SD10
Carex arenaria dune community

Synonymy
Carex arenaria community West 1936, 1937; *Corynephorus canescens* localities Marshall 1967 *p.p.*; *Carex arenaria* vegetation Noble 1982 *p.p.*

Constant species
Carex arenaria.

Rare species
Astragalus danicus, *Corynephorus canescens*.

Physiognomy
The *Carex arenaria* community includes very open to more or less closed swards in which the sand-sedge is the most abundant plant, where vascular associates are few in number and usually sparsely distributed and where there is hardly any contribution from mosses or lichens on what is often still a somewhat mobile sand surface. Where the sedge is invading freshly-deposited material, its initial cover may be very low, the shoots emerging, spaced out and generally single, in striking straight lines from the far-creeping rhizomes. If accretion continues at a fairly modest rate, well-established plants can keep pace but, as the sand starts to become stabilised, clones can thicken up very considerably with densely-packed shoots growing tiller-like from short, closely-spaced branches. Up to several hundred shoots per m^2 have been recorded in this vegetation, but vigour is affected by soil conditions in a particular stand and by grazing which can reduce the sedge to very squat proportions (Tidmarsh 1939, Noble 1982).

In younger stands, or where *C. arenaria* has pre-empted a site and remained strongly dominant, there may be very little else growing among it. Often, though, the sedge is accompanied by some *Festuca rubra* or *F. ovina*, the former tending to favour coastal situations, the latter the more common of the two in those few stretches of inland sands where this vegetation can be found. In coastal stands, too, there may be plants of *Elymus farctus* or *Ammophila arenaria*, though any abundance of these generally presages a spatial or successional shift to other dune communities. Around the East Anglian coast, the patches of bare, shifting sand where this vegetation develops may also be invaded by the rare grass *Corynephorus canescens*, and its dense tussocks of glaucous shoots may be locally abundant. Then, there is occasionally some *Holcus lanatus* and *Dactylis glomerata* while, among smaller grasses, *Koeleria macrantha* and *Agrostis capillaris* are sometimes found, particularly in transitions to grazed swards on more stable ground, with *Aira paraecox* sometimes making an appearance on sheltered open areas.

No dicotyledons occur frequently throughout the community but coarser weedy plants such as *Senecio jacobaea*, *S. vulgaris*, *Matricaria maritima* and *Epilobium angustifolium* are found in some stands, with *Plantago lanceolata*, *Achillea millefolium*, *Cerastium fontanum*, *Galium verum*, *Taraxacum officinale* agg., *Potentilla anserina* and *Rumex acetosella* also recorded occasionally. The community can also provide a locus for the rare *Astragalus danicus*, though this plant is not so characteristic here as in shorter, more closed swards with the sedge.

Cryptogams are rare, but very occasionally there may be small patches of *Hypnum cupressiforme s.l.* or *Ceratodon purpureus*.

Sub-communities

***Festuca rubra* sub-community.** *F. rubra* is a frequent associate in this kind of *Carex* vegetation or sometimes there is *Ammophila* or *E. farctus* at low to moderate cover, with *Corynephorus* locally prominent in some East Anglian stands. *Potentilla anserina*, *Plantago lanceolata* and *Matricaria maritima* occur occasionally and, where the community develops among foredunes, *Honkenya peploides*.

***Festuca ovina* sub-community.** *F. ovina* usually replaces *F. rubra* here and there can be frequent *H. lanatus*, with

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scattered *S. jacobaea* giving a weedy appearance to the vegetation. In other stands, small tussocks of *K. macrantha* and patches of *A. capillaris* give some continuity with closed grassy swards, and there is occasional *C. fontanum*, *G. verum*, *R. acetosella* and *P. lanceolata*.

Habitat

The *Carex arenaria* community is a pioneer vegetation type of freshly-deposited calcareous and acid sands in more sheltered places among dunes all around the British coast and at a few inland sites. It is especially common around the foot of lee slopes of mobile dunes and among blow-outs, or marking the track of recently-disturbed sand over more stable ground, usually forming a minor and relatively short-lived element of dune vegetation. Some stands are grazed and this may help perpetuate the dominance of the sedge, but animal activity can precipitate erosion and destruction of the community.

C. arenaria is ubiquitous around the seaboard of north-west Europe, its northern limit, coinciding roughly with the 0 °C isotherm for mean January air temperature, falling just beyond the latitude of Orkney (Noble 1982). Throughout this range, it is most characteristic of deep pure sands out of reach of tidal inundation and salt-spray, although it exceptionally invades mixtures of sand and shingle (Marshall 1967). In mainland Europe, it is common inland, extending far into the Baltic lowlands on the sandy plains of Sweden, Denmark, Poland and Germany and into The Netherlands whereas, with us, suitable substrates are virtually confined to coastal dune systems. British records away from such habitats are few (Perring & Walters 1962) and strongly concentrated on the small tracts of unreclaimed sand and sandy brown soils (Avery 1980) that remain in Breckland and Lincolnshire (Gibbons 1975, Trist 1979, Noble 1982).

In such situations in Britain, *C. arenaria* is a common and sometimes abundant member of a range of vegetation types but the dominance characteristic of this community is very much associated with the fresh deposition of wind-blown sand in relatively sheltered places. Establishment of the sedge from seed on such surfaces demands the maintenance of moist conditions, a certain temperature fluctuation, and freedom from burial or the predation of herbivores (Tidmarsh 1939, Noble 1982), conditions most likely to be met where sand movement impinges on damper, ungrazed hollows among the dunes. Elsewhere, colonisation often takes place by vegetative extension from individuals already present in the surrounding swards: the rhizomes of *C. arenaria* are able to grow for many metres, and branching and shoot production show renewed vigour as the underground stems penetrate into the loose bare sand, so that clone margins are able to extend and thicken up rapidly to form virtually monospecific stands as opportunity arises. Moreover, if accretion continues, the plants can keep pace to some extent by the production of series of tiered lateral rhizomes at successively higher levels, though deep and sudden burial may overwhelm the leading shoots (Tidmarsh 1939). Likewise, where young rhizomes grow into the face of a dune, apical dominance is lost, new laterals developing further back and consolidating the hold in the shallower sand (Noble 1982). If extensive invasion of this kind allows the sedge to pre-empt a site, big stands of the community can remain prominent even though the sand becomes fixed, as happened over parts of the Blakeney dunes in Norfolk after myxomatosis (White 1961). And, in Breckland, Watt (1937) considered that the abundance of *C. arenaria* in a variety of vegetation types in the 1930s marked the trail of a series of severe sand-storms that had occurred as long as three centuries before. For the most part, however, stands of this *Carex* community are a local and more short-lived feature of the dune environment, being replaced by other more species-rich assemblages as the surface becomes stabilised but recurring where and when bouts of wind erosion or other disturbance favour the renewed deposition of sand.

In this kind of dune habitat, shortage of water and nutrients are important factors influencing the nature of the vegetation. Although *C. arenaria* itself is very tolerant of widely differing ground moisture regimes and often establishes among developing slack vegetation on damp sand, or even where there is some winter flooding in dune hollows (Willis *et al.* 1959*b*, Willis 1985*b*) beneath this community, the sand surface is usually dry. At moderate elevations, the sedge may still be able to benefit from ground water and any nutrients dissolved in it, because it has robust sinker roots which can grow rapidly and penetrate deep, as far as 2–3 m (Tidmarsh 1939, Robards *et al.* 1979, Noble 1982) but, on dunes raised far above the water-table, it must rely much of the time on rain for its moisture supply, a mass of fine superficial roots absorbing the water as it quickly percolates away. A marked resistance to drought in *C. arenaria* equips well-established clones to survive the frequent periods of water shortage in such situations. Episodes of rain may also be important for flushing such nutrients as there are in the sand down the dune slopes into just those places where the sedge can thrive in this community with minimal competition from other species. In general, however, it seems likely that shortage of nitrogen and phosphorus in the raw sands where this vegetation gets a hold imposes the major constraint on the vigour of *C. arenaria* and its associates (Willis & Yemm 1961, Pemadasa & Lovell 1974*b*, Noble 1982).

Variation in soil reaction, on the other hand, seems to affect the sedge little. Where this community develops among younger dunes around our coasts, the sands are usually very lime-rich, often with a high proportion of

shell fragments and not yet subject to much leaching, such that the superficial pH is often 8 or more (Noble 1982). On sands derived from blow-outs among older, fixed dunes, the substrate may be more depleted of calcium and, rather locally, there is a plentiful supply of acid sands for the earlier stages of dune building, as at Winterton in Norfolk, where this vegetation is found on ground with a surface pH as low as 4 (Marshall 1967). Inland stands can also occur on highly acidic sands, as in Breckland (Watt 1936, 1957), but both here and around the coast, differences in soil reaction tend to make themselves felt among the flora in the later stages of sward development which succeed this community.

Although older stands of *Carex* vegetation can be found where there is little else growing among densely-packed ageing sedge shoots, it is usually the younger stages of colonisation that exhibit the more impoverished associated floras here, with other species appearing as the *C. arenaria* consolidates its hold and enters a mature phase of growth (Noble 1982). Such companions are often of rather sporadic and chancy occurrence at first, but prominent among them are plants well-adapted in one way or another to the inhospitable dune environment, particularly in the coastal stands of the *F. rubra* sub-community, where extensive tracts of vegetation with other potential invaders of freshly-turned sand generally surround the community. Some of these plants, like the rhizomatous grasses *Ammophila*, *F. rubra* and *E. farctus*, may get an early hold along with the sedge by vegetative spread from established individuals nearby. For the rare associate *Corynephorus*, invasion is a more precarious affair, being dependent on seed germination which requires dampening of the surface by rain, and but a modest amount of accretion if the seedlings are not to be overwhelmed. Even where these conditions are satisfied, survival among established *C. arenaria* is especially poor, competition for moisture tending to favour the sedge (Marshall 1967). More ephemeral plants, too, like *Matricaria maritima*, *Senecio vulgaris* and *Aira praecox*, may only be able to get a hold where there is more open, but stable, ground.

Mixtures of perennial and more short-lived associates also characterise developing stands of the *F. ovina* sub-community seen on inland sands, though in the non-maritime environment, there is little overlap with the flora of the *F. rubra* sub-community, the companions being mostly early invaders from the grassy swards and heaths established on the surrounding stable sandy soils.

Many of the dune systems among which the *Carex* community can be found are subject to grazing, and cattle, rabbits and hares commonly eat the young aerial shoots, particularly during late winter and early spring when the evergreen foliage offers a quite tender bite and little alternative herbage is available (Bhadresa 1977). Such predation may result in stunted growth and a severe curtailment of flowering if the grazing extends into the late spring (Tidmarsh 1939, Noble 1976), although it can help maintain species-poor stands of the community where more palatable invaders are selectively grazed out: in Breckland in the 1930s, for example, *Carex* vegetation commonly spread around rabbit burrows replacing the preferentially grazed *Calluna* heath (Tansley 1939). Heavy grazing, though, can be very destructive, even where such small herbivores as voles are responsible: these tunnel through the herbage and gnaw off the shoots at ground level (Tidmarsh 1939). Burrowing or scuffing of the sand and trampling may also damage the vegetation cover by direct injury to the rhizomes and shoots or by precipitating erosion. Human visitors to dunes can also encourage the destruction of the *Carex* community, though all these kinds of disturbance may release new supplies of sand for deposition elsewhere, with the possibility of further stands developing.

Zonation and succession

The *Carex arenaria* community is generally found as a minor element among zonations and mosaics of other vegetation types of coastal and inland sands, interrupting the patterns wherever the sedge has been able to capitalise on local deposition in sheltered places. It is replaced by other communities as more aggressive plants are able to dominate on still mobile sand or where, with increased stability of the surface, the vigour of the sedge wanes. Grazing may influence these successional changes or help bring about a renewed round of invasion on newly-disturbed ground.

On coastal sites, the *F. rubra* sub-community is sometimes found invading areas of sand among foredunes where the *Elymus farctus* community is the predominant colonising vegetation, but more often it appears among *Ammophila* and *Ammophila-Festuca* stands on somewhat older mobile dunes, where marram has not yet asserted, or reasserted, its dominance. Boundaries between the vegetation types in these patterns are marked by shifts in the proportions of the monocotyledons, although *Ammophila* can be quite common and abundant among developing *Carex* vegetation, while the sedge persists frequently, though never as more than a sub-dominant, in the *Carex* sub-community of *Ammophila* vegetation and in certain kinds of *Ammophila-Festuca* sward. The scattered occurrence throughout of associates like *F. rubra* and *S. jacobaea* can also accentuate the continuity among the vegetation cover.

Where accretion is rapid, *Ammophila* readily assumes dominance over the sedge with a succession to these other communities in a resumption of the main trend of development, although local deposition of sand in sheltered spots among the dunes and around blow-outs which subsequently form can favour a resurgence of

Carex vegetation. Indeed, such a return to this pioneer community is possible among stretches of fixed dunes where the *Festuca-Galium* vegetation is often the successor to the *Ammophila-Festuca* community where the sands remain calcareous. *C. arenaria* is a common associate in the sward and may be quick to take advantage of accretion, especially where *Ammophila* has become very debilitated. Boundaries are generally sharp in such situations, though the margins of the *Festuca-Galium* turf may become fretted away by wind erosion or animal disturbance or blurred by a thin overlay of sand and, if the surface becomes stabilised once again, the richer sward can re-establish itself around the margins or among the *Carex* vegetation. In certain situations, however, it seems as if the sedge community can remain in long occupation of fixed dunes, as on Blakeney where, with the disappearance of rabbits in the myxomatosis epidemic, *C. arenaria* attained a dominance that has not been readily challenged by *F. rubra* (White 1961).

Among coastal dunes built of more acidic sands, or where the surface has become strongly leached with time, the patterns are somewhat different. If accretion proceeds at a fairly modest rate, and especially where the sand is sufficiently acidic from the outset to inhibit the vigour of marram (Huiskes 1979), the sedge may play a more prominent role throughout the succession. Then, especially where the vegetation is grazed, the *Carex* community can give way to the *Carex-Festuca-Agrostis* or *Carex-Cornicularia* swards. In the former, mixtures of *C. arenaria* and smaller grasses usually dominate, with such *Ammophila* as is present often sparse and puny, and the early appearance among the developing sedge cover of plants like *Agrostis capillaris*, *H. lanatus*, *P. lanceolata* and *Achillea millefolium*, may make the boundaries between the vegetation types indistinct. Generally, however, high frequencies of *Anthoxanthum odoratum*, *Luzula campestris* and *Galium saxatile* characterise the later stages of sward development, together with the appearance of a variety of calcifuge bryophytes that hardly ever find a place on the still mobile sand. In other situations, perhaps where heavy rabbit grazing has played an important role in influencing the succession, the *Carex-Cornicularia* community can occupy much of the more stable sand surface. Here, again, the sedge retains a frequent and often abundant place in the vegetation, commonly with some *F. rubra* and sparse marram, but *Rumex acetosella* and a variety of diminutive ephemerals now appear and there is typically an extensive carpet of lichens, with *Cornicularia aculeata* and a variety of *Cladonia* spp. particularly prominent. Where either of these swards becomes disrupted with degeneration and wind erosion, the *Carex* community can reappear on drifts of accumulated sand. A striking feature of some sites with this kind of pattern, as at Winterton, is the prominence, early in the succession and re-seeding for a few years within the more close turf, of *Corynephorus* (Marshall 1967).

It is mixtures of grassy and lichen-rich swards that make up much of the vegetation context for the development of inland stands of the *Carex* community. Away from the coast, tracts of mobile sand are very localised though, in regions like Breckland, wind erosion of sandy soils has played an important part in the evolution of the landscape. Here, blow-outs have been observed forming (Watt 1937) as a result of the action of local cyclonic winds on degenerating *Calluna-Festuca* heath, *Carex-Cornicularia* or *Carex-Festuca-Agrostis* grasslands on sand-smeared podzols. Where these have become reduced to a mat of humus or a scabby carpet of lichens among decaying grass shoots, the surface is readily disrupted by the impact of sun, rain and wind, the sand accumulating in low dunes around the developing hollow or being blown away in shallow drifts by frontal erosion. It is on this newly-accreted material that the *F. ovina* sub-community of the *Carex* vegetation is able to get a hold, sometimes persisting for a considerable time in its impoverished form, in other places grading back into grazed swards. Then, the *Carex-Festuca-Agrostis* or *Carex-Cornicularia* communities may form a transition to the *Festuca-Agrostis-Rumex* grassland, the contribution of the sedge waning, and dominance passing to small tussock grasses, ephemerals and patches of lichens and bryophytes. Very occasionally in these fine mosaics, where there is a transition to less sandy soils of higher pH, the *Carex* community can be closely juxtaposed with the more basiphilous of the Breckland grassheaths of the *Festuca-Hieracium-Thymus* type (Watt 1940, Noble 1982).

On shallower, stabilising drifts of sand where there is little or no grazing, an alternative successional development is the reappearance of heath, because in such conditions *Calluna* is an important competitor to *C. arenaria* (Watt 1936, 1937). On Breckland sands, it is the *Calluna-Festuca* community that is the usual kind of sub-shrub vegetation and its *Carex* sub-community, with co-dominant mixtures of heather and sedge, can form a transitional zone in shifts from more to less mobile substrates (Tidmarsh 1939, Gibbons 1975). *C. arenaria* also remains a constant feature of many stands of heath which develop on the more stable, acid sands of ungrazed or lightly-grazed coastal dunes. Around parts of the East Anglian coast, *Calluna-Festuca* heath indistinguishable from that inland can be found in such situations but, elsewhere, *Calluna-Carex* heath is the usual community, with *Erica cinerea* or, much more locally, *Empetrum nigrum* spp. *nigrum*, invading along with the heather. Such heaths are sometimes subject to burning to regenerate the sub-shrub cover, and such treatment may help stimulate flowering among ageing *C. arenaria* (Tidmarsh 1939).

A further complication of such patterns is the appearance of *Pteridium aquilinum*, because the sedge and bracken are both able to spread rapidly on loose and deep, well-aerated substrates and, in both inland and coastal sites, the *Carex* community can be found in intimate association with bracken vegetation, the balance between the dominants along the boundaries being related to the cyclical upbuilding and ageing of the *Pteridium* along its front (Watt 1936, 1940; Tidmarsh 1939). More mature stands of bracken in such patterns on acid sands tend to be of the *Pteridium-Galium* type, with *Pteridium-Rubus* underscrub developing on less base-poor and impoverished substrates.

Distribution

The community occurs in suitable situations on dunes all around the British coast and inland in Breckland and Lincolnshire.

Affinities

The aggressive, gregarious character of sand sedge was early recognised, but accounts of British coastal dune vegetation have usually treated the species as little more than a locally prominent element in communities dominated by *Ammophila* (Tansley 1911, 1939), although Watt (1936, 1937), in his account of the vegetation of inland Breck sands, gave prominence to *Carex arenaria* stands, and Noble (1982) recognised a variety of assemblages with the sedge.

In phytosociological schemes, *C. arenaria* is seen as a characteristic plant of the Corynephorion, an alliance of pioneer swards on dry, acid sands which has been described from The Netherlands (Westhoff & den Held 1969), Germany (Ellenberg 1978, Oberdorfer 1978) and Poland (Matuszkiewicz 1981). Generally, however, the sedge is less prominent in the associations in the process of sand fixation, than *Corynephorus* and only in a very few sites in Britain can the sequence of vegetation types typical of this kind of succession be seen. Thus, although swards like those of the *Carex-Cornicularia* and *Carex-Festuca-Agrostis* communities would find a ready place among the Sedo-Scleranthetea, there might be some argument for retaining the *Carex* community itself in the Ammophilion.

Floristic table SD10

	a	b	10
Carex arenaria	V (5–10)	V (4–10)	V (4–10)
Festuca rubra	III (2–5)		II (2–5)
Ammophila arenaria	II (2–3)		I (2–3)
Elymus farctus	II (5–6)		I (5–6)
Potentilla anserina	II (3–5)		I (3–5)
Matricaria maritima	II (2–4)		I (2–4)
Honkenya peploides	I (2–4)		I (2–4)
Festuca ovina		IV (3–7)	II (3–7)
Senecio jacobaea		III (3)	II (3)
Holcus lanatus		III (3–7)	II (3–7)
Cerastium fontanum		II (3–4)	I (3–4)
Rumex acetosella		II (3–4)	I (3–4)
Koeleria macrantha		II (4)	I (4)
Galium verum		II (2–3)	I (2–3)
Astragalus danicus		I (3)	I (3)
Ceratodon purpureus		I (3)	I (3)
Plantago lanceolata	II (1–3)	II (3–4)	II (1–4)
Achillea millefolium	I (2)	I (3)	I (2–3)
Taraxacum officinale agg.	I (1–3)	I (1–3)	I (1–3)
Aira praecox	I (4)	I (3–4)	I (3–4)
Epilobium angustifolium	I (4)	I (3–5)	I (3–5)
Senecio vulgaris	I (1–2)	I (3)	I (1–3)
Agrostis capillaris	I (3)	I (3–5)	I (3–5)
Hypnum cupressiforme	I (4)	I (3–4)	I (3–4)
Dactylis glomerata	I (1)	I (3–5)	I (1–5)
Number of samples	18	18	36
Number of species/sample	8 (3–14)	8 (2–19)	8 (2–19)
Vegetation height (cm)	14 (1–50)	42 (5–50)	35 (1–50)
Vegetation cover (%)	62 (20–100)	93 (50–100)	77 (20–100)

a *Festuca rubra* sub-community
b *Festuca ovina* sub-community
10 *Carex arenaria* dune community (total)

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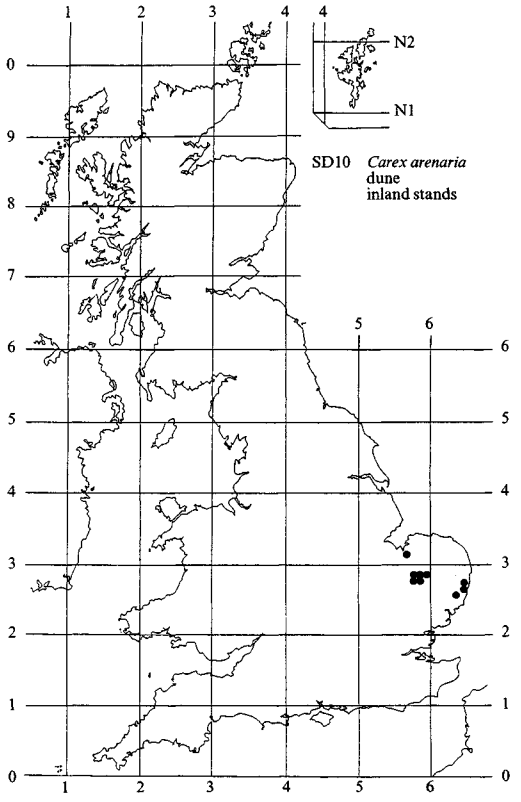

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