

SD12

Carex arenaria-*Festuca ovina*-*Agrostis capillaris* dune grassland

Synonymy

Dune grassland Pearsall 1934; Dune pasture Gimingham 1964a *p.p.*; *Astragalo-Festucetum arenariae* Birse 1980 *p.p.*

Constant species

Agrostis capillaris, *Ammophila arenaria*, *Carex arenaria*, *Festuca ovina*, *Poa pratensis*.

Rare species

Astragalus danicus.

Physiognomy

The *Carex arenaria*-*Festuca ovina*-*Agrostis capillaris* community comprises short, generally closed swards dominated by various mixtures of *Carex arenaria* and a number of grasses, of which *Festuca ovina*, *Agrostis capillaris* and *Poa pratensis* *s.l.* are the most frequent and abundant. *F. rubra* also occurs quite commonly, and *Anthoxanthum odoratum*, *Luzula campestris* and *Holcus lanatus* are variously represented in the different sub-communities, with *Koeleria macrantha* occasional. *Ammophila arenaria* persists at high frequency, too, though it hardly ever shows any vigour, being usually reduced to sparse and debilitated shoots.

Dicotyledonous herbs are rather few in number, but the assemblage is distinctive, with *Galium saxatile*, *Lotus corniculatus*, *Galium verum*, *Cerastium fontanum* and *Rumex acetosella* occasional to frequent throughout. In some stands, *Hypochoeris radicata*, *Thymus praecox* and *Hieracium pilosella* become more common, with *Campylosiphium rotundifolium*, *Viola riviniana* and *Achillea millefolium* occurring more often in others. Compared with more open dune swards, however, ephemeral plants are noticeably scarce. There are very occasionally some scattered bushes of *Calluna vulgaris*, frequently nibbled down, but any increase in the cover of ericoid sub-shrubs usually marks a transition to heath.

Bryophytes are fairly numerous and sometimes abundant in the sward and, though *Dicranum scoparium* is

very common, it is bigger pleurocarps that are generally more obvious, with frequent records for *Rhytidiadelphus squarrosus*, *Pseudoscleropodium purum*, *Hylocomium splendens* and *Pleurozium schreberi* and more occasional occurrences of *Rhytidiadelphus triquetrus* and *Hypnum cupressiforme*. *Brachythecium albicans*, *Polytrichum juniperinum* and *Ceratodon purpureus* also occur in some stands.

Lichens are generally not so numerous or extensive in their cover, and certainly nothing like so prominent as in the *Carex*-*Cornicularia* community. However, *Peltigera canina* is occasionally found and there can be patches of *Cladonia arbuscula*, *C. rangiformis* and *Cornicularia aculeata*.

Sub-communities

***Anthoxanthum odoratum* sub-community.** *F. ovina*, occasionally accompanied or sometimes replaced by *F. rubra*, is the usual dominant in this sub-community, with mixtures of varying amounts of *C. arenaria*, *A. capillaris*, *P. pratensis* and, preferentially frequent here, *Anthoxanthum*. *Ammophila* is constant but rarely of even moderate cover and usually distinctly moribund. *L. campestris* is also preferential at low cover, with occasional *K. macrantha* and, of more local occurrence, *Danthonia decumbens* and *Deschampsia flexuosa*. In contrast to the other sub-community, *H. lanatus* is not very common.

Among the dicotyledons of the community, *G. saxatile*, *L. corniculatus*, *C. fontanum* and *R. acetosella* remain frequent, with *G. verum*, *Trifolium repens* and *Veronica officinalis* more occasional while, among the preferentials, *Hypochoeris radicata* is often found. With the appearance of plants such as *Thymus praecox*, *Hieracium pilosella* and *Plantago lanceolata*, the sward may take on something of the look of a calcicolous grassland, while other stands can have *Potentilla erecta* and scattered clumps of *Calluna*, *Erica cinerea* or even *E. tetralix* in transitions to damper heath. In some sites, the

Anthoxanthum sub-community also provides a locus for *Astragalus danicus*.

The community mosses *D. scoparium*, *R. squarrosus*, *P. purum*, *H. splendens* and *Pleurozium schreberi* all remain common and each is able to show considerable local abundance, while *Rhytidiadelphus triquetrus* and *Hypnum cupressiforme* occur more occasionally, with *Polytrichum junipericum* preferential at low frequency and cover.

***Holcus lanatus* sub-community.** *C. arenaria* is generally the most abundant plant here, with *A. capillaris*, *F. ovina* (and occasional *F. rubra*) and *P. pratensis* making up much of the rest of the sward. However, in contrast to the previous sub-community, *H. lanatus* is very common and it can be moderately abundant, while *Anthoxanthum* and *L. campestris* are only occasional. *Ammophila* is also rather patchy in its occurrence here, though locally it may retain some vigour and show strongly tussocky growth.

G. saxatile and *R. acetosella* remain frequent in the sward, together with *L. corniculatus* and *C. fontanum*, but *H. radicata* is much less common and there is preferential *C. rotundifolia*, *V. riviniana* and *A. millefolium* with *Prunella vulgaris* and *Ranunculus repens* in some stands. Most of the bryophytes of the community remain frequent and *Ceratodon purpureus* is preferentially common, but these plants are not usually so abundant as in the *Anthoxanthum* sub-community.

Habitat

The *Carex-Festuca-Agrostis* grassland is characteristic of grazed stretches of fixed, acidic sands around the coasts of Britain, developing where quartz sand has become stabilised or more calcareous wind-blown sediments leached with the passage of time. It is thus most often found on areas of subdued relief among older dunes and on long-established sand plains, and is commoner towards the north and west where the wetter and cooler climate enhances leaching and providing some protection against drought.

Even more so than the *Festuca-Galium* grassland, this is a community of fixed sand surfaces, attaining its best development only where accretion has fallen to negligible levels and where erosion is limited to areas of disturbed ground. On more sheltered coasts, stands may be set back just a short way inland but this kind of vegetation is usually found on surfaces which are now far removed from sources of mobile material. Thus, although *Ammophila* persists at high frequency and may show a measure of renewed vigour locally when there is the occasional bout of fresh deposition of sand, it generally survives as a puny relic exerting next to no influence on the character of the substrate or the structure of the vegetation (Gimingham 1964a; Huiskes 1979). Also lim-

iting to its growth here is the fact that the sands are base-poor, at least in the upper layers, the surface pH being usually below 5 (Salisbury 1952, Willis *et al.* 1959a, b; Huiskes 1977a, 1979). In places where the wind-blown sediments are lime-rich, as where shell fragments make up a considerable proportion of the sands, such superficial acidity may develop only after very prolonged leaching (Ranwell 1972, Willis 1985b), which is one reason why this community is still of only local occurrence on many stretches of machair: there, despite the considerable age of the surfaces and the very wet climate, the ground often remains markedly calcareous. By contrast, on those dune systems where the sediments are largely made up of quartz sand, younger stable surfaces can offer a congenial substrate for this vegetation, even in regions where the climate is much drier.

The occurrence of suitably siliceous sands of Pliocene and Pleistocene origin around the coast of East Anglia gives the *Carex-Festuca-Agrostis* community some important outposts in the drier and warmer south-east of Britain, but most stands of this vegetation are found further north and west. There, annual rainfall of more than 800 mm (*Climatological Atlas* 1952), with usually over 140 wet days yr⁻¹ (Ratcliffe 1968), and mean annual maxima often below 25 °C (Conolly & Dahl 1970), help maintain the distinctive character of these swards on sands which were initially more calcareous. Also, the greater consistency of the rainfall and the cloudier character of the climate help protect the vegetation against the tendency of the ground to parching. Older soils here, with some accumulation of organic matter in their upper layers, can be more moisture-retentive than the raw sands of younger dunes, but the plants are still largely dependent on regular rainfall for sustained growth.

This combination of edaphic and climatic features gives the *Carex-Festuca-Agrostis* grassland much of its distinctive floristic and structural character. As in the *Festuca-Galium* swards, the waning of the dominance of *Ammophila* on the more fixed sand surface allows the smaller rhizomatous plants like *C. arenaria*, *P. pratensis* and *F. rubra* to increase their contribution, though here, perhaps with the reduction of any influence of salt-laden winds, *F. ovina* is often the more prominent fescue. More obvious than this, however, is the better representation of calcifuges. On these more acidic soils, *C. arenaria* itself thrives better than *Ammophila* (Huiskes 1979, Noble 1982), but more diagnostic against the *Festuca-Galium* grassland are *A. capillaris*, *Anthoxanthum* and *G. saxatile* which usually exceed in frequency plants like *L. corniculatus*, *G. verum*, *T. repens* and *P. lanceolata*. Then, among the bryophytes, there is the common occurrence of such species as *D. scoparium*, *H. splendens* and *P. schreberi*. When all of these are well represented, as in the *Anthoxanthum* sub-community, the impression is of

a Nardo-Galium grassland with little of the calcicolous or mesophytic aspect seen in many *Festuca-Galium* swards.

However, compared with the *Carex-Cornicularia* community, which is the other herbaceous vegetation of fixed, acidic sands, the *Carex-Festuca-Agrostis* grassland generally has a more closed and less tussocky cover, something which reflects the less droughty character of the soils here. In the *Carex-Cornicularia* swards, most of the perennials perform rather poorly, with even *C. arenaria* often in a senile phase (Noble 1982) and the grasses frequently patchy and prone to parching in summer. Here, by contrast, the sedge and grass matrix is more or less continuous and usually retains its fresh green colour throughout the year. *Poa pratensis* becomes constant, too, a good marker of better moisture supply within the sands and then, in the *Holcus* sub-community, there is the frequent appearance of *H. lanatus*, *V. riviniana* and *A. millefolium*. The development of this kind of *Carex-Festuca-Agrostis* grassland may reflect treatment differences, but it could also extend the community on to damper and less impoverished ground around dune hollows. Certainly, it has an aspect never seen in the *Carex-Cornicularia* community.

Even in the *Anthoxanthum* sub-community, however, there are other obvious floristic distinctions. Thus, while light-demanding perennial herbs such as *H. radicata*, *R. acetosella* and *T. praecox* remain quite common in the short swards, ephemerals able to capitalise rapidly on the appearance of bare patches are decidedly scarce. Then, among the cryptogams, it is not drought-tolerant lichens that dominate, with acrocarpous mosses colonising open areas, but moisture-demanding pleurocarpous mosses that form a sometimes abundant web among the turf.

In addition to these environmental effects, however, there is the influence of grazing because this is almost always a plagioclimax vegetation maintained by the predation of herbivores. More particularly, it is probably stock, as much as or more than rabbits, which are important here. With the *Carex-Cornicularia* community, rabbit grazing is (or has been) a very likely influence in maintaining the impoverished condition of the soils and favouring the abundance of lichens in the sward, as well as keeping the herbage very short. With the *Carex-Festuca-Agrostis* grassland, sheep and cattle can crop the vegetation close, helping to maintain some diversity among the vascular plants, but their heavier trampling is destructive of lichens. Further, because their faeces and urine are distributed over the sward, rather than concentrated into latrines, they can have a considerable manurial effect, enhancing the nutrient status of the sands and increasing moisture retention with the accumulation of an organic fraction. Such effects are perhaps especially important in the development of the more mesophytic

Holcus sub-community which may be associated with the greater enrichment and less assiduous cropping that cattle, rather than sheep, bring. But, whatever the herbivores, they are ultimately important in holding in check the invasion or spread of any ericoids or shrubs and trees and, without their predation, most stands would probably progress quickly to heath or woodland.

Zonation and succession

The *Carex-Festuca-Agrostis* community is typically found in zonation and mosaics with other grasslands and heath on the fixed sands of the hinterland of coastal dunes and sand plains, where the vegetation patterns are primarily determined by edaphic variation and differences in treatment. Relaxation of grazing mediates a succession to heath or woodland, but most stands are maintained by continuing use as pasture for stock. Where stretches of fixed dunes have been reclaimed for more intensive agricultural use or for forestry or amenity purposes, the *Carex-Festuca-Agrostis* grassland may survive more fragmentarily among improved swards or arable land, plantations or golf-course greens.

Among the other kinds of grassland found on fixed sands, the community is most often seen with some type of *Festuca-Galium* vegetation, grading to this where the ground is more base-rich, with substrates of shell-sand that is not so strongly leached or periodically renewed by very modest accretion. Species like *C. arenaria*, fescues and *P. pratensis* continue to provide much of the cover in a fairly short sward with just scattered tufts of *Ammophila*, but *F. rubra* generally exceeds *F. ovina*, and there is usually a more consistent occurrence of *G. verum*, *P. lanceolata*, *T. repens*, *L. corniculatus* and *A. millefolium*. In the *Luzula* sub-community, however, *L. campestris*, *A. capillaris*, *F. ovina* and *Anthoxanthum* become quite common and this sort of *Festuca-Galium* sward may pass imperceptibly to the *Anthoxanthum* sub-community of the *Carex-Festuca-Agrostis* grassland where there are gentle shifts in the base-richness of the sands. On somewhat moister and less impoverished ground, the *Holcus* sub-community of the *Carex-Festuca-Agrostis* grassland may grade to the *Prunella* type of *Festuca-Galium* sward.

Where the sand retains a greater degree of mobility with the move on to younger dunes, the *Festuca-Galium* grassland passes in turn to *Ammophila-Festuca* vegetation, where marram is still vigorous on the upbuilding surface and where the associates make up an often patchy cover between the tussocks. Sometimes, the *Carex-Festuca-Agrostis* grassland itself gives way to the *Ammophila-Festuca* community in places where the sand has become mobile again with disturbance of the surface, but more often, and particularly where the sands are acidic, it is the *Carex arenaria* community that is the secondary colonising vegetation. In that vegetation, the

cover can be much more open at first, with rejuvenated *C. arenaria* extending its rhizomes out through the loose sand, but the sedge may thicken up in time, and other associates appear, with tussocks of the fescues and scattered *R. acetosella* and *P. lanceolata* providing a measure of continuity with the more intact swards around. Indeed, on base-poor sands, this kind of invasion may be the natural line of primary succession that leads eventually to the development of *Carex-Festuca-Agrostis* grassland.

On coasts in warmer and drier parts of Britain, and more locally elsewhere, the community can also be found on acidic sands with the *Carex-Cornicularia* vegetation. In that assemblage, the sedge cover thins and the perennial grasses are reduced to scattered tussocks, with just occasional rosette herbs and patches of chamaephytes and, very strikingly, a switch to lichens rather than pleurocarps as the dominant cryptogams. Such a change can be associated with concentrated rabbit activity, but exposure to parching on sunnier dune slopes may also favour the development of the *Carex-Cornicularia* community on old erosion surfaces that have compacted and impoverished sands.

Both the *Carex-Cornicularia* and especially the *Carex-Festuca-Agrostis* community are prone to invasion by *Calluna* and other ericoids where grazing is lax. In drier parts of the country, where both these vegetation types can contribute to the swards on fixed acid sands, colonisation by heather usually leads to the development of the *Calluna-Festuca* heath, where *C. arenaria* can remain locally prominent with *F. ovina* and occasional *A. capillaris*, *G. saxatile* and *R. acetosella*, along with *D. scoparium* and *H. cupressiforme* in the ground carpet. *Erica cinerea* may also occur in such heath in East Anglia, but this plant becomes much more common in northern and western localities where the *Calluna-Carex* heath is the usual kind of dune ericoid vegetation. Here again, mixtures of sub-shrubs, *C. arenaria* and *F. ovina* provide a diagnostic element, but *L. campestris*, *Anthoxanthum* and various bryophytes give greater floristic continuity with the *Carex-Festuca-Agrostis* grassland. In this type of dune heath in eastern Scotland, *Empetrum nigrum* tends to replace *E. cinerea* as the associated sub-shrub.

Quite often, where grazing has fluctuated in intensity complex mosaics of heath and grassland occur on pas-

tured dunes, the expansion of the sub-shrubs within the *Carex-Festuca-Agrostis* community being held or pushed back by renewed predation by stock. Elsewhere, neglect has allowed the development of leggy heather which excludes virtually all associates until it begins to degenerate. Or, where seedling shrubs and trees get away, there may be transitions to scrub or woodland, with birch and pine, more locally oak, leading a succession to Quercion vegetation. Then, there may be patches of the *Pteridium-Galium* community where bracken has pre-empted the spread of heather in the grassland or shaded it out, with *Ulex-Rubus* scrub marking places that have been disturbed or enriched. Fragments of all these may survive, along with patches of the *Carex-Festuca-Agrostis* vegetation, around plantations on dunes, in field corners of improved pastures and on golf-course rough.

Distribution

The community has scattered localities around the coasts of south-east England, but it is commoner towards the north and west in those places where older, leached sands have been grazed. Were suitable substrates more widely distributed through north-west Scotland, it would probably be extensive there.

Affinities

More calcifuge dune vegetation of this kind has been described from a few sites around the British coast (Pearsall 1934, Gimingham 1964a), and it was included by Birse (1980, 1984) in the *Astragalo-Festucetum arenariae*, his grassland of fixed dunes on the less oceanic coasts of eastern Scotland. In this scheme, regional phytogeographic distinctions among the swards of less mobile dunes seem less obvious than those which reflect variation in the base-richness of the substrate, and throughout its range the *Carex-Festuca-Agrostis* grassland retains its integrity as the nearest approach to Nardo-Galion vegetation among dune communities. Because of the prevailingly calcicole character of much *Astragalo-Festucetum*, Birse (1980, 1984) grouped it within the Koelerion alliance of the Sedo-Scleranthetea, whereas the *Carex-Festuca-Agrostis* grassland as defined here would be best located in the Corynephorion of the same class.

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	a	b	12
<i>Agrostis capillaris</i>	V (1–9)	V (1–9)	V (1–9)
<i>Carex arenaria</i>	V (2–10)	IV (1–6)	V (1–10)
<i>Festuca ovina</i>	IV (2–6)	V (2–9)	IV (2–9)
<i>Poa pratensis</i>	IV (2–5)	IV (1–7)	IV (1–7)
<i>Ammophila arenaria</i>	V (2–8)	III (1–6)	IV (1–8)
<i>Anthoxanthum odoratum</i>	V (2–7)	II (2–4)	III (2–7)
<i>Luzula campestris</i>	V (1–4)	II (2–4)	III (1–4)
<i>Hypochoeris radicata</i>	III (1–5)	I (1)	II (1–5)
<i>Koeleria macrantha</i>	II (1–5)	I (1–2)	I (1–5)
<i>Hieracium pilosella</i>	II (1–6)		I (1–6)
<i>Polytrichum juniperinum</i>	II (1–3)		I (1–3)
<i>Plantago lanceolata</i>	II (1–4)		I (1–4)
<i>Thymus praecox</i>	II (1–6)		I (1–6)
<i>Potentilla erecta</i>	I (1–6)		I (1–6)
<i>Calluna vulgaris</i>	I (1–6)		I (1–6)
<i>Danthonia decumbens</i>	I (1–4)		I (1–4)
<i>Deschampsia flexuosa</i>	I (1–5)		I (1–5)
<i>Erica cinerea</i>	I (1–5)		I (1–5)
<i>Cladonia furcata</i>	I (1–3)		I (1–3)
<i>Carex pilulifera</i>	I (2–3)		I (2–3)
<i>Ononis repens</i>	I (1–3)		I (1–3)
<i>Astragalus danicus</i>	I (1)		I (1)
<i>Holcus lanatus</i>	II (1–6)	IV (2–8)	III (1–8)
<i>Campanula rotundifolia</i>	I (1–4)	III (1–4)	II (1–4)
<i>Viola riviniana</i>	I (1)	III (2–4)	II (1–4)
<i>Ceratodon purpureus</i>	I (1–4)	III (2–4)	II (1–4)
<i>Achillea millefolium</i>	I (2–4)	II (1–4)	I (1–4)
<i>Ranunculus repens</i>		I (2–4)	I (2–4)
<i>Prunella vulgaris</i>		I (2–4)	I (2–4)
<i>Lathyrus pratensis</i>		I (2–4)	I (2–4)
<i>Urtica dioica</i>		I (2–4)	I (2–4)
<i>Galium saxatile</i>	III (1–7)	III (2–5)	III (1–7)
<i>Dicranum scoparium</i>	III (1–7)	III (2–5)	III (1–7)
<i>Rhytidiadelphus squarrosus</i>	III (1–6)	III (2–5)	III (1–6)
<i>Lotus corniculatus</i>	III (1–6)	II (2–5)	III (1–6)
<i>Pseudoscleropodium purum</i>	III (1–8)	II (1–5)	III (1–8)
<i>Festuca rubra</i>	III (1–9)	II (2–4)	II (1–9)
<i>Hylocomium splendens</i>	II (1–9)	III (2–4)	II (1–9)
<i>Pleurozium schreberi</i>	II (1–7)	III (2–4)	II (1–7)
<i>Cerastium fontanum</i>	II (1–2)	III (2–4)	II (1–4)
<i>Rumex acetosella</i>	II (1–5)	II (2–4)	II (1–5)
<i>Galium verum</i>	II (1–6)	II (2–4)	II (1–6)
<i>Hypnum cupressiforme</i>	II (1–7)	II (2)	II (1–7)
<i>Rhytidiadelphus triquetrus</i>	II (2–5)	II (2–3)	II (2–5)
<i>Trifolium repens</i>	II (1–4)	I (2–4)	II (1–4)

<i>Veronica officinalis</i>	II (1–6)	I (2–4)	II (1–6)
<i>Brachythecium albicans</i>	I (1)	II (2–4)	I (1–4)
<i>Peltigera canina</i>	I (1–6)	I (2)	I (1–6)
<i>Senecio jacobaea</i>	I (1)	I (2–4)	I (1–4)
<i>Cerastium diffusum diffusum</i>	I (1–3)	I (2)	I (1–3)
<i>Cirsium arvense</i>	I (1)	I (2–4)	I (1–4)
<i>Cladonia arbuscula</i>	I (1–6)	I (2)	I (1–6)
<i>Rumex acetosa</i>	I (1–3)	I (2–4)	I (1–4)
<i>Vicia lathyroides</i>	I (1–2)	I (1)	I (1–2)
<i>Geranium molle</i>	I (2)	I (2)	I (2)
Number of samples	37	30	67
Number of species/sample	18 (10–27)	16 (5–28)	17 (5–28)

- a *Anthoxanthum odoratum* sub-community
- b *Holcus lanatus* sub-community
- 12 *Carex arenaria-Festuca ovina-Agrostis capillaris* dune grassland (total)

