SD11
Carex arenaria-Cornicularia aculeata dune community

Synonymy
Caricetum arenariae Tansley 1939 *p.p.*

Constant species
Carex arenaria, *Cornicularia aculeata*.

Rare species
Astragalus danicus, *Corynephorus canescens*.

Physiognomy
The *Carex arenaria-Cornicularia aculeata* community includes lichen-rich swards in which sand-sedge is the only constant vascular plant. It is, though, never a vigorous dominant here, only occasionally having high cover and more usually occurring as scattered tufts of shoots, sometimes distinctly moribund. Neither are any other herbs consistently abundant. *Festuca ovina* and *F. rubra* are quite commonly found, for example, but usually as small scattered tussocks and, though *Agrostis capillaris* occasionally forms patches in the turf, these are rarely dense. Then, although *Luzula campestris* is fairly frequent, it generally occurs as rather sparse individuals. Sometimes more abundant, though only very locally around the East Anglian coast, is the rare grass *Corynephorus canescens* which, while being essentially a pioneer plant of more open sands, can continue to seed into these swards for several years (Marshall 1967). Certain annual grasses like *Aira praecox*, *A. caryophyllea* and *Phleum arenarium* may also occur with considerable local abundance where bare patches develop. Finally, among the monocotyledons, *Ammophila arenaria* is a frequent feature of coastal stands of the community though, even more than *Carex arenaria*, it is characteristically of very debilitated growth, persisting as sparse, scattered tussocks.

Perennial dicotyledons are few and usually of low cover, though some can be locally prominent. Most common is *Rumex acetosella*, with occasional *Hypochoeris radicata*, *Galium saxatile* and *Sedum acre*, patches of this last sometimes quite plentiful and eye-catching with their yellow flowers. Then, there can be some *Thymus praecox*, *Galium verum*, *Plantago lanceolata* and *Viola canina* while, at certain localities, this vegetation provides a locus for the rare *Astragalus danicus*. More ephemeral herbs may be found, too, with *Senecio jacobaea*, *Viola tricolor*, *Filago minima*, *Erodium cicutarium* and *Teesdalia nudicaulis* coming and going on areas of open ground. Other stands can have a somewhat heathy appearance with small bushes of *Calluna vulgaris*, but the cover of this is never extensive.

Typically, all these plants are of low growth, and often grazed back into very stunted individuals, and it is the extent and diversity of the lichen carpet that generally forms the most impressive feature of the vegetation, its colour suggesting to some the epithet 'grey' for the kind of dunes on which it is found (Tansley 1939). Most frequent and plentiful of the lichens are *Cornicularia aculeata*, *Cladonia arbuscula*, *C. foliacea* and *C. impexa* with *C. furcata*, *C. tenuis*, *C. pyxidata*, *C. uncialis*, *C. gracilis*, *C. squamosa* and *Hypogymnia physodes* occasional to common in the different sub-communities, *C. fimbriata*, *C. rangiformis* and *C. rangiferina* more rarely represented.

Bryophytes may also contribute to the ground cover, though as a group they are nowhere near as abundant as the lichens. However, *Dicranum scoparium*, *Polytrichum piliferum*, *P. juniperinum*, *Ceratodon purpureus* and *Hypnum cupressiforme* occur quite frequently sometimes as extensive patches, with *Ptilidium ciliare*, *Brachythecium albicans*, *Racomitrium canescens*, *Tortula ruralis* ssp. *ruraliformis* and *Rhytidium rugosum* being found less commonly.

Sub-communities

***Ammophila arenaria* sub-community.** The constancy of small amounts of *Ammophila* is the most distinctive feature of the vascular element in this sub-community, with both *F. rubra* and *F. ovina* occurring occasionally. *A. praecox* is common, with *A. caryophyllea* and *P. arenarium* being recorded less frequently and it is in this kind

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of *Carex-Cornicularia* vegetation that *Corynephorus* can be found. *R. acetosella*, *H. radicata*, *S. acre* and *V. tricolor* are the commonest associated herbs, with *G. verum*, *T. praecox* and *V. canina* more occasional and, among the annuals, *E. cicutarium*, *L. minima* and *Teesdalia*.

The most frequent and abundant lichens are usually *Cornicularia aculeata*, *C. arbuscula* and *C. furcata* with *C. foliacea* and *Hypogymnia physodes* also very common, *C. impexa*, *C. fimbriata*, *C. tenuis* and *C. rangiformis* more occasional but sometimes extensive. *D. scoparium*, *P. piliferum*, *Ceratodon* and *H. cupressiforme* are fairly frequent and can be of locally high cover.

***Festuca ovina* sub-community.** The general appearance of this kind of *Carex-Cornicularia* vegetation is similar to the above but *Ammophila* is absent and the fescue in the sward is almost always *F. ovina*, mixtures of this with *C. arenaria*, *L. campestris* and *A. capillaris* generally forming the bulk of the rather sparse vascular cover. *R. acetosella* is frequent and *G. saxatile* occasional, with *Astragalus* occurring at some sites but associated herbs typically occur again as scattered individuals.

Cornicularia aculeata and *Cladonia arbuscula* remain very frequent and abundant in the lichen carpet, but *C. furcata* is scarce and the other most common species are *C. foliacea* and *C. impexa*, with *C. pyxidata*, *C. uncialis*, *C. gracilis* and *C. squamosa* preferentially frequent. Among the bryophytes, *D. scoparium*, *P. piliferum* and *H. cupressiforme* are occasional to common and locally plentiful.

Habitat

The *Carex-Cornicularia* community is characteristic of fixed and rather acid sands, or compacted mixtures of sand and shingle, where the ground remains very drought-prone and impoverished. It is a rather local community, better developed in the drier east of Britain, but it can be found on both coastal and inland sands, being most typical of flat areas that lie out of reach of the ground water-table between or behind old dune ridges or on stable sand plains. Heavy grazing by rabbits has probably been of considerable importance in maintaining this vegetation in the past, but trampling by stock and humans or disturbance by vehicles is very destructive of the lichen carpet and may help initiate erosion of the surface.

This community cannot become established on wind-blown sand until accretion has virtually ceased and, though the ground may become subject to renewed disturbance, stands are generally found in places beyond the reach of freshly-deposited material from beach sources, in areas of stable and subdued relief in the older parts of dune systems, or where old erosion surfaces have become compacted (Figure 15). Active invaders of mobile sand do not therefore have a vigorous role in the control of the physical environment here and play a minor part in the composition and structure of the sward. Where this vegetation occurs among coastal dunes, for example, *Ammophila* often persists, though it is as a debilitated relic, with the clones reduced to the typically senile clusters of shoots and scarcely ever flowering (Gimingham 1964*a*, Huiskes 1979). Edaphic changes initiated with increased stability of the sand surface probably play some part in this (Salisbury 1952, Willis *et al.* 1959*a*, *b*; Huiskes 1977*a*, 1979) because, compared with the immature sands beneath the *Ammophila-Festuca* community, and even the more fixed sediments of the *Festuca-Galium* vegetation, the superficial sand layers here are typically poor in lime, with a pH usually less than 5.5. Where the wind-blown material is initially calcareous, as in dune systems where shall fragments make up a considerable proportion of the beach sediments, such surface acidity can come about only through prolonged leaching (Ranwell 1972, Willis 1985*b*) though, with sands that are more acid from the start, younger surfaces may offer a congenial substrate, provided they are not actively accreting. Apart from leached or siliceous sands of beach origin, suitable sediments have been derived inland or along the coast from Pliocene and Pleistocene Crag on the Suffolk Sandlings, Greensand and glacial sands on the Norfolk Commons and the more acidic of the Pleistocene and aeolian deposits in Breckland (Watt 1940, Hodge & Seale 1966, Corbett 1973, *Soil Survey* 1983, Hodge *et al.* 1984).

Even where the soils are of considerable age, however, with the surface layers darkened by the accumulation of some organic matter and humic staining, their water-retentive capacity is generally very limited. Absent from those stretches of flat ground among dunes which are subject to winter flooding, indeed typically out of reach of any influence of ground water, this vegetation is thus dependent on rain for the bulk of its moisture. Characteristically here, such a source is limited because the *Carex-Cornicularia* community is largely confined to the drier east of Britain where annual precipitation is less than 800 mm (*Climatological Atlas* 1952) with often fewer than 120 wet days yr^{-1} (Ratcliffe 1968), and mean annual maxima frequently in excess of 27 °C (Conolly & Dahl 1970). The tendency to parching is thus very strong, particularly around the East Anglian coast and in Breckland where conditions are most markedly continental, with rainfall quite often below 500 mm annually and a high likelihood of a water deficit in late spring (Gregory 1957, Chandler & Gregory 1976, Smith 1976).

The other important feature of the sands is their nutrient-poor character, something that is inherently typical of siliceous sediments, but perhaps accentuated over many generations by particular kinds of biotic activity. Grazing by rabbits, for example, which defaecate their

re-ingested pellets in latrines, can continually remove nutrients from the system, perhaps appreciable amounts of phosphorus and nitrogen (Watt 1981*a*), and long histories of rabbit-rearing, and of sheep-grazing with folding on arable, have been characteristic of places like the Suffolk Sandlings and Breckland (Crompton & Sheail 1975, Sheail 1979, Chadwick 1982, Webb 1986). This, together with past generations of shifting cultivation on inland sands, has helped preserve stretches of suitably impoverished ground where the community has been able to persist.

These climatic and edaphic conditions affect the vegetation in a variety of ways. First, there is the generally open character of the vascular cover. *Carex arenaria*, for example, though better able than *Ammophila* to tolerate the base-poor soil environment (Huiskes 1979, Noble 1982) and strongly resistant to drought (Noble 1982), is usually in a senile phase of growth in this community. The fresh deposition of sand that favours active clone extension has ceased here and the vigour of the plants is severely constrained by the shortage of major nutrients (Willis & Yemm 1961, Noble 1982). Where rabbits remain numerous, they can graze off inflorescences in the spring (Ranwell 1960*a*, *b*) and perhaps completely prevent the establishment of new seedlings (White 1961, Noble 1982). Perennial grasses also fare badly. In fact, it has been suggested that colonisation by other species among senile *C. arenaria* is markedly inhibited by allelopathic compounds secreted by the sedge (Symonides 1979) but, even if this is ineffectual, the parched, oligotrophic character of the sands is likely to maintain the sparse and tussocky aspect of the swards, with the herbage often looking crisp and brown by midsummer. In this respect, the vegetation can contrast quite sharply with the *Carex-Festuca-Agrostis* grassland, which is typical of fixed acid sands in cooler and wetter parts of Britain. There, the swards are generally closed, with *C. arenaria* growing more vigorously, grasses like *Poa pratensis*, *Anthoxanthum* or even *Holcus lanatus* contributing to the cover, and dicotyledonous herbs such as *Viola riviniana* and *Cerastium fontanum* occurring more often.

In the *Carex-Cornicularia* community, such species are scarce or absent and, though the poor competitive ability of the grasses allows for a potentially large contribution from herbaceous associates, these are few in number and of particular kinds, the perennials being light-demanding and drought-tolerant, species like *Rumex acetosella*, *Hypochoeris radicata* and *Sedum acre* providing the most distinctive element. Patches of bare

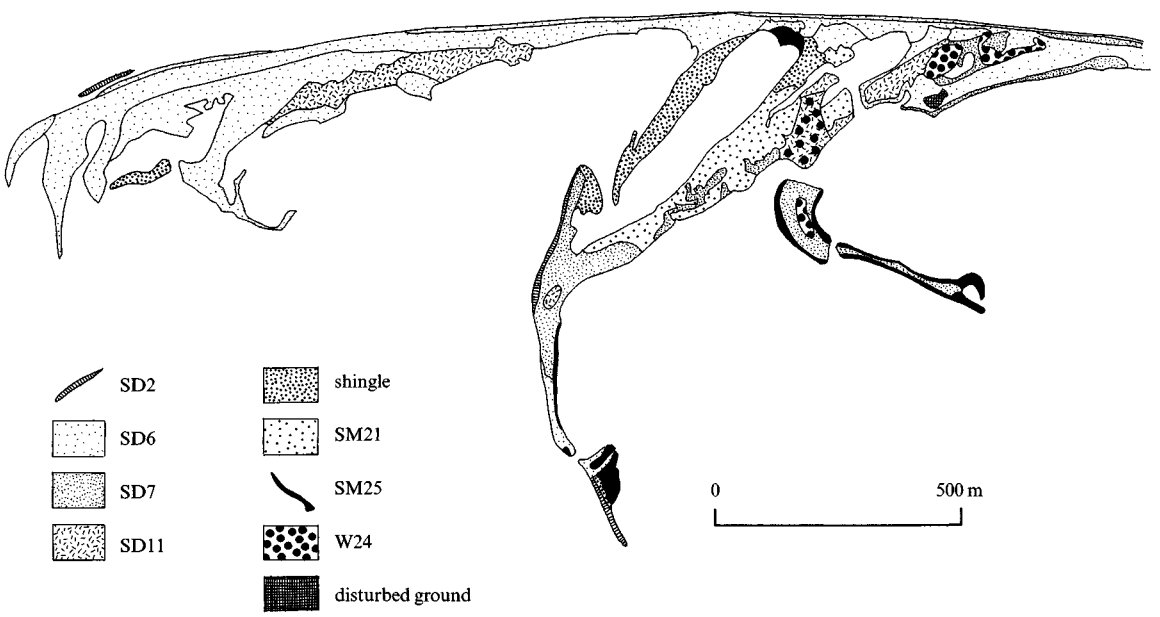

Figure 15. Sand dune and transitions to salt-marsh at Scolt Head Island, Norfolk.
The main spit comprises a shingle ridge with various kinds of SD6 *Ammophila* vegetation fronted, at the far point, by a very fragmentary SD2 *Honkenya-Cakile* strandline. Behind, on semi-fixed dune sand, is a zone of SD7 *Ammophila-Festuca* grassland with areas of the *Ammophila* sub-community of SD11 *Carex-Cornicularia* vegetation patchily colonised by W24 *Rubus-Holcus* underscrub. Shingle lows have stretches of vegetation resembling the SM21 *Suaeda-Limonium* community with SM25 *Suaeda vera* vegetation fringing the transition to the salt-marsh proper. (Redrawn from Hadley *et al.* 1990, by permission of the Joint Nature Conservation Committee.)

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ground, occasionally renewed by the demise of such perennials in severe droughts (Watt 1971*b*), also offer opportunity for the continued seeding-in of *Corynephorus*, and colonisation by ephemerals, sometimes coarse weedy plants like *Senecio jacobaea*, more usually diminutive annuals such as *Aira praecox*, *Phleum arenarium*, *Viola tricolor*, *Erodium cicutarium*, *Logfia minima* and *Teesdalia nudicaulis*. In the data available, such plants have been more frequently recorded in the coastal stands, but this is probably fortuitous.

The other component of the vegetation able to capitalise on the soil and climatic conditions here are the lichens, particularly the bulkier fruticose species like *Cornicularia aculeata*, *Cladonia arbuscula*, *C. furcata* and *C. foliacea*, some of these perhaps making an early appearance in the colonisation of compact erosion surfaces (Watt 1938). Bryophytes tend to be less prominent, though the most abundant are generally acrocarpous invaders of bare ground, with a noticeable scarcity of the pleurocarps common in *Carex-Festuca-Agrostis* swards, like *Rhytidiadelphus squarrosus*, *Pseudoscleropodium purum*, *Hylocomium splendens* and *Pleurozium schreberi*.

Natural environmental conditions may be sufficient to maintain the essential character of the *Carex-Cornicularia* swards but, quite apart from its influence on soils, grazing by rabbits and stock probably has other important influences on the vegetation. Close cropping can keep the herbage short, helping maintain the balance between perennial grasses and dicotyledons, and the annuals and cryptogams able to take advantage of open ground, while scuffing creates new bare patches for invasion. Grazing is also often very selective, with certain vascular plants like *Sedum acre* remaining uneaten. As far as rabbits are concerned, such choosiness may be especially beneficial to the lichens which they seem to avoid. Sheep, too, may have some effect on the composition of this element of the vegetation: in similar swards to these around the Baltic, selective grazing appears to modify the distribution of *Cladonia* spp. (Sjögren 1971) and such influences may contribute to the contrasts seen between the sub-communities here.

Trampling by stock, however, or by humans is detrimental to the lichen carpet and may help open up the surface to renewed sand movement. Although military manoeuvres can contribute to maintaining the sort of open landscape in which the *Carex-Cornicularia* community can survive (Sheail 1979), tracked army vehicles are very destructive of the vegetation.

Zonation and succession

The *Carex-Cornicularia* community is commonly found as a minor element in mosaics with calcifuge grasslands and heaths on the subdued topography of older dunes and sand plains. On siliceous sediments, these vegetation types may represent late stages in a distinctive line of succession, but they also develop where calcareous sands have been long-leached and may then occur among less mature and more basiphilous dune communities, particularly in coastal sites. This vegetation can also be part of secondary cycles of succession related to renewed erosion and is probably often dependent for its continuing survival on heavy grazing, particularly by rabbits. Where this is relieved, the community probably gives way to heath or, where the ground is less impoverished, to scrub and woodland.

In the heart of its distribution in East Anglia, the *Carex-Cornicularia* vegetation often occurs, at both coastal and inland sites, with the *Festuca-Agrostis-Rumex* grassland which, apart from the scarcity of *C. arenaria* can be very similar in its physiognomy and composition. In the *Cornicularia-Cladonia* sub-community of the grassland, for example, *Cornicularia aculeata*, *Cladonia arbuscula*, *C. tenuis*, *C. impexa*, *C. foliacea*, *C. uncialis* and *C. furcata* all remain frequent and abundant, with *D. scoparium*, *P. piliferum* and *R. acetosella*, among an open tussocky turf of *F. ovina* and *A. capillaris*. Transitions of this kind may reflect increasing stability of the surface, with the final extinction of the sand sedge, while in more scuffed and disturbed places, as along path edges, the *Carex-Cornicularia* community may give way to the *Erodium-Teesdalia* sub-community of the *Festuca-Agrostis-Rumex* grassland with its rich and varied suite of ephemerals. Gross disruption of the swards in such mosaics may result in erosion of the sand, with the development of blow-outs and tracts of freshly-deposited sediment (Watt 1938) and then there is an opportunity for renewed invasion by the sand sedge from rhizome fragments or by seed (Noble 1982), remnant stretches of sward occurring among young stands of the *Carex* community. Where the surface of such siliceous sands becomes quickly stable once again, the sedge decreasing in vigour and the spread of other perennials being restricted by inhospitable soil conditions, it is possible that the *Carex-Cornicularia* community re-establishes itself fairly quickly (Watt 1938) and this may represent a natural sequence on such base-poor sediments. In contrast to such situations in The Netherlands (Westhoff & den Held 1969), Germany (Oberdorfer 1978, Ellenberg 1978) and Poland (Matuszkiewicz 1981), however, *Corynephorus* plays a very restricted role with us in the earlier stages, being an important colonist at just a few coastal sites (Marshall 1967) and remaining now at only a single inland station (Trist 1979).

On sands which were initially more calcareous, as in many coastal dune systems, the persistence of *Ammophila* is a reminder that the *Carex-Cornicularia* community may represent a late stage in a rather different successional sequence, with marram playing the major

role in fixing the sediments before they become stable and leached. In such situations, the *Carex-Cornicularia* community can be found among older dunes, sometimes again with *Festuca-Agrostis-Rumex* swards or among stretches of *Festuca-Galium* grassland, particularly where the sands have not been so strongly decalcified. In the *Luzula* sub-community of such grassland, plants like *F. ovina*, *L. campestris* and *H. radicata* remain frequent in a turf with senile *Ammophila* and sometimes sparse *C. arenaria*, and where the *Carex-Cornicularia* community extends into eastern Scotland, *Astragalus danicus* can occur throughout the zonation. Increasingly, however, with the shift to the wetter and cooler part of Britain, the *Carex-Festuca-Agrostis* grassland becomes important as a transition between parched calcifuge swards of the *Carex-Cornicularia* type and the more closed grasslands of fixed dune sands. Then, such fragments of the former as remain, grade almost imperceptibly through a thickening turf into *Festuca-Galium* vegetation, species such as *Poa pratensis*, *A. capillaris*, *F. rubra*, *Galium verum* and *Lotus corniculatus* becoming increasingly important, and bryophytes occluding lichens as the major cryptogamic element.

Grazing is an important factor in maintaining mosaics of these different grasslands and some sites now betray ample evidence of the demise of rabbits or the cessation of sheep pasturing with an increase in size of the grass tussocks and a disappearance of the species demanding of open ground. A spread of *Calluna* is also very likely in such situations, the vegetation becoming increasingly heathy as the bushes multiply and enlarge. In East Anglia, such succession is usually to the *Calluna-Festuca* heath, among certain types of which *Carex arenaria* and lichens remain very frequent and patchily abundant. Where the climate is not so strongly continental, *Calluna-Carex* heath often develops from calcifuge dune grasslands, *Erica cinerea* being a common associate among lichen-rich vegetation with frequent *C. arenaria*, *F. ovina*, *L. campestris* and *A. praecox*. Disturbed and enriched ground may have patches of *Ulex-Rubus* scrub with fragments of calcifuge sward persisting among the gorse bushes, while deep, loose sands can support dense *Pteridium-Galium* vegetation. Invasion of birch or pine may presage a development to some kind of Quercion woodland, typically, in the heart of the range of the *Carex-Cornicularia* community, of the *Quercus-Betula-Deschampsia* type.

Distribution

The *Carex-Cornicularia* community is found mainly on the east coast of Britain, with the *Ammophila* sub-community concentrated on the coastal dunes of Norfolk and Suffolk, with some stands in eastern Scotland. The *Festuca* sub-community extends the range inland, on to the sands of Breckland.

Affinities

Although the cryptogamic component of this kind of vegetation was described from old fixed dunes at Blakeney by Richards (1929) and included within a *Caricetum arenariae* by Tansley (1939), the community figured little in early accounts of British dune vegetation. More recently, stands were listed in ecological studies of *Corynephorus* (Marshall 1967) and *Carex arenaria* (Noble 1982), where attention was drawn to the similarity between this sort of assemblage and Corynephorion communities described from coastal and inland sands from The Netherlands (Westhoff & den Held 1969), through Germany (Oberdorfer 1978, Ellenberg 1978) into Poland (Matuszkiewicz 1981). Closest among these to our own *Carex-Cornicularia* community is the *Spergulo morisonii-Corynephoretum canescentis* R.Tx. (1928) 1955 which has virtually identical suites of lichens and mosses, together with frequent records for *R. acetosella*, *Teesdalia* and *Filago minima*. Although *Corynephorus* is generally more important in sand fixation in such Continental vegetation than *Carex arenaria*, it seems sensible to locate British stands within the Corynephorion, and thus emphasise the genesis of at least some of them from a distinctive succession on initially acidic sands.

Floristic table SD11

	a	b	11
Carex arenaria	V (1–9)	V (4–8)	V (1–9)
Cornicularia aculeata	IV (1–6)	III (2–5)	IV (1–6)
Ammophila arenaria	IV (1–6)		III (1–6)
Cladonia furcata	III (1–7)	I (3)	III (1–7)
Aira praecox	III (1–5)	I (3)	II (1–5)
Hypogymnia physodes	III (1–5)		II (1–5)
Festuca rubra	II (1–3)		I (1–3)
Sedum acre	II (2–5)		I (2–5)
Hypochoeris radicata	II (2–5)		I (2–5)
Corynephorus canescens	II (1–7)		I (1–7)
Viola tricolor	II (1–4)		I (1–4)
Polytrichum juniperinum	II (2–7)		I (2–7)
Cladonia tenuis	II (2–5)		I (2–5)
Galium verum	I (1–3)		I (1–3)
Thymus praecox	I (3–7)		I (3–7)
Phleum arenarium	I (2–4)		I (2–4)
Cladonia coccifera	I (1–6)		I (1–6)
Viola canina	I (1–3)		I (1–3)
Racomitrium canescens	I (4–9)		I (4–9)
Cladonia rangiformis	I (2–8)		I (2–8)
Anthoxanthum odoratum	I (1–3)		I (1–3)
Erodium cicutarium	I (1–3)		I (1–3)
Logfia minima	I (1–5)		I (1–5)
Tortula ruralis ruraliformis	I (3–4)		I (3–4)
Cladonia rangiferina	I (1–6)		I (1–6)
Festuca ovina	I (2–5)	V (3–8)	I (2–8)
Cladonia pyxidata	I (2–4)	III (3)	I (2–4)
Cladonia uncialis	I (2–4)	III (1–5)	I (1–5)
Cladonia gracilis	I (2–3)	III (3–4)	I (2–4)
Calluna vulgaris	I (2)	II (3)	I (2–3)
Cladonia squamosa	I (3)	II (3)	I (3)
Astragalus danicus		I (2)	I (2)
Rhytidium rugosum		I (6)	I (6)
Cladonia arbuscula	III (1–9)	III (2–4)	III (1–9)
Cladonia foliacea	III (1–6)	III (2–3)	III (1–6)
Rumex acetosella	III (1–4)	III (2–4)	III (1–4)
Cladonia impexa	II (1–8)	III (2–4)	II (1–8)
Dicranum scoparium	II (1–5)	III (3–5)	II (1–5)
Luzula campestris	II (1–3)	II (4–5)	II (1–5)
Polytrichum piliferum	II (2–8)	II (3–4)	II (2–8)
Hypnum cupressiforme	II (2–8)	II (2–3)	II (2–8)
Agrostis capillaris	II (1–7)	I (4)	II (1–7)
Cladonia fimbriata	II (2–3)	I (3)	II (2–3)
Ceratodon purpureus	II (1–6)	I (3)	II (1–6)
Galium saxatile	I (2)	II (3)	I (2–3)

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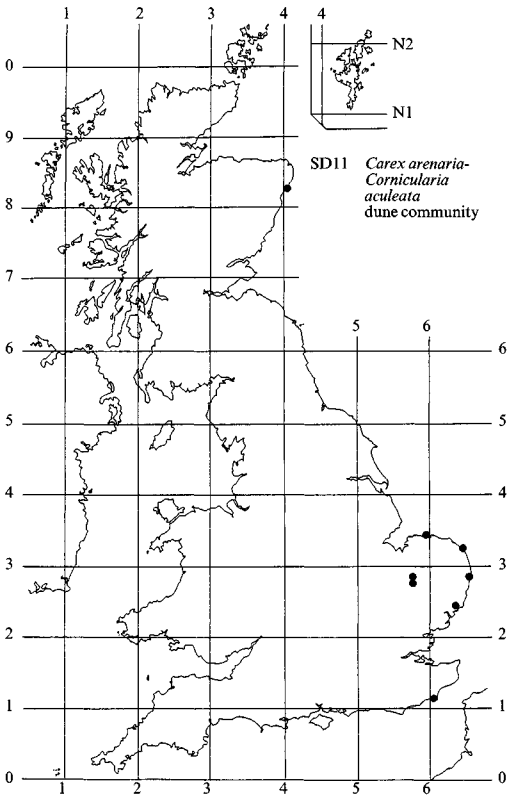
Ptilidium ciliare	I (1)	II (4–5)	I (1–5)
Brachythecium albicans	I (2–3)	I (4)	I (2–4)
Teesdalia nudicaulis	I (2)	I (4)	I (2–4)
Senecio jacobaea	I (1–2)	I (1)	I (1–2)
Plantago lanceolata	I (4)	I (3)	I (3–4)
Campanula rotundifolia	I (2)	I (3)	I (2–3)
Number of samples	46	7	53
Number of species/sample	12 (8–19)	17 (7–30)	16 (7–30)

a *Ammophila arenaria* sub-community
b *Festuca ovina* sub-community
11 *Carex arenaria-Cornicularia aculeata* dune community (total)



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