SD8
Festuca rubra-Galium verum fixed dune grassland

Synonymy
Dune grassland Tansley 1911, 1939, Gimingham 1964*a*; Dune pasture Gimingham 1964*a p.p.*; Machair Gimingham 1964*a*, 1974, Ranwell 1974; *Euphrasio-Festucetum arenariae* Birse 1980; *Astragalo-Festucetum arenariae* Birse 1980 *p.p.*

Constant species
Festuca rubra, *Galium verum*, *Lotus corniculatus*, *Plantago lanceolata*, *Poa pratensis*, *Trifolium repens*.

Rare species
Acaena novae-zelandiae, *Astragalus danicus*, *Dianthus deltoides*, *Epipactis atrorubens*, *Mibora minima*, *Oxytropis halleri*, *Primula scotica*.

Physiognomy
The *Festuca rubra-Galium verum* community consists of dune vegetation in which *Festuca rubra* and a variety of other grasses, dicotyledons and mosses make up a generally closed sward, occasionally rank, but usually just a decimetre or two tall, and sometimes closely cropped to a short, tussocky turf. *Ammophila arenaria*, the usual dominant with us on more mobile sand, remains common overall, but it is no longer a constant feature of the vegetation: indeed, in some sub-communities here, it is only occasional. Moreover, even where it is still frequent, the cover is rarely extensive and often reduced to small tufts of shoots noticeably lacking in vigour. *F. rubra*, by contrast, is usually abundant, the typical dominant in the sward, and commonly recorded as var. or ssp. *arenaria* with its far-creeping rhizome systems and rather lax tussocks of stiff leaves (Hubbard 1968, Tutin *et al.* 1980). Other grasses are generally subordinate but some can be quite common. *Poa pratensis* agg., for example, often obviously *P. subcaerulea*, is a constant of the community, though only exceptionally of more than moderate cover, and in regions of moister climate *Holcus lanatus* becomes very frequent. *Dactylis glomerata*, too, is occasionally seen and there are sometimes records for *Avenula pubescens*, though *Arrhenatherum elatius*, another bigger tussocky grass that is sometimes seen on dunes, is characteristically rare here. *Leymus arenarius* very occasionally maintains a place in the community but, along with *Elymus farctus* ssp. *boreali-atlanticus*, *E. pycnanthus* and *E. repens*, it is not really a typical feature of this vegetation.

Among smaller grasses, *Koeleria macrantha* can be quite frequent, this community providing an important locus for this species towards the north of its range where suitably dry soils are scarce. *Festuca ovina* may also sometimes accompany *F. rubra*, though this grass, together with *Agrostis capillaris* and *Anthoxanthum odoratum*, has a restricted role here compared with more calcifuge dune swards. *Agrostis stolonifera* can occur in damper places and becomes increasingly important in transitions to slacks. In stands close to improved areas of dune pasture, *Lolium perenne* and *Cynosurus cristatus* may seed-in in small amounts. In contrast to this diversity of grasses, sedges are few in number, with only *Carex arenaria* occurring at all frequently, although *C. flacca* becomes quite common in some sub-communities and very occasionally there is a little *C. caryophyllea*. *Luzula campestris* is also a frequent plant in certain situations here.

Along with these graminoids, there is in the *Festuca-Galium* community a characteristic variety of dicotyledons, more numerous and usually more abundant than in the earlier stages of dune vegetation, with the commonest among them reinforcing the impression of a mesophytic sward. *Galium verum*, *Plantago lanceolata*, *Trifolium repens* and *Lotus corniculatus* now become constant, while *Hypochoeris radicata* persists only very occasionally and *Ononis repens* is scarce, even among stands in southern Britain. Also distinctive, though somewhat more unevenly represented in the different sub-communities, are *Cerastium fontanum*, *Bellis perennis*, *Ranunculus acris*, *Euphrasia officinalis* agg., *Senecio jacobaea* and *Hieracium pilosella*. Then, occasional to frequent throughout, there are *Achillea millefolium*,

Thymus praecox, *Viola riviniana*, *Heracleum sphondylium* and *Thalictrum minus*, this last often showing the shorter stature and low-branching panicle that have sometimes been used to segregate a ssp. *arenarium* (Clapham *et al.* 1962). Among other perennials recorded at low frequency in the community are *Taraxacum officinale* agg., *Ranunculus bulbosus*, *Plantago major*, *P. maritima*, *P. coronopus*, *Primula vulgaris*, *P. veris* and *Equisetum arvense*, with *Veronica chamaedrys*, *Linum catharticum*, *Campanula rotundifolia*, *Prunella vulgaris* and *Trifolium pratense* becoming common in different kinds of *Festuca-Galium* vegetation. The community also provides an important northern locus for the nationally rare *Astragalus danicus* and around the north-west coast of Scotland in particular, stands can show a local profusion of orchids, with *Coeloglossum viride*, *Gymnadenia conopsea*, *Listera ovata*, *Dactylorhiza fuchsii*, *D. majalis* ssp. *purpurella*, *D. incarnata* and the rare *Epipactis atrorubens* all having been recorded here. In this part of Britain, too, where montane plants can be found virtually at sea-level, *Dryas octopetala* and *Oxytropis halleri* are very occasionally seen among *Festuca-Galium* swards, together with *Primula scotica*.

Apart from coarser ephemerals like *Senecio jacobaea* and occasional *Cirsium vulgare* and *Sonchus oleraceus*, short-lived plants tend not to be a prominent feature of this vegetation but *Rhinanthus minor* and *Odontites verna* are sometimes seen growing semi-parasitically among the sward, and scattered places where the turf is broken can provide an opportunity for very occasional records of *Gentianella amarella*, *Viola tricolor*, *Erodium cicutarium*, *Cerastium diffusum* ssp. *diffusum*, *C. semidecandrum*, *C. arvense*, *Medicago lupulina*, *Trifolium campestre*, *Vicia lathyroides*, *Veronica arvensis*, *Myosotis arvensis*, *M. ramosissima*, *Aira praecox* and the rare *Mibora minima*. Typically, however, the richer assemblages of the winter annuals seen among *Ammophila-Festuca* vegetation are rarely found here.

Mosses are quite often a prominent feature of the sward with locally high cover, though the species involved vary somewhat in the different sub-communities. Plants such as *Tortula ruralis* ssp. *ruraliformis*, *Homalothecium lutescens* and *Brachythecium albicans* can remain quite common but frequently it is pleurocarps like *Rhytidiadelphus squarrosus*, *R. triquetrus*, *Pseudoscleropodium purum*, *Calliergon cuspidatum* and *Hylocomium splendens* that give a distinctive look to this element of the vegetation, with *Hypnum cupressiforme*, *Plagiomnium rostratum*, *P. undulatum*, *Eurhynchium praelongum*, *Thuidium tamariscinum*, *T. delicatulum* and *Entodon concinnus* occurring more occasionally. Lichens are far fewer in number and only rarely abundant, but *Peltigera canina* can be quite frequent, with *P. rufescens* less common.

Sub-communities

Typical sub-community. *F. rubra* is generally an obvious dominant in this kind of *Festuca-Galium* vegetation, with *P. pratensis* very common but almost always of low cover, and *Ammophila* only moderately frequent, though sometimes quite abundant and vigorous where there is still some small measure of sand movement. *Dactylis* occurs occasionally and its tussocks can be quite prominent, but other grasses are rather sparse. *C. arenaria* is frequently found, though hardly ever in any abundance, and there is only rarely any *Luzula campestris*.

Dicotyledonous associates also tend to be fewer here than in most other kinds of *Festuca-Galium* vegetation. The community constants *G. verum*, *P. lanceolata*, *T. repens* and *L. corniculatus* are all well represented, and there is commonly some *A. millefolium* and *S. jacobaea* but, apart from these, it is usually just occasional *C. fontanum*, *Bellis*, *R. acris*, *Heracleum* and *T. minus* that provide variety in the sward. Mosses, too, are generally not very prominent, with just occasional *R. squarrosus* and rather infrequent *B. albicans* and *T. ruralis* ssp. *ruraliformis*.

***Luzula campestris* sub-community:** *Astragalo-Festucetum arenariae*, Typical subassociation Birse 1980. *F. rubra* is still usually the most abundant plant here, but the sward is considerably richer and more diverse than in the Typical sub-community and various associates can attain quite high cover. Among other grasses, tussocks of *Ammophila* are very frequent and locally abundant, and *P. pratensis* too can be moderately plentiful. Then, there is occasional *H. lanatus* and *K. macrantha* but, more distinctive, is the rather common occurrence of *Agrostis capillaris*, *Anthoxanthum* and *F. ovina* which, with very frequent *Luzula campestris*, can give a quite fine-grained character to much of the turf. *C. arenaria* is also often found.

Then, among shorter stretches of the sward, the typical dicotyledons of the community are frequently accompanied by chamaephytes or smaller rosette plants like *T. praecox*, *H. pilosella*, *Veronica chamaedrys* and *Hypochoeris radicata*, all of which tend to have their best representation in this kind of *Festuca-Galium* vegetation. *Astragalus danicus* is also occasionally found here along the east coast of Scotland. Less strikingly, there are sometimes records for *V. riviniana*, *T. officinale*, *S. jacobaea*, *L. catharticum* and *C. rotundifolia*, with *Rumex acetosella*, *Cerastium arvense*, *Myosotis arvensis* and *Veronica arvensis* seen in a few stands.

Moss cover can be quite high among these herbs, with *R. squarrosus* occurring commonly, *R. triquetrus*, *B. albicans*, *P. purum*, *H. lutescens* and *T. ruralis* ssp. *ruraliformis* more occasional, but all able to form extensive

patches, particularly where the swards are close grazed. *Peltigera canina* also occurs quite frequently.

***Tortula ruralis* ssp. *ruraliformis* sub-community.** In its vascular component, this vegetation is similar to the Typical sub-community in the quite impoverished and unvarying flora, although *Ammophila* is somewhat more common and abundant here, *P. trivialis* rather less so, and there are more frequent records for *Hieracium pilosella* and *Thymus*. *Sedum acre* and *Anthyllis* occur as preferential occasionals too and there can be a modest local abundance of annuals. Much more distinctive, however, is the constant occurrence and patchily high cover of *H. lutescens* and *T. ruralis* ssp. *ruraliformis*, with *R. squarrosus* also very common and locally abundant. Both *Peltigera canina* and *P. rufescens* are occasionally found.

***Bellis perennis-Ranunculus acris* sub-community:** *Euphrasio-Festucetum arenariae*, Typical subassociation Birse 1980. *F. rubra* is almost always the most abundant plant in this kind of *Festuca-Galium* vegetation, and is that much more noticeable with *Ammophila* reduced here to a usually low-cover occasional. However, *P. pratensis* and *H. lanatus* are also very common and there is quite often some *A. stolonifera*, particularly where this sub-community extends on to moister ground. *C. arenaria* is also sometimes accompanied by *C. flacca* and *L. campestris*. Also rather striking is the vigorous contribution of dicotyledons to the sward which, though commonly cropped quite short, is generally closed. Thus, along with the community constants, there is frequently much *E. officinalis* agg., *B. perennis* and *R. acris* with *S. jacobaea*, *A. millefolium*, *C. fontanum* all common and, more occasional, *L. catharticum*, *Prunella*, *Trifolium pratense*, *Heracleum* and *Thalictrum*. Bryophyte cover is somewhat patchy, but *R. squarrosus* is very frequent and *H. lutescens*, *C. cuspidatum* and *T. ruralis* ssp. *ruraliformis* also fairly common.

***Prunella vulgaris* sub-community:** *Euphrasio-Festucetum arenariae*, *Linum* subassociation Birse 1980. Some important features of this vegetation are similar to the *Bellis-Ranunculus* sub-community, such as the general prominence of *F. rubra*, the reduced contribution from *Ammophila*, and the frequency of *H. lanatus*, *C. flacca*, *E. officinalis* and *S. jacobaea*. Here, though, both *Bellis* and *R. acris* are only occasional and the most striking associates of the community constants are *L. catharticum*, *C. rotundifolia*, *T. pratense*, *G. amarella* and, most strongly preferential, *Prunella vulgaris*. More occasionally, there are records for *Centaurea nigra*, *Daucus carota*, *Leucanthemum vulgare* and *Ranunculus repens* with *Thalictrum*, *Thymus* and *C. fontanum* well represented among the community companions.

As for bryophytes, *R. squarrosus* remains the most frequent moss and it is often abundant, but *P. purum* is quite common, *H. splendens* occasional, and more obviously preferential are *R. triquetrus*, *C. cuspidatum*, *Plagiomnium undulatum* and the leafy liverwort *Lophocolea bidentata s.l.*

Habitat

The *Festuca-Galium* community is the characteristic grassland of more calcareous fixed sands on dunes and coastal plains all around Britain. Its floristics and structure are strongly influenced by the rather less droughty and impoverished conditions that come with long stability of the lime-rich sand surface, but climatic variation across the range of the community affects the processes of soil development, and grazing also often plays an important part in enhancing fertility and maintaining the physiognomy and variety of the sward. Especially striking and extensive stands of this vegetation contribute to the machair landscape of north-west Scotland and the Isles, though it is these same general factors, albeit in a particular combination, that give them their distinctive character.

The *Festuca-Galium* community cannot become permanently established on accumulations of wind-blown sand around our coasts until accretion has come to a virtual halt, and it is therefore typically found where distance or shelter put the ground beyond the reach of freshly-deposited material derived from beach sources, occurring on stable and usually gentle dune slopes and over stretches of low-relief sand plain. Localised areas of erosion and renewed deposition can develop within tracts of this kind of vegetation, but these generally support rejuvenated stages in dune colonisation, and it is a distinguishing feature of the *Festuca-Galium* community that invaders of mobile sand, so important on young dunes and secondarily exposed areas, now play a much less significant role. *Leymus arenarius*, for example, along those coasts where it assumes a prominent place in early invasion, and much more widely obvious, *Ammophila*, are past their peak of vigour here and no longer exert a dominating influence on either the physical environment or the character and disposition of the other elements of the vegetation. With marram, where shoot production ceases to be proliferative as accretion declines (Huiskes 1979) and flowering becomes less free (Huiskes 1977*a*), with but sparse regeneration from seed (Huiskes 1977*b*), the effects are seen among *Festuca-Galium* vegetation in a fall in tiller density and loss of the strong tussock habit in many stands, the frequent reduction of the clones to scattered, delibitated groups of shoots and the eventual loss of the plant altogether (Gimingham 1964*a*, Huiskes 1979).

The reasons for this decline in vitality are uncertain but probably relate to the edaphic changes that are set in

train with increased stability of the sand surface and the greater competition from other plants that can develop upon it (Carey & Oliver 1918, Benecke 1930, Tansley 1939, Salisbury 1952, Willis *et al.* 1959*a*, *b*; Huiskes 1977*a*, 1979). Very few quantitative data are available but, compared with the more immature sands beneath the *Ammophila-Festuca* community, the major developments here are an accumulation of organic matter in the upper few centimetres, an increased capacity for retention of moisture, still derived mostly from rain, and some enhancement of the trophic state (Salisbury 1952, Willis & Yemm 1961, Willis *et al.* 1959*a*, Ranwell 1972, Chapman 1976, Willis 1985*b*). Even with the passage of centuries, however, it seems that the changes may be relatively modest. Thus, although the surface layers of sand under the *Festuca-Galium* community are usually noticeably darkened by the incorporation of decaying plant material and humus staining, the amount of organic matter can remain as little as 2–3% (Salisbury 1952, Knox 1974). Major nutrients, particularly nitrogen and phosphorus, also continue to limit plant growth for very considerable periods of time (Willis *et al.* 1959*a*, Willis & Yemm 1961), and some trace elements, like copper and cobalt, can be in short supply (Knox 1974). As with the more open *Ammophila-Festuca* vegetation, then, the addition of balanced fertiliser to this kind of sward results in a marked response in growth, the turf filling up, fresh weight and height of the herbage increasing, though here there is an accompanying decline in diversity, particularly among dicotyledons and mosses (Willis 1963, 1985*b*). Furthermore, although there is increased leaching of calcium carbonate from the upper layers with time, specially where the *Festuca-Galium* community extends into regions of higher rainfall, the sands are generally so rich in lime from the outset that the effects of this are negligible. Typically, then, this is a vegetation type of dunes and sand-plains where shell fragments make up a considerable proportion of the beach sediment that has fed them. Where the *Festuca-Galium* swards occur on machair, for example, the amount of calcium carbonate is commonly more than 50% of the sand, sometimes well over 75% (Gimingham *et al.* 1949, Vose *et al.* 1957, Ritchie 1974) and, even where there is more siliceous sand, reduction of the surface pH may take a very long time (Ranwell 1972, Willis 1985*b*). Usually, then, the pH here is not very different from that beneath the *Ammophila-Festuca* community, being mostly between 6.5 and 8.5.

These general edaphic conditions are reflected through the *Festuca-Galium* vegetation as a whole in a number of ways. With the decline in accretion and the waning of the dominance of *Ammophila*, other plants can capitalise on the expanses of stabilised sand surface but, while moisture and nutrients remain limiting, they are unable to thicken up into anything like a luxuriant sward. In particular, although the rhizomatous grasses *F. rubra* and *P. pratensis*, and the far-creeping sedge *C. arenaria*, increase their cover here compared with most *Ammophila-Festuca* vegetation, they are still held in check, and coarser tussock species like *H. lanatus* and *D. glomerata*, or *Agrostis stolonifera*, only make any prominent contribution where the ground is kept a little moister. There thus remains ample room among them for the establishment of the numerous herbs characteristic of the *Festuca-Galium* community, many of them smaller rosette plants or low-growing chamaephytes susceptible to crowding out, together with the mosses that can find patchy representation among the herbage. With the maintenance of high pH, however, more calcifuge species are very scarce in this vegetation and, only in the *Luzula* sub-community, with its preferential records for *Agrostis capillaris* and *Anthoxanthum*, along with *L. campestris*, does the sward come at all close to the *Carex-Festuca-Agrostis* vegetation characteristic of siliceous or strongly surface-leached sands. Even in the *Luzula* sub-community, with the pH usually remaining about 6, the flora continues to be mixed, and the suites of more acidophilous mosses and lichens that are so striking a feature on acidic fixed dunes still do not make an appearance.

For the most part, then, the *Festuca-Galium* community has the look of a calcicolous sward, though one in which there is some modest amelioration of a harsh edaphic environment. The commonest plants are thus species like *G. verum*, *T. repens*, *L. corniculatus*, *P. lanceolata*, *A. millefolium*, *C. fontanum* and *E. officinalis* agg. which have a broad tolerance of fairly dry, quite nutrient-poor, base-rich soils and provide strong floristic continuity with a variety of inland grasslands of a less improved character. The ground is sufficiently limey and sharply-draining for the vegetation to provide an occasional place for the small tussock grass *K. macrantha*, and the frequent occurrence in some sub-communities of *T. praecox* enhances the similarity of the sward to the kinds of Mesobromion grasslands found on limestones in the warmer and drier south of Britain. However, it is interesting that, apart from very occasional *Ranunculus bulbosus*, very few of the other widely distributed calcicoles typical of rendziniform soils are found in the *Festuca-Galium* community and, and even where this sort of dune vegetation occurs around our warmer southern coasts, more thermophilous Mesobromion plants are likewise very scarce. With *Ononis repens*, which is very diagnostic of more southerly *Ammophila-Festuca* vegetation, this may have something to do with the fact that the *Festuca-Galium* swards are often grazed, but this would scarcely eliminate many of the pasture calcicoles. Only in the *Tortula* sub-community, which extends on to some of the most base-rich soils, with a pH often above 8, does the sward take on a little more of the

appearance of an open Mesobromion turf and, even then, with the patchy abundance of *T. ruralis* ssp. *ruraliformis* and *H. lutescens*, and scattered occurrence of *S. acre* and *A. vulneraria*, the resemblance is, not surprisingly, to the rather distinctive grasslands of some of the sandiest inland rendzinas, like those of Breckland.

Differences in regional climate have a marked effect on this general edaphic environment of the fixed sand surface, continuing and accentuating influences that have developed during earlier stages of dune colonisation and helping to distinguish the various sub-communities. Around our warmer and drier coasts, for example, south of the Solway–Forth line, mean annual maximum temperatures are usually above 25 °C (Conolly & Dahl 1970) and rainfall often as low as 1000 mm annually (*Climatological Atlas* 1952) with sometimes less than 140 wet days yr^{-1}, particularly to the south and east (Ratcliffe 1968). In these conditions, the fixed sands remain more drought-prone and the most widely-distributed sub-community in this part of the country, Typical *Festuca-Galium* vegetation, is often only a little less open and impoverished in its flora than the *Ammophila-Festuca* community of more mobile sands. More locally around these coasts, the *Luzula* and *Tortula* sub-communities bring some enrichment to the fixed dune swards, the first on the somewhat less base-rich surfaces, the second on those that are rather more so, but even here the herbage remains thin. It is among these kinds of *Festuca-Galium* vegetation, where open patches are more likely to develop in the sward in drier summers, particularly where there is heavy grazing by rabbits and locally by sheep, and where winter rains are insufficient to pose any threat of rotting to small rosettes, that winter annuals retain a somewhat better representation. Occasionally, then, species such as *Aira praecox*, *Erodium cicutarium*, *Cerastium diffusum* ssp. *diffusum*, *Viola tricolor*, *Vicia lathyroides* and *Trifolium campestre* bring additional diversity to the swards here.

Both the Typical and the *Luzula* sub-communities extend their range around the northern coasts of Britain, particularly to the east where, though mean annual maximum temperatures can fall below 24 °C (Conolly & Dahl 1970), with very cold winters (Chandler & Gregory 1976), the precipitation remains low (*Climatological Atlas* 1952, Ratcliffe 1968). The particular combination of climatic conditions favours the occurrence in the *Festuca-Galium* vegetation of this part of Britain of the Continental Northern *Astragalus danicus*, but apart from this there is often not much to distinguish these swards from more southerly stands. Along the west coast of northern Britain, however, the rainfall and temperature regimes are very different, with stretches of fixed dune often experiencing over 1200 mm precipitation annually (*Climatological Atlas* 1952) with more than 200 wet days yr^{-1} (Ratcliffe 1968), cool, cloud-ridden summers and relatively mild winters (Chandler & Gregory 1976, Page 1982). The influence of this is seen among the *Festuca-Galium* swards in this part of Britain, not so much in any striking phytogeographical response to the cool, oceanic conditions, but in the increased prominence of mesophytic plants benefiting from the more consistently moist character of the sand surface, even on ground that is well removed from the water-table. Thus, in the *Bellis-Ranunculus* and *Prunella* sub-communities, which make up much of the *Festuca-Galium* vegetation on the fixed sands of the western and northern Scottish coasts, through the Hebrides and on Orkney and Shetland, it is grasses like *H. lanatus* and, to a lesser extent, *A. stolonifera* and *Dactylis*, and dicotyledons such as *B. perennis*, *R. acris*, *P. vulgaris*, *E. officinalis* agg., *C. rotundifolia*, *T. pratense* and *R. repens* that give much of the distinctive character to the swards. Stands of these sub-communities can be all the more striking because they are often disposed over extensive stretches of the gently-undulating machair landscape, developed perhaps over many centuries where the profile of deposited sand has become closely adjusted to a low reception surface on hindshore rock platforms, raised beaches or terraces of drift (Ritchie & Mather 1974).

Throughout the range of the *Festuca-Galium* vegetation, grazing by rabbits, and often by stock, also has important effects on the composition and structure of the swards. For one thing, continual close cropping helps keep the herbage short, maintaining the diversity of smaller plants sensitive to shading by those able to make bulkier growth, and ultimately hindering any tendency to succession to ranker grasslands or scrub where soil conditions would favour this. Even on somewhat more fertile and moister sands, then, the community only locally takes on the look of Arrhenatherion or Rubion vegetation, with species like *Arrhenatherum elatius*, *Heracleum sphondylium*, *Daucus carota* and *Centaurea nigra* generally infrequent and nibbled back to short tufts or rosettes. Grazing animals also trample the sward and can disrupt the vegetation cover, making room for the spread of mosses or the fleeting appearance of annual plants in the community. More drastic disturbance, as by burrowing rabbits, can destroy stretches of the *Festuca-Galium* vegetation, precipitating renewed erosion of the sand, and perhaps a local rejuvenation of earlier stages in colonisation.

Sometimes, grazing works together with the edaphic and climatic conditions to maintain a generally harsh environment for the community. This is particularly the case where rabbit predation is heavy in *Festuca-Galium* vegetation around our drier southern coasts, when substantial removal of nutrients from the sward with the concentration of dung and urine latrines, can lead to a run-down of already droughty and impoverished soils, favouring a spread of plants like *Hieracium pilosella* and

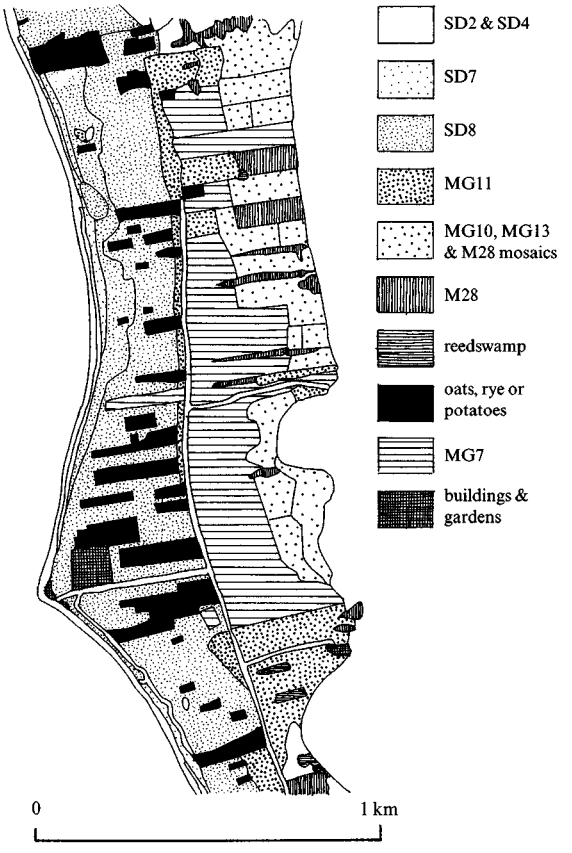
Homalothecium lutescens, which contribute to the distinctive character of the *Tortula* sub-community. In other cases, however, grazing animals may play an important part in enhancing the general trophic state of fixed dune soils by the distribution of urine and faeces across the sward. Sheep and, in some regions, cattle have been frequently pastured on stretches of *Festuca-Galium* vegetation, especially round our northern coasts, where enrichment from their manuring has combined with the moister climatic conditions to encourage the development of the more mesophytic character of the *Bellis-Ranunculus* and *Prunella* sub-communities. It is this particular kind of pastoral dune economy that has helped make the machair *Festuca-Galium* stands so distinctive because, through the Isles in particular, they have long provided important grazing on the township commons (Fraser Darling & Morton Boyd 1969, Knox 1974, Ranwell 1974). Under the old souming system, as it was called, these traditionally carried only moderate numbers of cattle, though they sometimes wintered larger burdens of stock, thus benefiting whole local areas by relieving the pressure on improved hill pasture. With an increasing switch to sheep since the early 1800s and the supplementing of natural manuring by the use of chemical fertilisers, the style and intensity of machair grazing has been much altered, and different patterns of past treatment may contribute to the floristic variations seen in the *Bellis-Ranunculus* and *Prunella* sub-communities.

It is also likely that machair stands of *Festuca-Galium* vegetation have often been influenced by the arable cultivation that began sporadically with the Viking occupation and which, over recent centuries, has brought large areas into rotational use, mainly for oats and potatoes, with resting under grass (Knox 1974, Ranwell 1974; see also Figure 13). Traditionally, seaweed has been spread on such fields, adding valuable bulk and nutrients to the light, infertile sands and such manuring may well have occurred on ground at present occupied by the community: certainly, in some places, the soils show a much deeper than usual dark loamy layer with beach cobbles betraying their past enrichment with loads of wrack (Fraser-Darling & Morton Boyd 1969). Also, there may be a local addition to the flora of *Lolium perenne* and *Cynosurus cristatus* from the seeded leys.

Zonation and succession

Where wind-blown sand has become stabilised over the surface of raised beaches, low shelves of rock or terraces of superficials set back but a little way from the shore, the *Festuca-Galium* community can occupy the first vegetated zone behind the beach top or cliffs. In more extensive dune systems, however, it typically occurs on older ridges or plains inland from tracts of somewhat more mobile sand, on which it is generally replaced by *Ammophila-Festuca* vegetation. There, with continuing modest accretion, *Ammophila* is more consistently prominent, retaining some vigour and holding its own against the smaller rhizomatous grasses, with more sporadic representation of the range of perennial herbs that only become really common as the surface is finally fixed. Often, though, the two communities intergrade, the boundaries between them depending on the varying proportions of marram and *F. rubra*, and the differing frequencies of associates such as *G. verum*, *L. corniculatus*, *P. lanceolata*, *C. fontanum*, *T. repens*, *H. radicata* and

Figure 13. Vegetation pattern in the machair landscape of the Outer Isles.
The dune system is fronted by narrow zones of SD2 *Honkenya-Cakile* and SD4 *Elymus farctus* vegetation and the SD7 *Ammophila-Festuca* community. Behind, the sand-plain has extensive areas of various kinds of SD8 *Festuca-Galium* grassland with scattered fields cultivated for oats and rye or potatoes or reverting as fallow to MG11 *Festuca-Agrostis-Potentilla* grassland. Behind large MG7 *Lolium* leys, are fields with mosaics of MG10 *Holco-Juncetum*, MG13 *Agrostis-Alopecurus* grassland and M28 *Filipendulo-Iridetum*, interspersed with purer stands of the last. (Redrawn from Dargie 1998, by permission of Scottish Natural Heritage).



https://doi.org/10.1017/CBO9780511541834.042 Published online by Cambridge University Press

Taraxacum. Around our southern coasts, the usual transition is from the *Ononis* sub-community of *Ammophila-Festuca* vegetation to the Typical or, more locally, the *Luzula* or *Tortula* sub-communities of the *Festuca-Galium* vegetation. Towards the north-west of Britain where, on the machair, stretches of stabilised sand are especially extensive, these generally carry the *Bellis-Ranunculus* or *Prunella* sub-communities, passing on younger dunes to Typical *Ammophila-Festuca* vegetation.

Particularly in southern Britain, locally bare areas within the *Festuca-Galium* Community often have patches of the *Tortulo-Phleetum*. With more abrupt transitions to areas of highly mobile sand, as where severe erosion has been precipitated among stable dunes following surface disturbance of some kind, stretches of *Festuca-Galium* vegetation can be punctuated by stands of the *Ammophila* community, where rejuvenated marram may be accompanied by little else at first among the shifting substrate. Or, where sand eventually settles in and around such blow-outs, the *Carex arenaria* community may develop, sharply marked off from the surrounding *Festuca-Galium* swards or grading to them as tillers of *F. rubra* and *Ammophila* spread in among the sedge.

Over fixed dunes where there is some variation in base-richness of the sand surface, the *Festuca-Galium* community is often accompanied by other swards, the zonations between the vegetation types being especially gradual where, as is frequently the case, grazing by stock or rabbits helps keep all the herbage short and diverse. Sometimes, it is the varied intensity of leaching of what seem to be fairly uniform sands that has produced differences in surface pH, but very commonly such patterns are influenced by contrasts in the lime-content of the wind-blown sediments, something which is usually dependent on the proportion of shell fragments to siliceous material. With a shift on to more acid sands, where the pH can fall from near 8 down to 5 or less, the *Festuca-Galium* community is often replaced by the *Carex-Festuca-Agrostis* grassland. There, marram remains similarly moribund but *F. rubra* is generally accompanied and sometimes replaced by *F. ovina* and, along with frequent and often abundant *C. arenaria*, there is commonly some *Agrostis capillaris* and *Anthoxanthum*, grasses which make only an occasional contribution to the *Festuca-Galium* community. Herbs such as *G. verum*, *L. corniculatus*, *C. fontanum*, *T. repens* and *Campanula rotundifolia* can remain fairly frequent, but *Galium saxatile* now becomes very common and, among the mosses, *Dicranum scoparium*, *Hylocomium splendens* and *Pleurozium schreberi* accompany *Rhytidiadelphus squarrosus* and *Pseudoscleropodium purum*. Generally, then, the sward has the look of a Nardo-Galion community rather than some kind of mesotrophic grassland although, again, transitions can be gradual, particularly where the *Luzula* sub-community of *Festuca-Galium* grassland passes to the *Anthoxanthum* sub-community of the *Carex-Festuca-Agrostis* vegetation, a zonation that is especially common in dune systems down the eastern Scottish and Northumberland coasts. In some places, such patterns are further complicated by the occurrence on compacted sand, or on sand–shingle mixtures, of the *Carex-Cornicularia* community, where the turf is much more open and where lichens such as *Cornicularia aculeata*, *Cladonia arbuscula*, *C. foliacea*, *C. impexa*, *C. furcata* and *C. fimbriata* are a very prominent feature.

Transitions from the *Festuca-Galium* community to more obviously calcicolous swards are much more local, but they can be seen where shell-sand has been deposited over exposures of limestone or calcareous drift with rendziniform soils. Along parts of the south Wales coast, for example, Carboniferous Limestone underlies some stretches of fixed dune, and in a few places the *Tortula* sub-community of *Festuca-Galium* vegetation passes to *Festuca-Hieracium-Thymus* grassland with the shift on to sandy rendzinas. *Ammophila*, *C. arenaria* and *F. rubra* largely disappear with this transition but among a grassy turf of *F. ovina* and *K. macrantha*, plants like *T. praecox*, *H. pilosella* and *S. acre* provide some continuity, together with *H. lutescens* and *P. purum* in what is often an extensive moss layer. Far to the north, where wind-blown sand has been deposited among exposures of Durness Limestone along the Sutherland coast, comparable zonations can be seen very locally between the *Bellis-Ranunculus* and *Prunella* types of *Festuca-Galium* grassland and the *Dryas-Carex* heath. Again, *Festuca-Galium* grassland and the *Dryas-Carex* heath. Again, *Ammophila* and *C. arenaria* drop out, while plants like *Dryas octopetala*, *Carex flacca*, *C. panicea*, *Plantago maritima* and *Antennaria dioica* become very common, but *L. corniculatus*, *B. perennis*, *G. verum*, *K. macrantha*, *T. praecox*, *H. pilosella* and *Homalothecium lutescens* continue to give character to many stands of the heath and some fine mosaics of the vegetation types have ill-defined boundaries.

The other important kind of edaphic variation that influences vegetation patterns on the fixed sands where the *Festuca-Galium* community occurs is related to the height of the ground water table. In depressions among undulating sand-plains or between ridges of immobile dunes, this can come close to the surface, keeping the ground very moist or waterlogged through much of the year, or even giving some flooding in winter. Then, the *Festuca-Galium* swards typically give way to some kind of slack vegetation, usually around the drier margins of more base-rich slacks, of the *Salix-Holcus* type. That community is quite varied, but some of the more moisture-tolerant plants of the *Festuca-Galium* vegetation

can run on into slacks with some frequency, *F. rubra*, *H. lanatus*, *C. arenaria*, *L. corniculatus*, *T. repens*, *Euphrasia officinalis* agg. and *Prunella* commonly making a contribution to the sward. With the appearance of *Salix repens*, however, and such associates as *Epipactis palustris*, *Carex panicea* and *Hydrocotyle vulgaris*, together with varied suites of other herbs and bryophytes, there is often little difficulty in discerning boundaries between the vegetation types, especially where sudden transitions to wetter ground occur among dunes in drier parts of the country with Typical *Festuca-Galium* forming the usual slack surround. In the wetter north-west of Britain, and particularly over the gently rolling sand-plains of the machair, the zonations can be less well defined because more moisture-demanding herbs extend further into the *Festuca-Galium* community and the slack vegetation tends not to be so strictly confined to lower depressions. Here, then, stretches of the more mesophytic *Bellis-Ranunculus* and *Prunella* sub-communities often pass more gradually into *Salix-Holcus* vegetation, sometimes with an intervening zone of the *Festuca-Agrostis-Potentilla* grassland. Wetter slacks then see a transition to the *Salix-Calliergon* or *Salix-Campylium* community. Where transitions to wetter ground also involve a reduction in the base-richness of the substrate, as with a shift on to moist acid sands, the *Potentilla-Carex* slack replaces the *Salix-Holcus* and these other communities in such sequences. There, it is the presence of mixtures of *P. anserina*, *C. nigra*, *S. repens*, *Galium palustre*, *Ranunculus flammula* and *Cardamine pratensis* that distinguish the damp swards, giving the look of a poor fen.

With the increased stability of the surface among fixed dunes, and the more hospitable nutrient and moisture regimes beneath the *Festuca-Galium* vegetation, there are enhanced possibilities of seral progression to scrub or woodland. Very commonly, though, such succession is held in check by the grazing of stock or rabbits, so that the community is maintained as a plagioclimax. Where there is some relief from the predations of herbivores, *Festuca-Galium* swards can grow more rank, grasses such as *F. rubra*, *H. lanatus* and *Dactylis* taking on a more tussocky appearance, and herbs like *Heracleum*, *Centaurea nigra* and *Daucus carota* growing up tall from their basal rosettes, producing something like a *Centaureo-Cynosuretum*. More locally, but especially along the north-east coast of England, the *Ammophila-Arrhenatherum* community can occur among *Festuca-Galium* vegetation where there is little or no grazing. Here, *F. rubra* and *Ammophila* can both persist in some quantity, with *P. pratensis*, *H. lanatus*, *A. millefolium*, *G. verum* and *L. corniculatus* also often present, but *Arrhenatherum* is a very common and sometimes abundant feature, with frequent *Dactylis*, *Veronica chamaedrys* and *Heracleum* confirming the character of an Arrhenatherion sward. On warmer dune slopes, the additional presence of *Geranium sanguineum* and patches of *Rosa pimpinellifolia* can mark out such transitions even more strikingly.

Continued freedom from grazing can allow the invasion of *Rubus fruticosus* agg. among the *Festuca-Galium* grassland producing patches of *Rubus-Holcus* underscrub, with rank growth of *F. rubra*, *P. pratensis*, *H. lanatus*, *Dactylis*, *Arrhenatherum* and umbellifers around the bramble, or bracken may spread in stands of *Pteridium-Rubus* vegetation. In other cases, the removal or demise of herbivores has allowed the direct invasion of trees, birch frequently figuring prominently in such successions, with conifers sometimes seeding in from nearby plantations. Where reduction of grazing has taken place on patchworks of *Festuca-Galium* grassland and *Carex-Festuca-Agrostis* swards on more acid sands, rank derivatives of the former often persist among some kind of *Calluna-Carex* heath, where mixtures of *Calluna vulgaris* with *Erica cinerea* or *Empetrum nigrum* ssp. *nigrum* are characteristically dominant among calcifuge herbs, bryophytes and lichens.

Landward patterns among stretches of *Festuca-Galium* vegetation are often further confused by various kinds of dune reclamation or improvement. Sometimes, but a small zone of natural fixed dune persists as a fringe to a golf course, on which the *Festuca-Galium* swards may survive only in a modified form in periodically mown rough, or to pasture where the community has been entirely replaced by sown *Lolio-Cynosuretum* or Lolio-Plantaginion leys. More strikingly, on the machair, *Festuca-Galium* grassland can be seen among extensive patchworks of rotational arable land, having escaped cultivation or being in various stages of reversion after short periods under the plough. Finally, on many dune systems, stands of the community give way abruptly to conifer plantations established on the stable sand.

Distribution

The *Festuca-Galium* grassland can be found on suitable stable dunes and sand plains all around the British coast. The Typical sub-community occurs throughout the range, and along our more southerly coasts it is the major type, with the *Luzula* and especially the *Tortula* sub-communities more locally represented. The *Bellis-Ranunculus* and *Prunella* swards, by contrast, are almost wholly confined to the north-west Scottish coast and the Isles.

Affinities

Although reference was made in early descriptions of British dune vegetation to grassland of this general type (Tansley 1911, 1939, Gimingham 1964*a*), there was no systematic attempt to characterise a distinct community or define the floristic variation within it. Likewise, accounts of machair vegetation, while stressing the

peculiarity of the habitat, have often been rather vague, doing little to distinguish this kind of grassland from other swards represented there, or to compare it with other assemblages of fixed dunes from elsewhere in Britain (Gimingham 1964*a*, 1974, Ranwell 1974). Only with Birse's (1980, 1984) scheme do we have anything like a broadly-based definition, and even then this gives us just a Scottish perspective. Birse also splits his samples of this sort of sward into two associations, his *Euphrasio-Festucetum* corresponding with our *Bellis-Ranunculus* and *Prunella* sub-communities, while what is here retained as a *Luzula* sub-community is separated off into an *Astragalo-Festucetum*. This also includes dune grassland which, while retaining frequent records for *A. danicus*, is more calcifuge in character than our *Festuca-Galium* vegetation, being included in our scheme in the *Carex-Festuca-Agrostis* community.

Birse (1980, 1984) placed his grassland of this kind within the Koelerion albescentis of the Sedo-Scleranthetea (or Galio-Koelerion of the Koelerio-Corynephoretea as Westhoff & den Held (1969) have it), but affinities with the emphemeral-rich swards of sandy soils are really only clearly seen here in the *Luzula* and *Tortula* sub-communities. An alternative view would be to retain the *Festuca-Galium* grassland within the Ammophilion, although *Ammophila* and other pioneer dune plants are by this time patchy in their representation. The other obvious affinity of this vegetation, especially well seen in the *Bellis-Ranunculus* and *Prunella* sub-communities, is with the grazed swards of among the Arrhenatheretalia. For all the particular character of the machair environment, the combination of habitat factors operative there tends to move the composition of the fixed dune grasslands close to some of the richer mesotrophic pastures of unimproved soils in lowland Britain.

Floristic table SD8

	a	b	c	d	e	8
Festuca rubra	V (1–10)	V (2–9)	V (2–9)	V (3–9)	V (5–10)	V (1–10)
Galium verum	V (1–7)	V (1–8)	V (2–6)	IV (1–7)	V (2–7)	V (1–8)
Plantago lanceolata	V (1–7)	IV (1–7)	IV (2–4)	V (1–8)	V (1–5)	V (1–8)
Trifolium repens	IV (1–8)	IV (1–6)	IV (2–6)	V (1–8)	IV (2–7)	IV (1–8)
Lotus corniculatus	IV (1–9)	V (1–7)	III (2–5)	IV (1–7)	IV (2–6)	IV (1–9)
Poa pratensis	IV (1–7)	V (1–7)	II (2–5)	IV (1–8)	IV (2–7)	IV (1–8)
Cerastium fontanum	II (1–4)	IV (1–5)	II (1–3)	III (1–4)	III (1–3)	III (1–5)
Luzula campestris	I (1–4)	IV (1–5)	I (2–3)	II (1–5)	II (2–3)	II (1–5)
Hieracium pilosella	I (1–5)	III (1–7)	II (3–4)	I (1–3)	II (2–3)	I (1–7)
Veronica chamaedrys	I (1–5)	III (1–5)	I (3)	I (2)	I (2)	I (1–5)
Agrostis capillaris	I (1–7)	III (1–7)	I (3)	I (1–6)		I (1–7)
Anthoxanthum odoratum	I (2–4)	II (1–8)	I (5)	I (2–5)	I (4–7)	I (1–8)
Brachythecium albicans	I (1–6)	II (1–7)	I (1)	I (1–5)		I (1–7)
Hypochoeris radicata	I (1–4)	II (1–6)		I (2)		I (1–6)
Festuca ovina	I (1–5)	II (1–7)		I (1–5)		I (1–7)
Climacium dendroides	I (2–4)	II (1–5)		I (2–7)		I (1–7)
Astragalus danicus	I (3–4)	II (2–7)				I (2–7)
Rumex acetosella		I (1–4)				I (1–4)
Cerastium arvense		I (1–4)				I (1–4)
Myosotis arvensis		I (1–3)				I (1–3)
Veronica arvensis		I (1–4)				I (1–4)
Homalothecium lutescens	I (1–4)	I (2–6)	V (2–7)	III (1–9)	I (2–3)	II (1–7)
Tortula ruralis ruraliformis	I (1–9)	I (1–6)	V (2–9)	I (1–8)	I (3–4)	I (1–9)
Polygala vulgaris	I (1–4)	I (1–4)	II (2–4)	I (1–5)	I (2–3)	I (1–5)
Sedum acre	I (1–4)	I (1–4)	II (2–4)	I (1–2)		I (1–4)
Anthyllis vulneraria	I (4)	I (1–7)	II (2–6)	I (1–4)		I (1–7)
Bellis perennis	II (1–8)	I (1–7)	III (2–6)	IV (1–6)	II (1–4)	III (1–8)
Ranunculus acris	II (1–5)	I (1–3)	III (1–4)	IV (1–5)	II (1–3)	III (1–5)
Agrostis stolonifera	I (2–5)	I (1–5)	I (2–3)	II (1–7)	I (3)	I (1–7)
Vicia cracca				I (1–3)		I (1–3)

Floristic table SD8 (*cont.*)

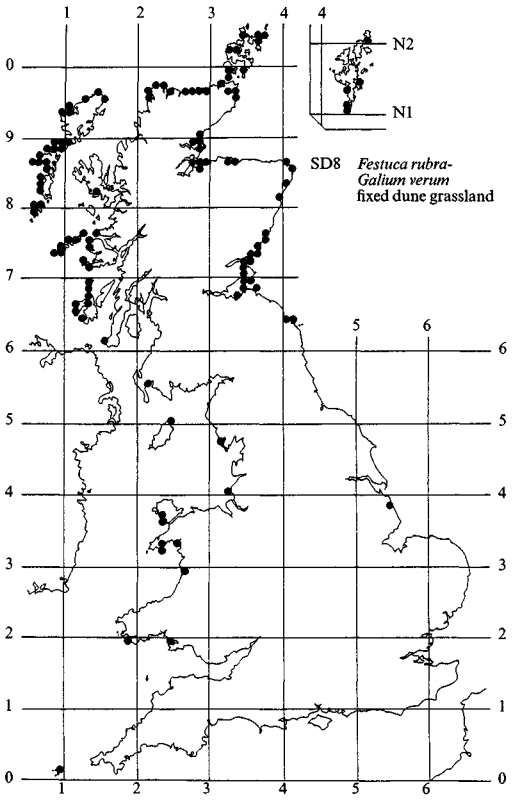
	a	b	c	d	e	8
Senecio jacobaea	III (1–5)	II (1–4)	III (1–5)	III (1–6)	IV (1–5)	III (1–6)
Euphrasia officinalis agg.	I (1–5)	I (1–6)	II (1–5)	IV (1–7)	V (1–6)	II (1–7)
Holcus lanatus	I (1–6)	II (1–8)	I (2–3)	III (1–6)	V (3–7)	II (1–8)
Linum catharticum	I (2–4)	II (1–5)	I (1–3)	II (1–4)	IV (1–5)	II (1–5)
Campanula rotundifolia	I (1–5)	II (1–5)	I (2–3)	I (1–2)	IV (1–4)	I (1–5)
Prunella vulgaris	I (2)	I (1–3)	I (2–6)	II (1–5)	IV (1–5)	I (1–6)
Rhytidiadelphus triquetrus	I (1–9)	II (1–9)	I (3–5)	I (1–8)	III (2–7)	I (1–9)
Calliergon cuspidatum	I (1)	I (1–6)	I (2–3)	II (1–8)	III (2–7)	I (1–8)
Trifolium pratense	I (1–4)	I (2–6)		II (1–6)	III (2–5)	I (1–6)
Carex flacca	I (1–6)	I (1–6)		II (1–6)	III (3–5)	I (1–6)
Gentianella amarella	I (3)	I (1–4)		I (1–4)	III (1–4)	I (1–4)
Centaurea nigra	I (1–7)	I (2–6)	I (1–4)	I (2–5)	II (2–7)	I (1–7)
Ranunculus repens	I (1–4)	I (1–4)	I (2–3)	I (1–6)	II (2–6)	I (1–6)
Lophocolea bidentata	I (1–4)	I (1–5)	I (3–5)	I (2–5)	II (2–7)	I (1–7)
Daucus carota	I (1–5)	I (3)	I (2–5)	I (1–4)	II (2–8)	I (1–8)
Plagiomnium undulatum	I (1–4)	I (1–6)		I (1–5)	II (2–4)	I (1–6)
Salix repens					I (3–8)	I (3–8)
Leucanthemum vulgare					I (3–8)	I (3–8)
Ammophila arenaria	III (2–9)	IV (2–8)	V (2–8)	II (1–6)	III (3–8)	III (1–9)
Rhytidiadelphus squarrosus	II (1–9)	III (1–8)	IV (2–7)	IV (1–8)	IV (2–8)	III (1–9)
Carex arenaria	III (1–7)	III (1–7)	III (2–5)	II (1–9)	II (1–3)	III (1–9)
Achillea millefolium	III (1–5)	II (1–4)	II (1–3)	III (1–8)	III (1–3)	III (1–8)
Thalictrum minus	II (1–7)	I (1–6)	III (2–6)	II (1–7)	III (1–7)	III (1–7)
Thymus praecox	I (1–8)	III (1–8)	II (2–7)	I (1–8)	III (1–7)	II (1–8)
Pseudoscleropodium purum	I (1–3)	III (1–7)	I (3)	I (1–4)	III (2–6)	II (1–7)
Koeleria macrantha	I (1–7)	II (1–7)	I (3–6)	I (2–6)	II (1–6)	II (1–7)
Viola riviniana	I (1–6)	II (1–6)	I (1–5)	I (1–5)	II (1–5)	I (1–6)
Heracleum sphondylium	II (1–8)	I (1–5)	I (2–3)	II (1–8)	II (2–5)	I (1–8)
Peltigera canina	I (5)	II (1–5)	II (2–3)	I (1–4)	I (1–3)	I (1–5)
Dactylis glomerata	II (1–8)	I (1–5)		I (1–6)	II (2–4)	I (1–8)
Viola tricolor	I (4)	I (1–7)	II (1–4)	I (1–4)	II (2–3)	I (1–7)
Hylocomium splendens	I (2–6)	II (1–8)		I (1–2)	II (1–5)	I (1–8)

Taraxacum officinale agg.	II (1–5)	II (1–4)		I (1–5)		I (1–5)
Ranunculus bulbosus	I (1–3)	I (1–5)	I (1)	I (1–4)	I (1–4)	I (1–5)
Hypnum cupressiforme	I (1–7)	I (1–9)	I (3)	I (1–5)	I (2)	I (1–9)
Elymus repens	I (1–6)	I (1–5)	I (2)	I (2–4)	I (2)	I (1–6)
Succisa pratensis	I (4)	I (3)	I (3)	I (2–4)	I (1–3)	I (1–4)
Elymus farctus	I (1–4)	I (1–2)	I (3–4)	I (1–3)	I (3)	I (1–4)
Avenula pubescens	I (2–8)	I (2–4)	I (4–5)	I (2–8)	I (2–4)	I (2–8)
Plagiomnium rostratum	I (2)	I (1–3)	I (3)	I (2–4)	I (2–3)	I (1–4)
Primula vulgaris	I (1–7)	I (1)	I (3)	I (2–4)	I (2–3)	I (1–7)
Plantago major	I (1–4)	I (2)	I (3)	I (2)	I (2–3)	I (1–4)
Plantago coronopus	I (1–4)	I (1–3)	I (2–4)	I (1–3)		I (1–4)
Cirsium vulgare	I (1–3)	I (1)	I (1–2)	I (1)		I (1–3)
Erodium cicutarium	I (1–4)	I (1–5)	I (3–4)	I (2–3)		I (1–5)
Rhinanthus minor	I (1–7)	I (1–4)		I (1–6)	I (2–4)	I (1–7)
Lolium perenne	I (1–6)	I (4)		I (1–5)	I (3–5)	I (1–6)
Primula veris	I (4)	I (1–6)		I (1–2)	I (3–4)	I (1–6)
Eurhynchium praelongum	I (1–3)	I (1–4)		I (1–3)	I (2–4)	I (1–4)
Equisetum arvense	I (1–2)	I (1–4)		I (1–3)	I (1–3)	I (1–4)
Crepis capillaris	I (1–4)		I (2–3)	I (1–4)	I (3)	I (1–4)
Entodon concinnus	I (6)		I (3–8)	I (2–3)	I (2–8)	I (2–8)
Cirsium arvense	I (1–3)		I (2)	I (1–3)	I (1)	I (1–3)
Plantago maritima	I (2–4)	I (1–5)			I (2–3)	I (1–5)
Trisetum flavescens	I (1–5)	I (1–3)		I (1)		I (1–5)
Leymus arenarius	I (1–6)	I (1–4)		I (1)		I (1–6)
Potentilla anserina	I (2–3)	I (1)		I (1–7)		I (1–7)
Poa trivialis	I (1–3)	I (2)		I (1–5)		I (1–5)
Aira praecox	I (3–7)	I (1–4)		I (1)		I (1–7)
Leontodon autumnalis	I (2–4)	I (1–3)		I (1–6)		I (1–6)
Rumex acetosa	I (1–3)		I (1–3)	I (1–4)		I (1–4)
Peltigera rufescens	I (1)		I (2–3)	I (2–4)		I (1–4)
Cerastium semidecandrum	I (1–3)		I (2–3)	I (1–3)		I (1–3)
Angelica sylvestris	I (1–5)		I (3)		I (3)	I (1–5)
Odontites verna	I (2–4)			I (2–4)	I (2–5)	I (2–5)
Ditrichum flexicaule			I (2–4)	I (2–4)	I (3–5)	I (2–5)
Thuidium tamariscinum		I (1–3)		I (3–4)	I (3–4)	I (1–4)
Arrhenatherum elatius	I (1–4)				I (3)	I (1–4)

Floristic table SD8 (*cont.*)

	a	b	c	d	e	8
Cerastium diffusum diffusum	I (1–3)				I (2)	I (1–3)
Medicago lupulina	I (1–5)				I (3)	I (1–5)
Cynosurus cristatus	I (1–4)				I (2–3)	I (1–4)
Elymus pycnanthus	I (1–4)	I (2)				I (1–4)
Carex caryophyllea	I (1)	I (1–4)				I (1–4)
Rosa pimpinellifolia	I (1–5)	I (2–8)				I (1–8)
Trifolium campestre	I (1–3)	I (1–4)				I (1–4)
Vicia lathyroides	I (1–3)	I (1–4)				I (1–4)
Ononis repens	I (1–6)		I (1–7)			I (1–7)
Pleurozium schreberi		I (2–5)		I (2)		I (2–5)
Cladonia rangiformis		I (1–5)			I (2)	I (1–5)
Myosotis ramosissima		I (1–4)			I (2)	I (1–4)
Sonchus oleraceus			I (1–2)	I (2)		I (1–2)
Thuidium delicatulum		I (1–2)			I (3–4)	I (1–4)
Listera ovata		I (2)			I (1–4)	I (1–4)
Coeloglossum viride				I (1–3)	I (2–3)	I (1–3)
Number of samples	111	117	36	129	25	418
Number of species/sample	15 (7–26)	23 (15–33)	18 (9–25)	20 (14–30)	24 (16–32)	20 (7–33)
Vegetation height (cm)	19 (1–80)	16 (2–70)	18 (2–50)	12 (2–84)	19 (3–63)	16 (1–84)
Vegetation cover (%)	85 (30–100)	82 (40–100)	No data	88 (60–100)	No data	84 (30–100)
Slope (°)	7 (0–40)	7 (0–45)	25 (0–60)	7 (0–40)	8 (0–50)	8 (0–60)
Soil pH	7.8 (4.6–9.3)	7.2 (4.7–9.0)	8.5 (8.3–9.2)	8.2 (7.5–8.9)	8.2 (7.7–8.6)	7.8 (4.6–9.3)

a Typical sub-community
b *Luzula campestris* sub-community
c *Tortula ruralis* ssp. *ruraliformis* sub-community
d *Bellis perennis-Ranunculus acris* sub-community
e *Prunella vulgaris* sub-community
8 *Festuca rubra-Galium verum* fixed dune community (total)



https://doi.org/10.1017/CBO9780511541834.042 Published online by Cambridge University Press