SD7
Ammophila arenaria-Festuca rubra semi-fixed dune community

Synonymy
Ammophiletum arenariae Moss 1906, Tansley 1911, 1939, all *p.p.*; *Elymo-Ammophiletum arenariae* Br.-Bl. & De Leeuw 1936.

Constant species
Ammophila arenaria, *Festuca rubra*, *Hypochoeris radicata*, *Poa pratensis s.l.*

Rare species
Acaena novae-zelandiae, *Epipactis dunensis*, *Euphorbia paralias*, *Mibora minima*, *Oenothera stricta*, *Vulpia fasciculata*.

Physiognomy
The *Ammophila arenaria-Festuca rubra* community is the major vegetation type of less mobile coastal sands where *Ammophila arenaria* is still usually the dominant, but where conditions are such as to allow the development of a fairly rich and often abundant associated flora over the stabilising dune surface. The marram tussocks may be big, with the shoots generally reaching 60–100 cm in height, but the tillers are not so densely packed or vigorous as in younger plants, and the accretion of bare sand among them much less rapid than in the earlier stages of colonisation. Where the tussocks are growing close together, the canopy of arching foliage can be quite extensive, but beneath this and particularly among more widely spaced marram, a variety of other herbs and also bryophytes can gain a hold, forming a patchy carpet of shorter vegetation that may be of locally high cover.

Along with the *Ammophila*, other sand-binding grasses are of only minor significant in this community. The hybrid × *Ammocalamagrostis baltica* occurs in some places, a natural associate in stands in Northumberland and on some Norfolk dunes, and of planted origin elsewhere in East Anglia (Hubbard 1968, Huiskes 1979), and *Leymus arenarius* remains of occasional importance here on dunes of moderate size and in disturbed situations, mostly along the east coast. *Elymus farctus*, however, a fairly common survivor in the *Ammophila* community where marram has invaded foredunes, is very scarce on this less mobile sand. Much more obvious throughout this kind of vegetation is *Festuca rubra*, often recorded as the var. or ssp. *arenaria* (Hubbard 1968, Tutin *et al.* 1980), here a constant companion of *Ammophila*, often sub-dominant to it and occasionally, in more open stretches of dune, the more abundant grass. *Poa pratensis s.l.* (probably *P. subcaerulea* in many cases: Hubbard 1968, Tutin *et al.* 1980) is also very common in the community, not usually of such high cover as *F. rubra*, though particularly noticeable in stands around our northern coasts. Other perennial grasses found much more occasionally are *Holcus lanatus*, *Arrhenatherum elatius* and *Dactylis glomerata*, the tussocks of which can be quite prominent, *Agrostis capillaris* and *Elymus repens*. At some sites, *E. pycnanthus* is locally abundant. The sand-sedge *Carex arenaria* also becomes very frequent here as a component of the sward among the marram, though it is never dominant.

Among the grassy matrix, a variety of perennial dicotyledons are characteristic of the *Ammophila-Festuca* community. The most frequent of these are *Hypochoeris radicata*, *Taraxacum officinale* agg. and *Senecio jacobaea* (sometimes behaving as a biennial) with *Hieracium pilosella*, *Lotus corniculatus* and *Galium verum* more unevenly distributed among the various sub-communities, but altogether commoner than in the *Ammophila* vegetation of more mobile dunes. In southern Britain and locally up the eastern Scottish coast, a further constant, *Ononis repens*, becomes very characteristic of the community, its patches of procumbent sticky shoots sometimes quite abundant.

More occasional associates of the *Ammophila-Festuca* vegetation, usually represented as scattered plants, are *Cerastium fontanum*, *Plantago lanceolata*, *Leontodon taraxacoides*, *L. hispidus*, *Luzula campestris*, *Achillea millefolium*, *Viola riviniana*, *Veronica chamaedrys*, *Trifolium repens* and *Anthyllis vulneraria*, with *Calystegia soldanella*, *Eryngium maritimum*, *Euphorbia paralias* and

E. portlandica a distinctive feature of some stands around our southern coasts. More patchily distributed and never really very common are *Viola canina*, *V. tricolor*, *Thymus praecox*, *Sedum acre*, *Campanula rotundifolia*, *Rhinanthus minor*, *Leontodon autumnalis* and *Ranunculus bulbosus*. Then, very locally, there can be clumps of *Rubus fruticosus* agg., *R. idaeus*, *R. caesius* or *Epilobium angustifolium*. Among more unusual perennials, the Australasian wool-alien *Acaena novae-zelandiae* (at one time thought to be *A. anserinifolia*) has become well established in this vegetation at certain of its coastal localities, notably in Northumberland, since its accidental introduction into Britain around the turn of the century (Gynn & Richards 1985). The rare and rather nondescript orchid *Epipactis dunensis* is also sometimes found in the community close to transitions to dune-slack surrounds.

Coarse weedy herbs tend to be rather less noticeable here than in the *Ammophila* vegetation but, along with *S. jacobaea*, there are occasional plants of *Cirsium arvense*, *C. vulgare*, *Rumex crispus*, *Senecio vulgaris*, *Sonchus arvensis*, *S. asper* and *Tragopogon pratensis*. Trailing masses of *Vicia sativa* ssp. *nigra* are also prominent in some stands. The South American evening primrose *Oenothera stricta* has also become well established in this vegetation on a number of dune systems around our southern coasts where it occasionally overwinters.

Compared with the *Ammophila* community, bryophytes are a more consistent feature here and they can be locally very extensive among the herbs, although the common species are rather few and none of these occurs frequently throughout. However, *Tortula ruralis* ssp. *ruraliformis* and *Hypnum cupressiforme s.l.* are characteristic of different kinds of *Ammophila-Festuca* vegetation, with *Brachythecium albicans*, *Homalothecium lutescens* and *Ceratodon purpureus* more occasional, *Brachythecium rutabulum*, *Eurhynchium praelongum*, *Pseudoscleropodium purum*, *Bryum capillare* and *B. argenteum* sparse. Lichens can also occur in small amounts, with records for *Cladonia fimbriata*, *C. impexa*, *C. furcata*, *C. rangiformis*, *C. pyxidata*, *Peltigera canina* and *P. rufescens*.

Sub-communities

Typical sub-community. *Ammophila*, or mixtures of *Ammophila* and *F. rubra*, dominate here, with very frequent and locally quite abundant *P. pratensis*, and in some stands patches of *Leymus arenarius* and occasional tussocks of *Dactylis*. Scattered plants of *H. radicata*, *T. officinale* agg. and *S. jacobaea* occur very commonly and there is often some *Carex arenaria*, but no other plants are frequent and the variety of associates is limited, so the vegetation is often rather species-poor and the cover of herbs among the grasses fairly open. Rather strikingly, there is never any *Ononis repens* in this sub-community.

Occasionals include *Hieracium pilosella*, *Galium verum*, *Lotus corniculatus*, *Cerastium fontanum*, *Plantago lanceolata* and *Cirsium arvense* with only rather sparse records for the various annuals found in the community. Bryophytes, too, are few in number but *T. ruralis* ssp. *ruraliformis*, *B. albicans* and *O. purpureus* occur quite commonly, with more infrequent *H. cupressiforme* and *Homalothecium lutescens.*

***Hypnum cupressiforme* sub-community.** *Ammophila*, or occasionally mixtures of *Ammophila* and *F. rubra*, are dominant in this sub-community, with *P. pratensis* still constant but generally subordinate. As in Typical *Ammophila-Festuca* vegetation, *H. radicata*, *T. officinale* agg., *S. jacobaea* and *C. arenaria* are all very common, but *Hieracium pilosella*, *Lotus corniculatus* and *Galium verum* all increase in frequency, and there is also occasional *Cerastium fontanum*, *Leontodon taraxacoides* and *Luzula campestris* in a cover of perennials that is usually more extensive.

Again, *Ononis repens* is not a characteristic plant but a number of preferentials give a distinct stamp to the vegetation. *Viola canina*, for example, is commoner here than elsewhere in the community and in Northumberland, prostrate patches of the alien *Acaena* can be very abundant. Then, along with annuals of the community like *Aira praecox* and *Cerastium semidecandrum*, *Arenaria serpyllifolia* and *Phleum arenarium*, others such as *Myosotis ramosissima*, *Valerianella locusta* and *Veronica arvensis* have been commonly recorded with more occasional *Vicia lathyroides* and *Erodium cicutarium*.

Equally striking in this sub-community is the frequency and often the abundance of *Hypnum cupressiforme s.l.* which, together with more patchy *Rhytidiadelphus squarrosus*, *R. triquetrus*, *Dicranum scoparium*, *Brachythecium albicans* and *Tortula ruralis* ssp. *ruraliformis*, can form an extensive carpet over the sand. Lichens, too, are often rather more conspicuous and varied here than elsewhere in the community, with fairly common *Cladonia fimbriata*, *C. impexa*, *Peltigera canina* and *P. rufescens*.

***Ononis repens* sub-community.** *Ammophila* usually dominates in this vegetation, with *F. rubra* constant though typically subordinate and *P. pratensis* rather reduced in frequency and rarely of appreciable cover. The commonest herbs are those of the Typical sub-community, *H. radicata*, *T. officinale* agg., *S. jacobaea* and *C. arenaria*, though even these can be rather patchy. Very distinctive here, though, is the constant occurrence, sometimes in considerable abundance, of *Ononis repens*.

Among the occasional associates, more thermophilous dune plants, like *Calystegia soldanella*, *Eryngium*

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maritimum, *Euphorbia paralias* and *E. portlandica*, are also found more commonly here, and there can be occasional *Galium verum*, *Lotus corniculatus*, *Plantago lanceolata*, *Leontodon taraxacoides* and *Cirsium arvense*. On more open areas, annuals such as *Aira praecox*, *Vulpia fasciculata*, *Phleum arenarium*, *Arenaria serpyllifolia*, *Cerastium semidecandrum* and *C. diffusum* ssp. *diffusum* make an occasional appearance. Bryophytes are less frequent here though scattered patches of *Brachythecium albicans* and *Tortula ruralis* ssp. *ruraliformis* can sometimes be found.

***Elymus pycnanthus* sub-community.** *Ammophila* remains abundant in this sub-community together with usually smaller amounts of *F. rubra* and *P. pratensis* but it is consistently accompanied by *Elymus pycnanthus* which can itself attain high cover. In this grassy ground, frequent associated herbs are few with even species like *Taraxacum officinale*, *Senecio jacobaea* and *Carex arenaria* being only occasional. Bryophyte cover is low, with just *Brachythecium albicans* showing any frequency.

Habitat

The *Ammophila-Festuca* community is the characteristic vegetation type of less mobile sands on dune systems all around the British coast, developing where accretion has become appreciably slower and erosion more rare, but where edaphic changes beneath the stabilising surface are not yet very great. Some of the floristic and structural variation in the community reflects the degree of fixity of the sand, but climatic differences through the season of growth and across the range of this vegetation are also influential with temperature and rainfall in particular having important effects on the representation of associates here on substrates that are still generally drought-prone and impoverished.

The rate and disposition of sand movement within particular dune systems around our coasts are complex functions of sediment supply and the development of dune-building vegetation on whatever material is able to accumulate behind the beach. In the establishment of an *Ammophila* cover, which is the controlling element in the colonisation of wind-blown coastal sands with us, the grass grows best where accretion is rapid and substantial, itself encouraging accumulation and keeping pace with burial of up to 1 m a year (Ranwell 1972). Eventually, though, there comes a point when reduced deposition of sand is matched by a waning in the vigour of the marram and, in this *Ammophila-Festuca* community, where accretion is probably less than 5 cm annually, we can see the early effects of that process. Only in young mobile dunes, or where there is some local spur to rejuvenation, is shoot production in the grass proliferative and, as death of the tillers comes to outstrip their replacement, the density of live shoots falls: here, there may be just half or so of the 150–200 tillers m^{-2} characteristic of the *Ammophila* community (Huiskes 1979). For some reason, too, flowering is not so free among the more fixed sand so, though the number of spikelets per inflorescence remains fairly constant, the output of ripe caryopses per unit area is reduced (Huiskes 1977*a*). Burial of the seed by wind-blown sand, which is highly inimical to germination (Huiskes 1972), is much less likely among the *Ammophila-Festuca* vegetation, but areas of bare ground in which seedlings might get a hold are that much sparser, and germination seems to be best adapted to the strongly-fluctuating soil temperatures typical of the open sandy surfaces of mobile dunes (Willis *et al.* 1959*b*, Stoutjesdijk 1960). In the field, seedlings of marram are rarely found away from the youngest dune ridges (Huiskes 1977*b*) and the tussocks of the *Ammophila-Festuca* community are probably almost always the thinning remnants of clones established early in the colonisation process (Huiskes 1979).

The reasons for the decline in *Ammophila* vitality are unclear. It has been suggested (Marshall 1965) that reduced accretion deprives the grass of the opportunity to put out new roots on freshly-buried internodes, but this seems an inadequate explanation (Hope-Simpson & Jefferies 1966, Huiskes 1977*a*). More likely are the impacts of increased competition for the very limited amounts of nutrients and water with other plants that are now able to establish on the less mobile surface, and the edaphic changes consequent upon the greater stability of the sand and the development of the vegetation upon it (Carey & Oliver 1918, Benecke 1930, Tansley 1939, Salisbury 1952, Willis *et al.* 1959*a*, *b*, Huiskes 1977*a*). In general terms, such changes involve an increase in the amount of organic matter, a leaching of carbonate and a reduction in pH within the surface layers of sand, but such developments can take several centuries and are much influenced by the initial character of the wind-blown sediment, particularly by the proportion of shell fragments, and the local climate (Salisbury 1952, Wilson 1960, Ranwell 1972, Willis 1985*b*). We do not know how far the changes have progressed with the shift from the *Ammophila* community of very mobile dunes to this next stage of *Ammophila-Festuca* vegetation, but perhaps not much. There is generally very little incorporated humus, even where there is an extensive moss carpet, and the superficial pH is usually between 7 and 8. The main response here may thus be to the increased physical stability of the sand surface.

The earlier stages of vegetation change are seen in the Typical and *Ononis* sub-communities characteristic of the lee faces of young dunes and tracts of semi-mobile sand. These can appear little different in general composition form the *Festuca* and *Poa* types of the *Ammophila* community on more shifting sand, but the increased

cover of the two smaller grasses, together with the more consistent occurrence of herbs like *Hypochoeris radicata*, *Taraxacum* and *Senecio jacobaea*, is testimony to the reduced accretion among marram that is not quite so vigorous nor so influential on its environment and associates. Both *F. rubra* ssp. *arenaria* and *P. subcaerulea* have far-creeping rhizome systems that can spread extensively among the *Ammophila* tussocks, but their shoots are easily overwhelmed by the deep and more sustained burial characteristic of earlier stages of dune growth. For *Carex arenaria*, too, it is only now that conditions begin to become more generally congenial: this sedge can readily accommodate to some measure of accretion by producing tiered lateral rhizomes (Tidmarsh 1939), but its increasing prominence in these kinds of vegetation is best seen as an indication of recently-declining sand mobility (Noble 1982). For the first time, also, the substrate is sufficiently stable for *Ononis repens* to find a frequent place in stands of the *Ammophila-Festuca* community around our warmer southern shores, and for the occasional appearance of plants like *Lotus corniculatus*, *Galium verum*, *Plantago lanceolata*, *Leontodon taraxacoides*, *Luzula campestris*, *Thymus praecox* and *Sedum acre*, smaller hemicryptophytes and chamaephytes that can never gain a permanent hold on more shifting sand.

In the *Hypnum* sub-community, the further increase in frequency of these herbs, the sharp rise to constancy of *Hieracium pilosella*, a plant well adapted to dry, nutrient-poor but stable soils, and the much more important contribution to the vegetation cover from mosses, all reflect the continuing reduction in accretion and the further fixing of the sand surface on more sheltered situations in semi-mobile dunes and altogether older ridges. Here, there may be but a very gentle upbuilding of the surface: *Tortula ruralis* ssp. *ruraliformis* and *Brachythecium albicans*, for example, can grow with their shoots crammed around with sand right to their tops, but rapid burial overwhelms them.

Throughout the development of the *Ammophila-Festuca* community, however, the composition of the vegetation reflects interactions between this changing physical character of the sand surface and the climatic conditions under which the dunes are being built. In the first place, among both younger and older stands of the community, the major floristic contrasts betray some effect of regional differences in rainfall and temperature. The Typical and *Hypnum* sub-communities, for example, occur most extensively north of the Solway–Forth line, with more local occurrences down to Northumberland and East Anglia and, in the West, to Cumbria and North Wales. Around these coasts, the combination of a cooler climate, with mean annual maxima usually below 25 °C (Conolly & Dahl 1970), and generally higher rainfall, especially in the west, where there are more than 160 wet days yr^{-1} (Ratcliffe 1968), results in a more humid atmosphere and reduced droughtiness in the dune sands. The greater abundance of *Poa subcaerulea* in these kinds of *Ammophila-Festuca* vegetation is probably a response to these conditions and continues a trend that has begun to appear in northern stands of the *Ammophila* community. The persistence of the Oceanic Northern *Leymus arenarius* in the Typical sub-community is also related to the cooler and moister climate around these coasts, although it is a scarce plant even there away from smaller and usually younger semi-mobile dunes or disturbed places.

By contrast, the *Ononis* sub-community is predominantly southern in its distribution, extending very little beyond the Solway–Forth line, particularly in the west. Here, *P. subcaerulea* has reduced frequency and cover, but more noticeably there is the common occurrence in this kind of *Ammophila-Festuca* vegetation of *Ononis repens*, a plant that is largely confined to warmer and drier parts of Britain, though not of course to coastal situations, except in the far north of its range, where suitably dry soils become scarce inland (Perring & Walters 1962). Other thermophilous associates of the *Ammophila-Festuca* community like the Oceanic Southern *Eryngium maritimum*, *Euphorbia paralias*, *Phleum arenarium* and the rare *Mibora minima* and *Vulpia fasciculata*, and the Oceanic West European *Euphorbia portlandica*, are also largely confined to the *Ononis* sub-community and, where numbers of these occur together, they create a very different impact from that seen in the Typical and *Hypnum* sub-communities.

The second kind of interaction between climate and soils which influences the *Ammophila-Festuca* community is evident among both northern and southern stands in the appearance of a range of diminutive ephemerals, more especially winter annuals. These usually have their best representation on our dunes in the later stages in the development of this kind of vegetation, providing some of the character of the *Hypnum* sub-community and representing a transition to the *Tortulo-Phleetum* which often occurs among it, though their contribution is by nature rather varied, local and sporadic.

Zonation and succession

In ageing dune systems, the *Ammophila-Festuca* community can occupy the first zone inland of the strandline on sand which has become more or less fixed but, where growth is still active, this vegetation is characteristically set back behind banks of foredunes and mobile dunes supporting different communities, only finding a place further towards the shore where there is a measure of local shelter. Inland, it can give way over ridges and sand-plains to dune grasslands and heath typical of

largely stabilised surfaces, the sequence of vegetation types sometimes clearly representing a succession. However, the patterns are often interrupted by zonations to slack communities, where the height of the water-table mediates the vegetation gradient, and are much influenced landwards by treatments and land improvement or reclamation.

In the most abbreviated beach-top sequences, where accretion and erosion are much reduced, there can be a sharp transition from the shore, sometimes with a strip of strandline vegetation, to more open stands of the *Ammophila-Festuca* community. Generally, though, even where the sand supply has become much reduced, the exposed face of the most seaward dunes carries the *Ammophila* community, the *Ammophila-Festuca* vegetation being limited to the lee slopes where the material is much less mobile. In southern Britain, it is the *Ononis* sub-community which is characteristic of these younger sheltered faces, with a zone of the *Festuca* sub-community of the *Ammophila* vegetation sometimes interposed in the transition to very open marram on the exposed, shifting sand. Around northern coasts, Typical *Ammophila-Festuca* vegetation replaces the *Ononis* sub-community, with the *Poa* type of *Ammophila* vegetation occurring where there is a more gradual shift to the immature marram. Then, especially down the east coast, and where the dunes remain low, these early sequences can be complicated by the persistence of *Leymus arenarius*, the *Festuca* sub-community of *Leymus* vegetation sometimes occurring on more mobile or disturbed surfaces among tracts of Typical *Ammophila-Festuca* grassland.

Where the zonations continue on to sand which is becoming more fixed, the *Ononis* and Typical sub-communities usually give way to the *Hypnum* type, the different vegetation types sometimes being found as distinct zones but more usually disposed in complex mosaics over surfaces of individual dunes or ridges where there is a diversity of aspects variously sheltered from the wind and sun. Locally severe erosion may result in a rejuvenation of the *Ammophila* community or the spread of *Carex arenaria* vegetation in blow-outs within such patterns. More local appearance of bare but still quite stable sand is often marked by patches of the *Tortulo-Phleetum*, particular on dune systems in the warmer and drier south of Britain.

In bigger dune systems, where there are expanses of fixed sand which have not been reclaimed, the more mature kinds of *Ammophila-Festuca* vegetation are frequently transitional inland to closed dune grassland, usually of the *Festuca-Galium* type. Here, *Ammophila* often remains very common, but it is generally much reduced in vigour, with *Festuca rubra* and *Poa pratensis* now typically providing the bulk of the grass cover. By this stage, the sands have become somewhat richer in organic matter and nutrients, and are more water-retentive, so the swards fill up and take on a more mesophytic character. Plants that are generally only occasional in the *Ammophila-Festuca* community become very frequent with *Galium verum*, *Plantago lanceolata*, *Trifolium repens*, *Lotus corniculatus* and *Achillea millefolium* especially distinctive, *Ranunculus acris*, *Bellis perennis* and *Euphrasia officinalis* agg. sometimes important, and a variety of other grasses, sedges and dicotyledons appearing that hardly ever figure on the more mobile, droughty and impoverished sands. Mosses such as *Tortula ruralis* ssp. *ruraliformis* and *Homalothecium lutescens* remain common but some pleurocarpous species like *Rhytidiadelphus squarrosus*, *R. triquetrus*, *Calliergon cuspidatum* and *Pseudoscleropodium purum* also occur among the turf. Grazing also has a more obvious effect upon the appearance of the vegetation than is the case with the communities of more mobile dunes sometimes trimming down the herbage to a short sward, but open patches are scarce and, where scuffing or droughting of the surface creates a gap, the appearance of assemblages of annuals is usually best seen as a transition to recurring *Ammophila-Festuca* vegetation. As with the communities of more mobile sand, there are some regional differences among the various kinds of *Festuca-Galium* grasslands, some of the most striking and extensive zonations occurring over the sand-plains along the very wet north-west seaboard of Scotland. There, the Typical and *Hypnum* sub-communities of *Ammophila-Festuca* vegetation on the semi-mobile dunes give way on the stretches of machair to the *Ranunculus-Bellis* and *Prunella* sub-communities of the *Festuca-Galium* grassland.

More locally, rather different zonations can be seen. Where there is little or no grazing on less mobile sands, a rather rare kind of situation on British dunes, the *Ammophila-Festuca* community can give way to the *Ammophila-Arrhenatherum* vegetation. This is a generally rather rank sward which has a number of characteristic plants in common with other assemblages of surfaces that are becoming fixed, like *Festuca rubra*, *Poa pratensis*, *Ononis repens*, *Galium verum*, *Lotus corniculatus* and *Achillea millefolium*, but the transition differs from zonations to the *Festuca-Galium* grassland in the prominence of *Arrhenatherum elatius* and *Dactylis glomerata*. These, and plants such as *Heracleum sphondylium* and *Lathyrus pratensis* often bring the vegetation close to an inland Arrhenatherion sward, but in some places the *Ammophila-Festuca* community passes on sunny, south-facing dune faces to a more striking kind of *Ammophila-Arrhenatherum* in which *Geranium sanguineum* is a constant feature, with scattered bushes of *Rosa pimpinellifolia*.

A more common variation occurs where the sands have become more sharply surface-leached on the fixed dune surfaces, when the *Ammophila-Festuca* commu-

nity can give way to the *Carex-Festuca-Agrostis* grassland. Here, again, *Ammophila* is often reduced to a minor and not very vigorous component in the swards, but *F. rubra* and *P. pratensis* are now usually matched in frequency and often in cover by *F. ovina*, *A. capillaris* and *C. arenaria*. Plants like *Hypochoeris radicata*, *Lotus corniculatus* and *Galium verum* remain fairly common but, with the increased importance of *Galium saxatile*, *Luzula campestris*, *Rumex acetosella* and acidophilous bryophytes, the vegetation approaches a dry calcifuge grassland in its appearance, especially where it is grazed, as is often the case. Transitions of this kind may also involve the local occurrence of patches of the *Carex-Cladonia* community on areas of open but compacted sand and, where ericoids gain a hold, there can be stands of *Calluna-Carex* heath.

All these different kinds of zonations may be interrupted by the occurrence of slack vegetation where the ground water table comes sufficiently close to the surface between the dunes to keep the sand permanently moist or at least seasonally flooded. On more calcareous sands, the *Salix-Holcus* community often occurs around the slack edges, with drier kinds of *Potentilla-Carex* vegetation on substrates that are less base-rich but, in both cases, boundaries are usually much sharper where the *Ammophila-Festuca* community occurs over the surrounding dune slopes, than where the *Festuca-Galium* vegetation provides the context. *F. rubra* often maintains some representation in the slacks, with herbs like *Lotus corniculatus*, *Ranunculus acris*, *Trifolium repens* and *Euphrasia officinalis* variously recorded, but *Ammophila* disappears sharply at the slack surrounds and plants such as *Poa pratensis* and *Carex arenaria* sometimes penetrate little further.

Distribution

The *Ammophila-Festuca* community occurs all around the British coast where there are suitable semi-mobile sands, with the *Ononis* sub-community found largely south of the Solway–Forth line, the Typical and *Hypnum* forms to the north, with an area of overlap along the coast of Northumberland.

Affinities

Although many accounts of the development of dune vegetation in Britain draw attention to the changes occurring with the reduction in sand mobility, there have never been any convincing attempts to systematically distinguish the various assemblages occurring between the foredunes and the fixed dunes in different parts of the country. In early schemes, then, the *Ammophila-Festuca* community would have been subsumed within a general *Ammophiletum* (Moss 1906, Tansley 1911, 1939), though it is sufficiently distinct in its floristics, structure and ecological relationships to warrant separation from the more immature *Ammophila* community, as well as from the *Festuca-Galium* vegetation of fixed dunes.

Phytosociologically, some of our southern stands in the *Ononis* sub-community approach the *Euphorbio-Ammophiletum* Tx. 1945, a more thermophilous association reported from semi-mobile dunes along the French Atlantic coast (Géhu & Géhu 1969) and from Eire (Braun-Blanquet & Tüxen 1952, Ivimey-Cook & Proctor 1966, Beckers *et al.* 1976, Schouten & Nooren 1977, Ni Lamhna 1982). With us, however, *O. repens* tends to be a better distinguishing species of this kind of dune vegetation around our warmer coasts than plants like *Calystegia soldanella*, *Euphorbia paralias* or *Eryngium maritimum*. Further north, the absence of these plants brings the Typical and *Hypnum* sub-communities close to the *Elymo-Ammophiletum* Br.-Bl. & De Leeuw 1936. Here again, though, there is no attempt in Continental schemes to distinguish earlier and later stages in the development of either of these communities.

Floristic table SD7

	a	b	c	d	7
Ammophila arenaria	V (1–9)	V (3–8)	V (1–10)	IV (1–9)	V (1–10)
Festuca rubra	V (2–9)	V (1–8)	V (1–10)	V (2–10)	V (1–10)
Poa pratensis	V (1–7)	V (1–8)	III (1–7)	V (1–7)	IV (1–8)
Hypochoeris radicata	IV (1–7)	IV (1–6)	III (1–4)	III (1–7)	IV (1–7)
Taraxacum officinale agg.	IV (1–5)	IV (1–3)	III (1–5)	II (1–2)	III (1–5)
Senecio jacobaea	IV (1–3)	IV (1–3)	III (1–5)	II (1–4)	III (1–5)
Carex arenaria	III (1–5)	IV (1–4)	II (1–5)	II (1–7)	III (1–7)
Ceratodon purpureus	II (1–6)	I (3)	I (1–4)	I (1–5)	I (1–6)
Leymus arenarius	II (1–5)		I (1–6)	I (2–5)	I (1–6)
Dactylis glomerata	II (1–5)		I (1–5)	I (1–4)	I (1–5)
Hypnum cupressiforme	I (1–8)	V (1–8)	I (1–4)	I (6)	II (1–8)
Hieracium pilosella	II (1–5)	IV (1–6)	I (1–3)	I (1–5)	II (1–6)
Galium verum	II (1–4)	III (1–6)	II (1–7)	I (3)	II (1–7)
Acaena novae-zelandiae	I (2–8)	III (1–6)	I (1–5)		I (1–8)
Myosotis ramosissima	I (1–2)	III (1–3)	I (1–2)	I (1)	I (1–5)
Valerianella locusta	I (1–2)	III (1–3)	I (1–2)	I (1–3)	I (1–4)
Viola canina	I (1–3)	III (1–3)	I (1–2)	I (3)	I (1–3)
Epilobium angustifolium	I (2–6)	II (1–3)	I (2–5)	I (2–4)	I (1–6)
Rhytidiadelphus squarrosus	I (2–3)	II (2–6)	I (1–3)		I (1–6)
Cladonia fimbriata	I (1–4)	II (1–3)		I (1–2)	I (1–5)
Dicranum scoparium	I (1–4)	II (1–5)		I (2)	I (1–6)
Veronica arvensis	I (1)	II (2–3)		I (1–2)	I (1–3)
Rhytidiadelphus triquetrus	I (1)	II (2–9)		I (3)	I (1–9)
Cladonia impexa		I (2–4)			I (2–4)
Vicia lathyroides		I (1–2)			I (1–2)
Erodium cicutarium		I (1–2)			I (1–2)
Peltigera rufescens		I (1–2)			I (1–2)
Ononis repens		I (2)	V (1–8)	I (2–6)	III (1–8)
Calystegia soldanella			I (3–4)		I (3–4)
Elymus pycnanthus	I (1–3)		I (2–6)	V (4–10)	II (1–10)

Floristic table SD7 (*cont.*)

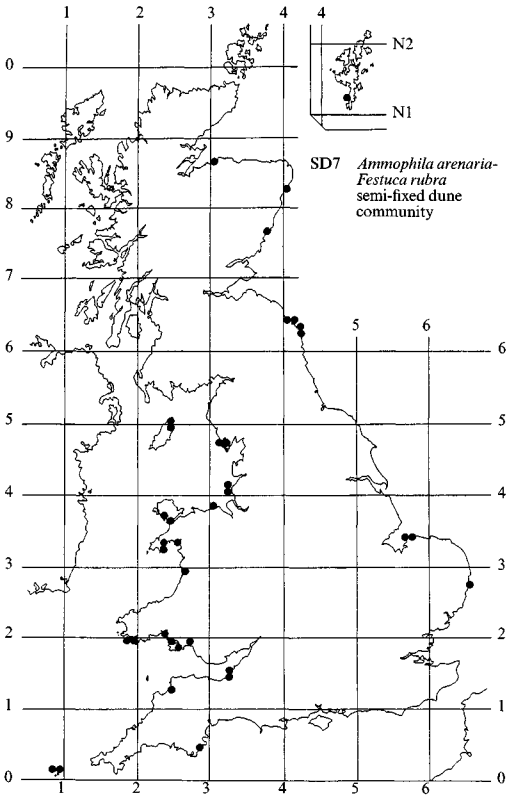
	a	b	c	d	7
Lotus corniculatus	II (1–9)	III (1–7)	II (1–8)	II (1–6)	II (1–9)
Cerastium fontanum	II (1–4)	II (1–3)	I (1–3)	I (1–4)	II (1–4)
Brachythecium albicans	II (1–9)	II (2–4)	I (1–5)	III (1–7)	II (1–9)
Plantago lanceolata	II (1–5)	I (3)	II (1–6)	I (2–6)	II (1–6)
Cirsium arvense	II (1–4)	I (2)	II (1–4)	II (1–3)	II (1–4)
Tortula ruralis ruraliformis	II (1–8)	II (2–7)	I (1–9)	II (1–7)	II (1–9)
Viola tricolor	I (1–3)	I (1–2)	I (1–4)		I (1–5)
Thymus praecox	I (1)	I (1–7)	I (1–8)		I (1–8)
Homalothecium lutescens	I (1–8)	I (1–5)	I (2)		I (1–8)
Arenaria serpyllifolia	I (1–3)	I (3)	I (2–4)	I (1–3)	I (1–4)
Phleum arenarium	I (1–3)	I (1–4)	I (1–4)	I (1–3)	I (1–5)
Sedum acre	I (1–4)	I (1–2)	I (1–5)	I (5)	I (1–5)
Cerastium diffusum diffusum	I (1–4)	I (1–2)	I (1–3)	I (1–2)	I (1–4)
Leontodon taraxacoides	I (1–4)	II (1–2)	II (1–5)	I (3–4)	I (1–5)
Aira praecox	I (2–4)	II (2–3)	I (1–4)	I (1–3)	I (1–5)
Luzula campestris	I (1–3)	II (1–3)	I (2)	I (1)	I (1–4)
Cerastium semidecandrum	I (1–2)	II (1–3)	I (1–4)	II (2–4)	I (1–6)
Peltigera canina	I (1–7)	II (1–3)			I (1–7)
Brachythecium rutabulum	I (1–8)	I (1)	I (1–6)	I (1–4)	I (1–8)
Holcus lanatus	I (1–4)	I (2–5)	I (1–5)	I (6)	I (1–6)
Arrhenatherum elatius	I (1–3)	I (3)	I (1–6)	I (3–6)	I (1–6)
Achillea millefolium	I (2–3)	I (3)	I (1–3)	I (1)	I (1–3)
Viola riviniana	I (1–5)	I (1–2)	I (1–2)		I (1–5)
Leontodon hispidus	I (3–4)	I (1–3)	I (1–2)	I (2–3)	I (1–5)
Eurhynchium praelongum	I (1–5)	I (4)	I (1)	I (3)	I (1–5)
Agrostis capillaris	I (1–7)	I (1)	I (2)		I (1–7)
Veronica chamaedrys	I (1–2)	I (1)	I (3–4)		I (1–4)
Linum catharticum	I (3)	I (1–3)	I (1)	I (1–3)	I (1–5)
Trifolium repens	I (1–5)	I (1–3)	I (1)		I (1–5)
Anthyllis vulneraria	I (1–3)		I (2–7)		I (1–7)
Trifolium arvense	I (2–5)		I (1–2)	I (2–6)	I (1–6)
Crepis capillaris	I (1–3)		I (1–4)	I (2–3)	I (1–4)

Euphorbia paralias	I (1)		I (1–5)	I (2)	I (1–5)
Eryngium maritimum	I (1)		I (2–6)	I (2–3)	I (1–6)
Campanula rotundifolia	I (1)		I (1–2)	I (2)	I (1–3)
Rumex crispus	I (1)		I (1–2)	I (2–4)	I (1–4)
Rubus fruticosus agg.	I (2)		I (1–2)	I (3–4)	I (1–4)
Centaurium erythraea	I (2–4)	I (1)		I (1–3)	I (1–4)
Pseudoscleropodium purum	I (1–4)	I (2–5)		I (3–7)	I (1–7)
Cladonia furcata	I (1)	I (1–3)		I (5)	I (1–5)
Cladonia rangiformis	I (1)	I (1–4)		I (2–6)	I (1–6)
Rhinanthus minor	I (1–4)	I (3)	I (1–3)	I (1–3)	I (1–4)
Elymus repens	I (1)	I (3)	I (3–6)		I (1–6)
Leontodon autumnalis	I (1–4)	I (3)	I (2)	I (1–2)	I (1–4)
Senecio vulgaris	I (1–2)	I (3)	I (2)		I (1–3)
Sonchus arvensis	I (4)	I (1)	I (1–2)	I (1–4)	I (1–4)
Vicia sativa nigra	I (2–4)	I (3)	I (2–5)	I (3)	I (2–5)
Tragopogon pratensis	I (1)	I (3)	I (1–2)	I (1)	I (1–3)
Erophila verna		I (2–3)	I (2)	I (1)	I (1–3)
Ranunculus bulbosus		I (1)	I (1)		I (1)
Trifolium campestre	I (2–3)			I (1–3)	I (1–3)
Bryum capillare	I (4–6)			I (5–9)	I (4–9)
Lophocolea bidentata	I (1–3)				I (1–3)
Tussilago farfara	I (1–4)		I (2)	I (3–4)	I (1–4)
Centaurea nigra	I (1–2)		I (1)		I (1–2)
Elymus farctus	I (1–4)		I (1–5)	I (1–8)	I (1–8)
Plantago coronopus	I (1–2)		I (4)	I (2)	I (1–4)
Bryum argenteum	I (1–5)		I (1)		I (1–5)
Heracleum sphondylium	I (1)		I (1–5)	I (1–2)	I (1–5)
Ranunculus repens	I (2)	I (1)			I (1–2)
Cladonia pyxidata	I (1)	I (1–2)			I (1–2)
Cirsium vulgare		I (1)	I (1)	I (1–3)	I (1–3)
Vulpia fasciculata			I (1–7)		I (1–7)
Rubus caesius			I (1–9)	I (1)	I (1–9)
Euphorbia portlandica			I (1–3)		I (1–3)
Sonchus asper			I (1–3)	I (1)	I (1–3)

Floristic table SD7 (*cont.*)

	a	b	c	d	7
Number of samples	52	21	74	54	201
Number of species/sample	15 (7–28)	19 (14–30)	13 (7–25)	11 (4–26)	14 (4–30)
Herb height (cm)	27 (1–80)	17 (3–50)	32 (2–100)	no data	27 (1–100)
Herb cover (%)	66 (40–100)	89 (75–98)	79 (25–100)	no data	80 (25–100)
Bryophyte height (mm)	30 (10–50)	19 (15–20)	9 (4–30)	no data	13 (4–50)
Bryophte cover (%)	39 (5–85)	21 (10–40)	7 (1–80)	no data	17 (1–85)
Slope (°)	9 (0–40)	12 (0–40)	11 (0–70)	no data	11 (0–70)
Soil pH	7.8 (5.3–8.8)	7.8 (7.0–8.9)	7.7 (5.5–8.7)	no data	7.8 (5.3–8.9)

a Typical sub-community
b *Hypnum cupressiforme* sub-community
c *Ononis repens* sub-community
d *Elymus pycnanthus* sub-community
7 *Ammophila arenaria-Festuca rubra* semi-fixed dune community (total)



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