemerals and cryptogams able to take advantage of the intervening patches of bare ground. Surface scuffing also produces a shifting patchwork of open areas available for repeated colonisation by the therophytes and for the successional re-establishment of the longer-lived elements of the sward (e.g. Watt 1938).

Grazing also contributes to the distinctive character of this vegetation by its selectivity, which can enhance the local abundance of particular unpalatable plants and produce what is often a rather marked degree of local diversity in the sward, even within small stands of a single sub-community or over short periods of time. Many of the annuals, for example, are generally avoided by rabbits, as are Senecio jacobaea, the Sedum spp. and, often, the foliage of Hieracium pilosella (Meylaender et al. 1968), although the flowers of this last species are frequently eaten by rabbits, which can thus exert a powerful control over whether the plant increases by sexual or clonal spread (Bishop et al. 1978, Bishop & Davy 1984). Many of the bryophytes and the lichens also seem to be avoided. Preferences among sheep are less well documented though, in similar vegetation on Öland in the Baltic, selective grazing seemed to modify the distribution of *Cladonia* spp. (Sjögren 1971). Other plants particularly associated with the Festuca-Agrostis-Rumex grassland appear to flourish best in the absence of large herbivores and are thus associated with neglected areas of sward: Thymus serpyllum, for example, though it cannot compete well in rank turf, is grazed out in some localities (Pigott 1955) and Silene otites can flourish and spread if protected (Watt 1971b).

The other important effect of grazing is on the trophic state of the system. Rabbits defaecate their re-ingested pellets in latrines, favouring the development of small patches of lusher, eutrophic vegetation on the moistened and enriched soils, where occasionals in the community like *Urtica dioica*, *U. urens* and *Stellaria media* tend to be concentrated. But, at the same time, they are continually removing nutrients, perhaps quite appreciable quantities of nitrogen and phosphorus, from the bulk of the sward (Watt 1981a). Generations of this kind of effect, together with the traditions, in areas like the Suffolk Sandlings and Breckland, of folding sheep on arable land or on ground about to be ploughed after manuring (Sheail 1979, Chadwick 1982, Webb 1986), could have played a major part in the impoverishment of the soils and the maintenance of swards like the *Festuca-Agrostis-Rumex* grassland over extensive areas.

Changes in the community consequent upon decline of grazing are today very widely seen, although it is possible that, with the resurgence in rabbit numbers, these are being reversed in some places. However, although it is clear that surviving stretches of the community are often but fragments of their former extent and often look generally rank and impoverished, close study of the changes has not been so detailed as among their calcicolous counterparts in the Festuca-Hieracium-Thymus grassland. Again, it is to Watt (1960a, 1971a,b) that we owe most knowledge of actual developments in particular stands, and study of his results, together with general comparisons of this vegetation today with that described in the early classic accounts (Farrow 1915, Tansley 1939, Watt 1936, 1940). suggests that, though the community can still retain the same general character under light grazing, the alterations can be considerable. The more universal dominance of F. ovina these days is one obvious result of neglect, with A. capillaris and, even more noticeably in some places, A. stolonifera and A. canina ssp. montana, showing a strong decline. Galium saxatile, too, is much less common through the community as a whole than it seems to have been in the past. Most obvious of all in many places where the Festuca-Agrostis-Rumex grassland has persisted is the occlusion of the open ground between the grasses, F. ovina usually retaining its tussocky habit, but individuals increasing in size and number and crowding out species sensitive to competition. The rich ephemeral flora is often the first element to suffer from such a change, then light-demanding perennials like R. acetosella. Acrocarpous mosses and the lichens are also reduced in extent, although, as the grass plants age and die, there is an opportunity for the re-establishment of some of the lichens over the matted and decaying foliage that lines the hollows in the turf.

Other kinds of disturbance, apart from the scuffing that rabbits and stock produce, have probably also been important in helping maintain the community, most notably the sporadic cultivation of the ground for arable crops or hay, an activity which perhaps dates right back to Neolithic times and which continued until relatively recent years over many of our lowland heaths (Webb 1986). Because of the inherent infertility of the profiles beneath the Festuca-Agrostis-Rumex grassland and associated ericoid vegetation themselves, such cultivation was often concentrated over areas of better soils among and around the impoverished sands. However, where these were disturbed they could accumulate a reservoir of ephemeral weeds able to recolonise the adjacent ground after it was abandoned, as it commonly was after cropping poorly. In Breckland, such shifting cultivation was a more integral feature of the heath landscape itself over many centuries – indeed, the word 'breck' means a ploughed-up portion of ground – and, though modern arable farming has facilitated permanent reclamation of extensive areas of once intractable land, stands of the community can still be found there on fragments of ploughed ground that have escaped planting. Disturbance from other activities, too, such as is associated with forestry among heaths or military manoeuvres, both again important features of the Breckland scene, can create open ground available for development of the community (see below).

Some of these activities, together with visitors drawn to the attractive open scenery still to be found on some lowland heaths, result in trampling of the sward. This helps keep the vegetation low and open and, though some elements of the flora, like the lichens, can suffer greatly, others like the chamaephytes and ephemerals can thrive. For the winter annuals, too, which need a moist surface on which to germinate in autumn, compaction of the ground and consequent slow run-off of rain may be of crucial importance to their successful establishment. *Crassula tillaea* is specifically associated with such winter-wet sites (Watt 1971b, Crompton & Sheail 1975).

Floristic variation in the community is a product of differences in these climatic, edaphic and biotic factors. The Typical sub-community is the most widely distributed kind of Festuca-Agrostis-Rumex grassland, occurring throughout the moderately dry and summerwarm parts of the range, where there are less than 800 mm rain and fewer than 140 wet days yr -1 (Climatological Atlas 1952, Ratcliffe 1968) and where the mean annual maximum temperature is over 27 °C (Conolly & Dahl 1970), a zone which takes in much of the lowland north-east of England, all of the Midlands and East Anglia, but which excludes most of The Weald and the south-west of the country. This vegetation can have sporadic representation of the more widespread ephemerals of the community, but its generally impoverished and grass-dominated character is perhaps testimony to the infrequency of grazing now and the general isolation of stands among overgrown heaths or intensive agricultural landscapes.

Such Typical Festuca-Agrostis-Rumex grassland can now be found quite commonly in Breckland and, although no detailed information is available to associate these stands specifically with known reduction in grazing or relatively recent reversion from arable, they do not represent the full potential richness of this vegetation in this part of Britain. That is seen in the Erodium-Teesdalia sub-community, the composition of which is sometimes approached locally elsewhere through the range of the Typical sub-community, but which is now confined to Breckland where, for various reasons, conditions are especially congenial. In the first place, it is there that the climate makes its closest approach to the truly continental. Rainfall is especially low, with under 120 wet days yr⁻¹ (Ratcliffe 1968), and annual rainfall of less than 600 mm, indeed quite often below 500 mm (Gregory 1957, Chandler & Gregory 1976). Summer temperatures are high and the potential water deficit in late spring especially marked (Smith 1976), though the winters are comparatively dry and cold, with little or no snow-lie but frequent and late frosts (Salisbury 1932, Ratcliffe 1968). As well as being especially suitable for the winter annuals, such conditions also favour the occurrence in the Breckland stands of ephemeral and perennial steppe plants, Teesdalia nudicaulis, Potentilla argentea, Silene conica, S. otites and Scleranthus perennis. Salisbury (1932) proposed that such species might need a dry winter to avoid rotting and a hot, dry early summer for seed-ripening.

The second feature of the Breckland environment favouring the development of the Erodium-Teesdalia sub-community is the extensive occurrence of suitably sharply-draining and base-poor soils, which in the particular climate of the area are susceptible to frost-heave in winter and wind erosion in the flat, open landscape, two further factors which help keep the swards open. And then there is the long and intensive history of land use in the area which even within relatively small areas like Lakenheath Warren (Crompton & Sheail 1975) or the Stanford Practical Training Area (Sheail 1979) can be surprisingly complex. Especially intensive sheep- and rabbit-grazing have been particularly important through Breckland, perhaps exacerbating the tendency for soil erosion and impoverishment. But also of great consequence is the way in which, for many generations, stretches of the ground, both in the arable fields around and within the grass-heaths themselves, went in and out of cultivation, maintaining a shifting pattern of disturbance over a whole landscape. Postgate (1960) and Sheail (1979) have shown how tenurial problems, the high cost of extending traditional treatments like marling, the uncertain efficacy of new fertilisers on the highly impoverished soils and the vagaries of the market for crops which remained unreliable, all helped postpone the impact of the Agricultural Revolution in Breckland, delaying gross transformation of the landscape until the present century with its state-funded forestry, farm improvement and military training grounds. Of these land uses, it is the last which has proved most compatible with maintenance of the conditions favouring the development of the *Erodium-Teesdalia* sub-community.

The other characteristic type of Festuca-Agrostis-Rumex grassland strongly concentrated in this part of Britain is the Cladonia sub-community, which can represent an early stage in the recolonisation of eroded areas (Watt 1938) or perhaps persist long over stabilised sand. The inland dune landscape among which this vegetation is often best seen is now virtually gone from Britain, fragments surviving at Wangford Warren and two other sites in Breckland and at Risby near Scunthorpe (Ratcliffe 1977). However, some sands around the south-east coast carry the Cornicularia-Cladonia sub-community and there is little doubt that it could occur more widely through the more continental parts of Britain were suitable habitats to persist. This is one kind of Festuca-Agrostis-Rumex grassland which cannot stand much trampling or crushing by tracked army vehicles.

A shift on to somewhat less parched soils and ones which are perhaps less impoverished than usual is marked by the occurrence of the Anthoxanthum-Lotus sub-community. This too, occurs throughout East Anglia where it may indicate the presence of more argillic profiles derived from less sandy drift, but it also extends the range of the Festuca-Agrostis-Rumex grassland decisively into The Weald, where annual rainfall exceeds 800 mm, approaching 1000 mm towards the western end (Climatological Atlas 1952). Here, too, and at scattered localities around Dartmoor, up the Welsh Marches and around the Pennines, where precipitation rises above 1000 mm with more than 140 wet days yr⁻¹ (Climatological Atlas 1952, Ratcliffe 1968), the Potentilla-Galium sub-community can be found on soils which sometimes show little tendency to parching and where the atmosphere is somewhat more humid. This vegetation is decidedly scarce in East Anglia, though it is occasionally seen on the Norfolk Commons and the Suffolk Sandlings, where the climate is less continental than in the interior.

With the decisive shift to more oceanic conditions through south-western England and into Wales, where rainfall can rise to over 1200 mm yr⁻¹ (Climatological Atlas 1952) and winter accumulated temperatures above zero day-degrees C (Page 1982), and where the local maintenance of a suitable topoclimate becomes paramount for the survival of this vegetation, the Hypochoeris sub-community is the usual form of Festuca-Agrostis-Rumex grassland. F. rubra begins to acquire some representation here, as a prelude to its dominance through a wide variety of more maritime cliff grasslands, and Sedum anglicum and Umbilicus rupestris add a

particular regional phytogeographic element. The coincidental occurrence of dolerite towards the inland limit of this more oceanic zone at Craig Breidden adds a further distinctive floristic character to stands of the *Hypochoeris* sub-community there, more broadly calcicolous species such as *Helianthemum nummularium* and *Thymus praecox*, together with the rare *Lychnis viscaria*, occurring on soils which are base-poor but quite calcium-rich (Jarvis & Pigott 1973, Jarvis 1974).

Zonation and succession

The Festuca-Agrostis-Rumex grassland usually survives now as fragments among mosaics of sub-shrub vegetation, bracken, scrub and woodland on lowland heaths where, after often long and complex treatment histories, response to neglect is generally the major factor in determining the pattern of communities. In other places, reclamation of such landscapes has been so complete as to leave small stands of the grassland isolated on more intractable or temporarily disturbed ground among intensive pasture, arable or forestry plantations, with some kinds of urban wasteland providing new habitats in a totally artificial context. All the more valuable, then, are those places where the community persists as a fairly extensive element of open, semi-natural scenery, as in parts of Breckland where there is the added interest of wide variation in soil conditions. Even in this most continental environment, the Festuca-Agrostis-Rumex grassland is largely a plagioclimax community ultimately dependent on grazing for its survival.

In this light, the community can be regarded as the usual product of clearance and long-continued pasturing over parched, acid soils through the drier lowlands of Britain, where it has been closely associated with heath vegetation, grazing and burning maintaining the characteristic patchwork of communities. The particular kinds of heath with which the Festuca-Agrostis-Rumex grassland is still found are, however, quite diverse, its own distribution spanning the ranges of a variety of distinct sub-shrub communities. Through its heartland, in East Anglia, it characteristically occurs with the Calluna-Festuca heath in the extensive grassheath mosaics of Breckland and the Suffolk Sandlings and among the drier vegetation of the Norfolk Commons; here the Typical, Erodium-Teesdalia and Cornicularia-Cladonia sub-communities come especially close to the heath in their floristics. Further south, on the commons of the wetter Weald, the Potentilla-Galium sub-community becomes frequent and its usual sub-shrub companion is the Calluna-Ulex minor heath; and then, in the South-West Peninsula, along the Welsh coast, up the Marches and around the south-western Pennine fringes, this is replaced by the Calluna-Ulex gallii heath, a community which recurs in close association with the Festuca-Agrostis-Rumex grassland at scattered localities around the East Anglian coast. The *Hypochoeris* sub-community is also found with the *Calluna-Ulex gallii* heath in some of its cliff-top stations around the south-western seaboard, where the sub-shrub vegetation is often of the *Scilla* sub-community. Such situations are scarcely maritime in the strict sense and, where there is any salt-spray influence, the *Festuca-Agrostis-Rumex* grassland is replaced by the *Armeria-Cerastium* maritime therophyte community.

All these sub-shrub communities are dry heaths and the various kinds of Festuca-Agrostis-Rumex grassland essentially represent their herbaceous element, in which the ericoids and gorse species are kept in check by the continual predation of herbivores. The proportions of grassland and heath at any site, and the sharpness of the boundaries between the vegetation types, are thus ultimately dependent upon the disposition and intensity of the grazing, with burning episodes offering periodic opportunities for the grassland to gain ascendancy over the heath on shallower soils where pasturing after the fire is heavy. Even then, however, the parched and impoverished character of the ground prevents the Festuca-Agrostis-Rumex grassland developing the kind of vigorous post-burn sward that is produced over moister soils in central southern and south-western heaths by Agrostis curtisii.

Except in very extreme situations, the continuing open nature of the vegetation means that, if grazing and burning cease, colonisation by woody plants tolerant of the dry and oligotrophic conditions readily occurs. With the almost universal abandonment of traditional heath management, then, and after the demise of rabbits, the contribution of the Festuca-Agrostis-Rumex grassland has generally shrunk, with a spread of heath and direct invasion of the sward by Betula pendula and pines, these latter able to seed in from nearby plantations, with Ouercus robur sometimes appearing or, more locally, as at Sandringham Warren, Rhododendron ponticum. Even where the shade is not too dense, the grassland species mostly succumb quite quickly and there is little doubt that most stands of the community would progress eventually to Quercus-Betula-Deschampsia woodland, the climax forest of acid and free-draining soils through lowland Britain and variously dominated by oak, birch or pine. The other very common element of the neglected heath landscape is bracken, although Pteridium aguilinum tends to avoid soils subject to pronounced parching and to make little headway in direct expansion into the Festuca-Agrostis-Rumex grassland.

Typically, then, the community now persists mainly on patches of more inhospitable ground where invaders cannot flourish, along pathways and around trampled picnic spots and viewing points among dense patchworks of rank heath, bracken and woodland. Periodic disturbance may allow a resurgence of the *Festuca*-

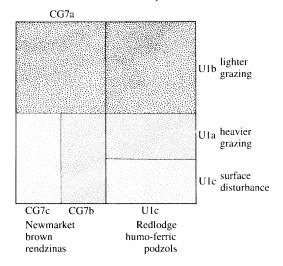
Agrostis-Rumex grassland but, where the ground becomes enriched, such places are likely to be directly invaded by *Ulex europaeus* to form *Ulex-Rubus* scrub, or by brambles to produce *Rubus-Holcus* or *Pteridium-Rubus* underscrub, or by rank grasses and tall herbs, all of which shade out the smaller plants of the grassland.

Towards the wetter part of its range, it is often among such vegetation types as these that the Festuca-Agrostis-Rumex grassland persists in rocky field corners and in the disturbed ground around settlements, forming part of the untidy patchwork of semi-natural vegetation typical of landscapes which have seen marginal improvement for grazing. Through the drier lowlands, reclamation has been more extensive and drastic, though it often came late because of the inherent difficulties which the soils pose for good cropping, being lime- and often copper-deficient, droughty and liable to wind erosion. But they are readily cultivated and, particularly in East Anglia, have often gone to arable, mostly for sugar-beet and barley (Hodge et al. 1984). Afforestation has also been an attractive alternative where agricultural yields are low and, in the first 30 years of its existence, the Forestry Commission had acquired 40% of Breckland where by far the largest and most interesting stands of the community survived. There, then, the Festuca-Agrostis-Rumex grassland often remains as fragments on the wider sandy ridges between plantations of pine, or in the corners of ploughed fields which have escaped planting and treatment with chemical fertilisers and herbicides. Stands taken in to airfields and military training grounds sometimes preserve more extensive and semi-natural zonations and mosaics by virtue of the prohibition on such improving activities, and the community can develop over a surprising range of man-made surfaces there. Within urban or industrial areas, too, in the warm dry lowlands, the Festuca-Agrostis-Rumex grassland can occur over sharplydraining derelict ground among a wide variety of more eutrophic grasslands, tall-herb vegetation and scrub.

Where the most extensive stands of the community remain, in parts of Breckland, there is the additional striking influence of variations in base-richness among the sharply-draining, impoverished soils depending on the proximity to the surface of the underlying Chalk and the amount of calcareous material among the superficials (Figure 31). Such differences exert the major control over the renowned suite of grass-heaths, first fully described by Watt (1936, 1940), and grouped in this scheme within the Festuca-Hieracium-Thymus grassland (Watt's A and B swards) and the Festuca-Agrostis-Rumex grassland (D-G). The zonations, which can be seen still in whole or part, on the Lakenheath-Elveden, Icklingham and Stanford-Wretham heaths (Ratcliffe 1977), run from the most calcifuge swards on Redlodge humo-ferric podzols, through transitions over Worlington and Methwold sands, to the most calcicole on Newmarket brown rendzinas (Corbett 1973, Hodge et al. 1984). Where Calluna-Festuca heath occupies the more acidic profiles, its boundaries are generally very obvious but zonations among the grasslands can be very gradual or form complex mosaics, often depending directly on heterogeneity in the superficials; where grazing has been relaxed, the boundaries often become further blurred by expansion throughout of F. ovina. Even in the close-cropped swards, some of the perennials and many of the ephemerals and cryptogams run throughout but the preference of Thymus praecox, T. pulegioides, Leontodon hispidus, Cirsium acaule, Sanguisorba minor, Avenula pratensis and, less obviously, Koeleria macrantha, is for the Festuca-Hieracium-Thymus grassland; and that of Rumex acetosella, Teesdalia and Galium saxatile is for the Festuca-Agrostis-Rumex grassland. In some Breckland sites, too, Carex arenaria can become prominent among these mosaics, marking a shift to Carex or Carex-Cladonia dune communities where sand has been eroded and re-deposited (Watt 1937, Noble 1982), with some possibility of redevelop-

Figure 31. Breckland grass-heaths in relation to soils and treatments.

CG7a Festuca-Hieracium-Thymus grassland,
Koeleria sub-community
CG7b Festuca-Hieracium-Thymus grassland,
Cladonia sub-community
CG7c Festuca-Hieracium-Thymus grassland,
Ditrichum-Diploschistes sub-community
U1a Festuca-Agrostis-Rumex grassland,
Cornicularia-Cladonia sub-community
U1b Festuca-Agrostis-Rumex grassland, Typical
sub-community
U1c Festuca-Agrostis-Rumex grassland, ErodiumTeesdalia sub-community



ment of the *Festuca-Agrostis-Rumex* grassland over stabilised surfaces (Watt 1938). Similar zonations can be seen at scattered localities around the East Anglian coast, too.

Distribution

The Festuca-Agrostis-Rumex grassland occurs widely over suitable substrates throughout the warm and dry lowlands of England and Wales, becoming increasingly local towards the wetter west and north of the country. The most extensive and distinctive stands, of the Erodium-Teesdalia and Cornicularia-Cladonia sub-communities, are found in Breckland, although it is possible that much Typical Festuca-Agrostis-Rumex grassland could approach their richness had not the habitat of the community become fragmented and overgrown through much of its range. The Anthoxanthum-Lotus, Potentilla-Galium and Hypochoeris sub-communities each have distinctive distributions in relation to regional differences in climate and soils.

Affinities

This vegetation received scarcely any attention prior to the classic accounts by Watt (1936, 1940; see also Tansley 1939) of the Breckland stands, where the emphasis was on the floristic variation through the whole range of grass-heaths. Certainly, the continuity in composition and physiognomy through the entire suite of vegetation types described by Watt is very clear, but there is no doubt that, in a national context, they are best seen as closely juxtaposed examples of two rather distinct communities, with the major disjunction occurring in his grassland C. In this scheme, the more calcicolous swards are readily included within the Festuca-Hieracium-Thymus grassland, our nearest approach in Britain to the more basiphile steppe-grasslands of the Festucion valesiacae and the Koelerio-Phleion phleiodis (Ellenberg 1978, Oberdorfer 1978). The more calcifuge, on the other hand, Watt's grasslands D–G, are best seen as the most distinctive examples of this rather widely distributed and, for the most part, fairly nondescript *Festuca-Agrostis-Rumex* grassland, a vegetation type which can then also clearly include other kinds of acidophilous swards of sandy soils which received passing mention in Tansley (1911).

The community represents an obvious geographical counterpart to the Festuca-Agrostis-Galium grassland, the major calcifuge sward of the wet and cool submontane zone of north-west Britain, occupying a similar ecological position in relation to woodland and heath vegetation. But, whereas that is clearly a kind of Nardo-Galion community, the Festuca-Agrostis-Rumex grassland is perhaps better located among the vegetation types of sandy soils included in the Sedo-Scleranthetea, of which Myosotis ramosissima, Potentilla argentea, Rumex tenuifolius, Scleranthus perennis, Sedum anglicum, S. acre, Taraxacum laevigatum, Veronica verna, Brachythecium albicans, Ceratodon purpureus and Polytrichum piliferum are regarded as character species (Ellenberg 1978). More particularly, it can find a place in the Thero-Airion alliance, of which Aira praecox, Logfia minima, Ornithopus perpusillus and Teesdalia nudicaulis are diagnostic, with Continental equivalents such as the Festuco-Thymetum serpylli R. Tx. (1928) 1937 described from The Netherlands and north-west Germany (Tüxen 1937, Westhoff & den Held 1969), the Airetum praecocis (Schwickerath 1944) Krausch 1967 and Airo caryophylleae-Festucetum ovinae R. Tx. 1955 from various parts of Germany (Oberdorfer 1978) and Poland (Matuszkiewicz 1981). Among the range of such vegetation types described from Britain, the Festuca-Agrostis-Rumex grassland and its maritime counterpart the Armeria-Cerastium community, can be seen as transitional between the grassier calcifuge swards of the Nardo-Galion and the stonecrop-dominated vegetation of fractured rocky outcrops.

Floristic table U1

	a	ь	С
Festuca ovina	V (3–9)	V (3-10)	V (3-9)
Agrostis capillaris	II (2-3)	IV (2–8)	IV (3-5)
Rumex acetosella	IV (2-5)	IV (2–6)	IV (2-4)
Dicranum scoparium	IV (3–8)	I (2–6)	II (2–7)
Cornicularia aculeata	IV (2-4)	I (4)	II (4–7)
Cladonia arbuscula	IV (2-6)		I (3-6)
Polytrichum piliferum	III (2-7)	II (1–7)	II (3–6)
Cladonia tenuis	III (2–6)	I (3–4)	II (2-5)
Cladonia impexa	III (2-7)	I (3)	I (3)
Cladonia foliacea	III (2-3)	I (3-6)	I (2-3)
Cladonia uncialis	III (2-5)	, ,	I (3-5)
Cladonia furcata	II (2–3)	I (2-4)	II (3–5)
Cladonia squamosa	II (2–3)	I (2-3)	I (2-3)
Cladonia gracilis	II (2–3)	I (2)	I (3-4)
Ptilidium ciliare	II (2–6)	,	I (2)
Pohlia nutans	II (1–4)		I (3-4)
Cladonia fimbriata	II (3–4)		I (3)
Cladonia pyxidata	II (3–4)	I (2)	I (3-4)
Campylopus introflexus	I (3–8)	· · ·	,
Silene otites		I (3–4)	
Silene conica		I (3)	
Scleranthus perennis		I (2-3)	
Brachythecium albicans	I (4–5)	III (2-7)	IV (3-6)
Aira praecox		II (3–6)	IV (2–6)
Erodium cicutarium		I (3-4)	IV (2-7)
Cerastium fontanum		II (2-7)	III (3-4)
Teesdalia nudicaulis		I (3)	III (2-4)
Aphanes arvensis		I (3-5)	III (2-5)
Myosotis ramosissima		I (2-3)	III (2–4)
Erophila verna		I (3)	III (2-5)
Astragalus danicus		I (3)	III (2–3)
Veronica arvensis		I (3)	III (2–3)
Sedum album		` '	III (2–5)
****			` '

Floristic table U1 (cont.)

	a	ь	c
Trifolium dubium		I (3)	II (2-3)
Ornithopus perpusillus		I (2-4)	II (3-4)
Plantago media		I (3–4)	II (3)
Arenaria serpyllifolia			II (2–4)
Geranium molle		I (4)	II (2–4)
Logfia minima		I (4)	II (2-4)
Cerastium arvense			II (3-4)
Trifolium sp.			II (2-3)
Campanula glomerata			I (2-4)
Viola tricolor curtisii			I (2-3)
Tortula ruralis ruraliformis			I (4–5)
Thymus serpyllum			I (4)
Arabidopsis thaliana			I (3)
Rhytidium rugosum			I (4)
Veronica agrestis			I (2)
Arabis hirsuta			I (3)
Plantago lanceolata		III (3–4)	III (3-4)
Anthoxanthum odoratum		I (2-5)	I (3-5)
Lotus corniculatus		I (3-4)	I (3-4)
Galium verum		I (3-5)	II (2-3)
Holcus lanatus	I (3-4)	I (1-6)	II (1-4)
Achillea millefolium		II (2-4)	II (2-4)
Campanula rotundifolia		I (2-4)	I (2-3)
Quercus robur seedling			
Urtica dioica			
Galium saxatile	I (2)	I (2-5)	I (2-3)
Potentilla erecta			
Deschampsia flexuosa			
Ulex europaeus			I (1)
Ulex minor			
Hypochoeris radicata		I (2-3)	I (2)
Centaurium erythraea		I (3–4)	I (3–4)

d	e	f	1
I (3-4)	I (3)	I (1-4)	I (1–4)
I (3)	I (4)	I (1–3)	I (1–4)
1 (3-4)	I (2)		I (2-4)
I (3–6)		I (1-3)	I (1–6)
I (3-4)			I (2-4)
			I (2-4)
I (3)			I (3-4)
I (3)			I (2-3)
			I (2-4)
			I (2-3)
I (4)			I (4-5)
			I (4)
			I (3)
			I (4)
			I (2)
			I (3)
IV (3-4)	I (3)	III (1–4)	III (1–4)
IV (3-5)	II (3-5)	I (1–6)	II (1–6)
IV (3-5)	II (3-5)	I (1)	II (1–5)
IV (3-5)	I (3)		II (2-5)
III (3-4)	I (4–5)	II (1-4)	I (1–6)
III (3-5)	I (2-4)		I (2-5)
II (2–4)	I (2–3)		I (2-4)
II (2–3)			I (2-3)
I (3-4)			I (3–4)
I (4)	IV (2-5)		II (2–5)
	III (2 -4)		I (2-4)
	III (3–4)		I (3–4)
I (2-4)	II (2-5)	I (1–2)	I (1–5)
	II (2–3)		I (2-3)
		IV (1-4)	I (1-4)
		II (1–4)	I (1–4)

I (3) I (2) II (3–4) II (2–8)	II (2–8) II (1–4) II (2–4) II (4–5)	II (1-7) III (1-3) II (3-5)
I (2) II (3-4) II (2-8)	II (1-4) II (2-4) I (4-5)	III (1–3)
I (2) II (3-4) II (2-8)	II (1-4) II (2-4) I (4-5)	III (1–3)
I (2) II (3-4) II (2-8)	II (1-4) II (2-4) I (4-5)	III (1–3)
I (2) II (3-4) II (2-8)	II (1-4) II (2-4) I (4-5)	III (1–3)
I (2) II (3-4) II (2-8)	II (1-4) II (2-4) I (4-5)	III (1–3)
I (2) II (3-4) II (2-8)	II (1-4) II (2-4) I (4-5)	III (1–3)
II (3-4) II (2-8)	II (2-4) I (4-5)	
II (2–8)	I (4-5)	II (3-5)
		()
I (2)	II (2 2)	II (3-5)
I (2)	II (2–3)	II (2-5)
* (<i>~)</i>	II (2-3)	
	II (3–5)	II (2-4)
I (1-2)	I (3–4)	II (3–4)
II (3–4)	I (4)	I (3-4)
	I (3-5)	II (2-5)
I (5)	I (3-5)	II (3–6)
	I (4)	II (3-7)
	I (2–4)	II (2–4)
I (2-3)	I (3-4)	I (4)
I (2)	I (4)	I (3–6)
	I (5)	I (3-7)
I (2)	I (3)	I (2-3)
	I (3–4)	I (2-5)
	I (2-3)	I (2-4)
	I (3)	I (3)
	I (2)	I (3)
	I (2-3)	I (3)
	I (2–6)	I (4)
	I (2-3)	I (2-4)
	I (3-5)	I (2-4)
	I (2)	I (4)
	I (3–4)	I (2–8)
	I (3-6)	I (2-3)
	I (3)	I (3–4)
	I (3)	I (2-3)
	I (2-4)	I (3-5)
	II (3-4) I (5) I (2-3) I (2)	II (3-5) I (1-2) II (3-4) II (3-4) II (3-5) I (4) I (3-5) I (5) I (3-5) I (4) I (2-4) I (2-4) I (2-4) I (2) I (3) I (3-4) I (2) I (3) I (3-4) I (2-3) I (3-4) I (2-3) I (2-6) I (2-3) I (3-5) I (2) I (3-4) I (3-6) I (3-6) I (3-6) I (3)

I (3-4)		II (1–4)	I (1-4)
		II (1–4)	I (1-4)
		II (1-4)	I (1–4)
		II (1-3)	I (1-3)
		I (1-2)	I (1-2)
		I (1-2)	I (1-2)
		I (1–4)	I (1–4)
III (3–8)	II (3-7)	I (1)	II (1–8)
III (1-5)	II (3–5)		II (1-5)
II (3-4)		I (1-3)	II (1-5)
II (3-6)		II (1–4)	II (1-5)
II (3)	II (3)	I (1)	II (1-5)
II (2-4)	II (2-3)	I (1)	II (1-4)
I (3-5)	I (4)	II (1–4)	II (1-5)
I (3-4)	I (2-3)	II (1–4)	I (1-4)
I (3)		II (1–9)	I (1-9)
I (3-4)	I (3)	II (1–8)	I (1-8)
II (2-7)			I (2-7)
II (3-4)		I (1)	I (1-7)
II (3–7)		. ,	I (2-7)
I (3)	I (2-3)	I (1)	I (1-4)
I (3–6)	I (4-5)	I (1-3)	I (1–6)
I (5)	I (5)	I (1-3)	I (1-7)
I (2-4)	. ,	` ,	I (2-4)
I (3-6)	I (2-4)		I (2-6)
I (2-4)	I (3–5)		I (2-5)
I (3)	I (2)		I (2-3)
I (3)	I (5)		I (2-5)
I (4)	I (1-4)		I (1-4)
I (3)	,	I (1–2)	I (1-6)
I (3-4)		I (1)	I (2-4)
I (3)		. ,	I (2-5)
I (3)			I (2-4)
I (5)			I (2–8)
I (2)			I (2-6)
I (3-5)			I (3-5)
I (3-5)			I (2-5)
ζ,	I (3-5)		I (2-5)

Floristic table U1 (cont.)

	a	b	c	d	e	f	1
Sagina procumbens		I (3–4)	I (2-4)			I (1-4)	I (1-4)
Teucrium scorodonia		I (3–4)		I (3-5)	I (3)		I (3–5)
Bromus hordeaceus hordeaceus		I (4)			I (5)	I (1–3)	I (1-5)
Pleurozoium schreberi	I (2)		I (3-4)				I (2-4)
Agrostis canina montana		I (3)	I (3)				I (3)
Sagina apetala		I (2-3)	I (3)				I (2-3)
Filaginella uliginosa		I (2-4)	I (3)				I (2-4)
Veronica polita		I (4)	I (2)				I (2–4)
Sedum acre		I (2-4)		I (3–4)			I (2-4)
Phleum pratense		I (3)		I (3)			I (3)
Potentilla reptans		I (4)		I (3)			I (3-4)
Vicia sativa		I (3)		I (3-5)			I (3–5)
Potentilla argentea			I (3-4)	I (2-3)			I (2-4)
Reseda lutea			I (3)	I (3)			I (3)
Trifolium campestre			I (3)	I (4)			I (3–4)
Stellaria graminea				I (3)	I (3)		I (3)
Bromus sterilis					I (2-7)	I (1–3)	I (1-7)
Number of samples	18	69	30	29	41	16	203
Number of species/sample	14 (7–20)	13 (5–27)	24 (15–35)	17 (6–28)	14 (9–32)	15 (7–27)	16 (6–35)
Herb height (cm)	10 (1–20)	11 (2–40)	7 (1–30)	13 (2–40)	8 (4-20)	6 (1–15)	9 (1–40)
Herb cover (%)	50 (10-100)	80 (35–100)	66 (50–100)	89 (60-100)	95 (60–100)	61 (10–100)	71 (10–100)
Ground layer height (mm)	24 (10-50)	21 (10–100)	20 (5-50)	26 (10–80)	18 (10–30)	17 (5–40)	15 (5–100)
Ground layer cover (%)	65 (10–90)	16 (0–80)	26 (0–60)	26 (0–100)	4 (0–25)	27 (0–95)	23 (0–100)
Altitude	29 (15–47)	40 (10–110)	22 (4–41)	30 (8–170)	102 (12–200)	95 (1–360)	41 (1–360)

a Cornicularia aculeata-Cladonia arbuscula sub-community

b Typical sub-community

c Erodium cicutarium-Teesdalia nudicaulis sub-community

d Anthoxanthum odoratum-Lotus corniculatus sub-community

e Galium saxatile-Potentilla erecta sub-community

f Hypochoeris radicata sub-community

¹ Festuca ovina-Agrostis capillaris-Rumex acetosella grassland (total)

