SD6

Ammophila arenaria mobile dune community

Synonymy

Ammophiletum arenariae Moss 1906, Tansley 1911, 1939, all *p.p.*; *Elymo-Ammophiletum arenariae* Br.-Bl. & De Leeuw 1936; *Ammophila arenaria* stands Gimingham 1964*a p.p.*

Constant species

Ammophila arenaria.

Rare species

Allium ampeloprasum ssp. *babingtonii*, *Corynephorus canescens*, *Euphorbia paralias*, *E. portlandica*, *Scrophularia scorodonia*.

Physiognomy

The *Ammophila arenaria* community includes virtually all the vegetation of more mobile coastal sands in which the robust perennial grass *Ammophila arenaria* plays a dominant role in the dune-building process. In young stands, or where newly eroded surfaces among established dunes are being recolonised, the cover of the plant is often low, with just a few sparse shoots emerging from freshly-blown sand that may be otherwise quite bare. Growth can become very vigorous, however, in actively-accreting material where *Ammophila* can spread its horizontal rhizomes far and keep pace with burial of up to 1 m a year, the expanding clones putting up densely-branching tillers that become aggregated into the characteristic tussocks (Gemmell *et al.* 1953, Greig-Smith 1961, Ranwell 1972). The shoots enhance accretion even more, continuing to proliferate among the upbuilding sand, until they can be packed at 150–200 m^{-2}. Adjacent tussocks, with their spreading foliage reaching 1 m or more in height, can thus enlarge to form an extensive cover of the grass over stretches of still shifting sand that is being built into often substantial dunes. As the substrate becomes more fixed, however, the vigour of the *Ammophila* in older stands of the community declines, with a reduction in shoot density to about half that in mobile sand, although bouts of erosion can stimulate fresh bursts of growth and a renewal of this vegetation in blow-outs (Tansley 1939, Ranwell 1960*a*, Huiskes 1979).

Almost all British *Ammophila* is *A. arenaria* ssp. *arenaria*, although the North American *A. breviligulata* (differing only in its truncate ligule and sometimes regarded as *A. arenaria* ssp. *breviligulata*: Maire 1953) was planted on some our dune systems following the 1953 coastal floods (Hubbard 1968) and persists as an element in the community at Newborough in Gwynedd (Huiskes 1979). The hybrid marram × *Ammocalamagrostis baltica*, a sterile intergeneric cross with *Calamagrostis epigejos* and a bulkier plant even than *Ammophila*, can also be found among this vegetation on dunes in Norfolk and Northumberland. These populations, like that on the cliffs of Handa in Sutherland seem to be of natural origin, although this grass, too, is regarded as a valuable sand-binder (Huiskes 1979) and was introduced at some new sites along the East Anglian coast after 1953 (Hubbard 1968).

In many stands, particularly where the sand remains very mobile, marram is the only plant in this vegetation and it is the sole constant of the community. Some other grasses, though, have a subordinate but locally prominent place here, and they provide important links with different kinds of dune vegetation. In younger stands, for example, where *Ammophila* is invading foredunes, *Elymus farctus* can persist for some time before being overwhelmed by the accumulating sand. Then, especially along the north-east coast of Britain, *Leymus arenarius* is a common colonist ahead of or along with *Ammophila* and it can remain as dense tufts or clusters of shoots, often a little taller than the marram and a more striking grey-green, in stands of the community on mobile dunes of up to moderately large size. Much less structurally important, but noticeable here as an invader of more open areas among the *Ammophila* where sand has recently settled is *Carex arenaria*. On somewhat more stable dunes, on the other hand, *Festuca rubra* often becomes the most frequent associate in this vegetation, being commonly recorded as the var. or ssp. *arenaria* with

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its stiff tufts of rather glaucous leaves and extensively creeping rhizomes (Tutin *et al.* 1980). In the moister and cooler climate of northern Britain, this is frequently accompanied by what is grouped here as *Poa pratensis* agg., but which is probably often *P. subcaerulea*, a plant that is not so strongly tufted as *P. pratensis s.s.* and where both glumes have three veins (Tutin *et al.* 1980). Even these commoner grasses never form anything like a continuous turf beneath the *Ammophila* in this community, but much more occasional, and usually only of very patchy abundance even on less mobile sand, are *Elymus repens*, *E. pycnanthus*, *Holcus lanatus*, *Dactylis glomerata*, *Agrostis stolonifera* and *Poa annua*. A further interesting species which sometimes finds a place in this vegetation at a few localities along the East Anglian coast is *Corynephorus canescens*, a nationally rare perennial grass that can become locally abundant among the *Ammophila* provided accretion is not too rapid, at least when the plant is establishing (Marshall 1967).

As with the grasses, no other associates occur at all frequently throughout the community, though the commonest group comprises more short-lived herbs, often of a rather coarse and weedy character, which can take advantage of periodically stable conditions among the developing dunes. Closer to the strandline, for example, where this vegetation can develop on foredunes, plants like *Cakile maritima* and various *Atriplex* spp. may figure, together with surviving patches of the perennial *Honkenya peploides*. Then, *Sonchus arvensis*, *S. asper*, *Senecio vulgaris*, *S. jacobaea*, *S. squalidus*, *Cirsium vulgare*, *C. arvense* and *Rumex crispus* all occur with varying degrees of frequency through the community, sometimes becoming locally abundant over particular stretches of dune, only to disappear completely in the next season. More especially characteristic of the sandy maritime habitat, though confined to stands in the warmer, southerly part of the range of this vegetation, are *Eryngium maritimum*, *Calystegia soldanella* and the rarities *Euphorbia paralias* and *E. portlandica*, these often establishing as scattered individuals but, except for the last, able to persist for some years where the sand is not too mobile. The community can also provide one of the loci for the rare *Scrophularia scorodonia* and *Allium ampeloprasum* var. *babingtonii* on some dune systems in south-west England (Perring & Farrell 1977).

Other plants found here, though usually where the sand has become somewhat stabilized, include *Hypochoeris radicata*, *Taraxacum officinale*, *Ranunculus repens*, *Trifolium repens*, *Galium verum*, *Tussilago farfara*, *Cynoglossum officinale*, *Linaria vulgaris* and *Erodium cicutarium*. More local, though usually noticeable by virtue of their tall stature are *Heracleum sphondylium*, *Angelica sylvestris* and *Epilobium angustifolium* and *Rubus fruticosus* agg., this last sometimes forming small patches among the *Ammophila*. The Californian *Lupinus arboreus* has also become naturalised in this community on various dune systems around our southern coasts in dense bushy growth 2 or 3 m high (Nicholson 1985).

Bryophytes are much more a characteristic feature of the *Ammophila-Festuca* vegetation that develops on less mobile sand than is usual here, but a few species begin to make an appearance at very low overall frequencies but occasionally with some abundance where the surface has become more stable: *Ceratodon purpureus*, *Tortula ruralis* ssp. *ruraliformis* and *Brachythecium albicans*.

Sub-communities

***Elymus farctus* sub-community.** Small amounts of *E. farctus* are a constant feature among the *Ammophila* here in what is often very open vegetation, with occasional low patches of *Honkenya* but otherwise just sparse individuals of *Cakile maritima*, *Senecio jacobaea*, *S. vulgaris*, *Sonchus arvensis*, *S. asper*, *Cirsium vulgare*, *C. arvense*, *Eryngium maritimum* and *Calystegia soldanella*.

***Elymus farctus-Leymus arenarius* sub-community:** *Elymo-Ammophiletum typicum* Br.-Bl. & De Leeuw 1936 *sensu* Birse 1980 *p.p.* Both *E. farctus* and *L. arenarius* accompany *Ammophila* in this sub-community, one or other or both sometimes sub-dominant, with occasional records for *Atriplex* spp. and very much the same associates as in the above.

***Leymus arenarius* sub-community:** *Ammophila* with scattered *Elymus* Gimingham 1964*a*; *Elymo-Ammophiletum typicum* Br.-Bl. & De Leeuw 1936 *sensu* Birse 1980 *p.p.* *L. arenarius* is a constant with *Ammophila* here and sometimes quite abundant, but other plants are usually very few, just sparse individuals of the weedy community associates, often without strandline survivors.

***Ammophila arenaria* sub-community.** *Ammophila* is often overwhelmingly dominant in this sub-community with scattered records for a wide variety of associates, but no consistency of enrichment from stand to stand. *Senecio jacobaea* is the commonest companion, but *Sonchus asper* and *Cirsium arvense* are also fairly frequent and each may be locally quite abundant. Less common, but rather striking on some of our more southerly dune systems, are *Calystegia soldanella*, *Eryngium maritimum*, *Euphorbia paralias* and *E. portlandica*. *Rumex crispus*, *Hypochoeris radicata* and *Festuca rubra* occur occasionally, too, and there can be very sparse bryophytes.

***Festuca rubra* sub-community.** *Ammophila* is still very much the dominant here, accompanied in some stands

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by smaller amounts of *Leymus*, but the vegetation cover between the tussocks and the variety of the associated flora are considerably increased. Most obviously, *F. rubra* is a constant companion, usually growing as scattered plants, though sometimes occurring with moderate local abundance, with *Senecio jacobaea*, *Hypochoeris radicata* and *Cirsium arvense* becoming quite common. *Eryngium*, *C. soldanella* and the *Euphorbia* spp. continue to add a distinctive character to more southern stands and then, along with occasional records for community associates like *Sonchus* spp., *Senecio vulgaris* and *Rumex crispus*, there can be scattered individuals of *Taraxacum officinale* agg., *Ranunculus repens*, *Galium verum*, *Trifolium repens* and *Tussilago farfara*. Rather more striking on this kind of dune, though never very frequent, are *Cynoglossum officinale*, *Erodium cicutarium*, *Linaria vulgaris* and *Trifolium arvense*. Then, there can be very occasional taller herbs like *Angelica*, *Heracleum* and *Epilobium angustifolium* with sparse patches of *Rubus fruticosus* agg. and, at some sites, bushes of invading *Lupinus*. Other grasses apart from *F. rubra* can sometimes occur, such as *Holcus lanatus*, *Dactylis glomerata*, *Elymus repens* and *E. pycnanthus*, but these are usually no more than scattered tussocks, and *Poa pratensis* is very scarce. Bryophytes can form locally quite extensive patches.

***Poa pratensis* sub-community:** *Elymo-Ammophiletum*, *Festuca rubra* Subassociation Br.-Bl. & De Leeuw 1936 *sensu* Birse 1980. *F. rubra* remains very frequent between the dominant *Ammophila*, but *P. pratensis* is also constant in this sub-community, these two grasses, occasionally with *Elymus repens* and a little *Holcus lanatus* or *Dactylis glomerata*, sometimes forming a moderately extensive, though still patchy, cover. *Senecio jacobaea*, *Cirsium arvense* and *Sonchus arvensis* are again quite common, with occasional *Heracleum sphondylium*, *Cynoglossum officinale*, *Angelica sylvestris*, *Epilobium angustifolium*, *Ranunculus repens*, *Trifolium repens* and *Galium verum*, but more thermophilous herbs of southern dunes are very scarce. As in the *Festuca* sub-community, bryophytes may be locally quite abundant.

***Carex arenaria* sub-community.** Usually this vegetation comprises little more than abundant *Ammophila* with sparse to quite plentiful *C. arenaria*, the sedge often extending out in its distinctive runs of shoots over the bare sand among the marram.

Habitat

The *Ammophila* community is the most widespread and extensive colonising vegetation of mobile sands above the limit of tidal inundation all around the British coast, dominating on young dune ridges and in blow-outs until such time as reduced accretion limits the vigour of the marram and allows an increase in the extent and diversity of the associated flora. Variation in the floristics and structure of the vegetation relates largely to the waning influence of tidal disturbance towards the lower limit of marram invasion and, in the opposite direction, to the increased stability of the sand surface.

Ammophila is the most important colonist of wind-blown sand above the tidal limit around the entire coast of Britain and the plant best adapted to the inhospitable environment characteristic of the mobile dunes that can develop there. Our own ssp. *arenaria* is widely distributed around the seaboard of north-west Europe, its northern limit at the 0 °C January isotherm (Salisbury 1952) occurring well beyond our shores in the Faeroes and in southern Norway, and only very locally in this country is its invasive and dune-building potential on suitable substrates out of reach of the tides rivalled. Planted × *Ammocalamagrostis* can be more vigorous, perhaps because, being sterile, it needs to spare no resources for seed production (Huiskes 1979), but *Leymus arenarius*, though a vigorous colonist along with *Ammophila* along our north-eastern shores, is eventually overwhelmed by more than a few metres of accumulated sand. The *Leymus* sub-community here is thus generally characteristic of younger mobile dunes, or the lower seaward faces of bigger sandhills carrying this kind of vegetation.

Leymus is also tolerant of occasional tidal inundation and can invade sandy patches closer to the strandline than is possible for *Ammophila*. Marram needs a substrate with less than 1% sea salt (Huiskes 1979), indeed experimentally it is almost always killed by salinities of only 1.5% (Benecke 1930), so it only becomes an important colonist where the beach level has already been raised out of reach of even extreme tides. However, where *Ammophila* invades foredunes, more salt-tolerant strandline survivors can persist for some time, *Honkenya*, *Cakile* and *Atriplex* spp., as well as *Elymus farctus*, the grass most tolerant of tidal submersion, providing a distinctive character to the *Elymus* and *Elymus-Leymus* sub-communities.

In such situations, *Ammophila* can colonise from both seed and rhizome fragments. Seed production in well-established plants can be prolific, Salisbury (1952) estimating an average of 20000 caryopses annually from vigorous tussocks, and dispersal occurs readily by wind. Viability is high, and germination succeeds best in the strongly-fluctuating temperature regime characteristic of mobile dunes (Kinzel 1926, Willis *et al.* 1959*b*, Stoutjesdijk 1961) with a marked flush in April and May after a winter chilling (Huiskes 1979). Even slight burial, however, beneath just a few centimetres of sand, greatly reduces germination and subsequent disturbance of the surface or desiccation kills many survivors (Huiskes 1979). Dampening of the ground greatly increases the

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chance of seedlings getting away (Huiskes 1977*b*), particularly on the more open surfaces in younger dunes, although even then, it is at least two years before inflorescences are produced.

Meanwhile, however, the young plant can get a firm hold in the substrate, a main shoot developing from the caryopsis or bud on the rhizome fragment, axillary buds giving rise to daughter tillers or new rhizomes, these growing upwards and outwards with repeated sympodial branching (Greig-Smith *et al.* 1947, Gemmell *et al.* 1953, Greig-Smith 1961). Once established, vegetative spread of the clones by such rhizome extension and proliferative shoot production is far more important within stands of the community than reproduction from seed (Huiskes 1979), though where conditions are suitable new seedlings can continue to find a place among the older tussocks, helping to infill the cover. However, only in foredune stands, or where the community develops around young slacks, does shoot production continue to result in a net increase in tillers per unit area, a process which continues until what is apparently the shoot-carrying capacity of the ground is reached. The tillers are, in fact, monocarpic although, even in mobile sand where inflorescences are mainly found, many tillers die from other causes and, in established stands, shoot production involves mainly a regenerative replacement of tillers that have died (Huiskes 1977*a*, 1979).

The real key to the success of *Ammophila* in this environment, however, is its impressive ability to keep pace with burial by the blown sand. The rhizomes and roots help bind the substrate against erosion and the densely-crowded tillers enhance accretion by reducing the speed and sand-carrying capacity of the wind (Willis *et al.* 1959*b*) but, when buried, the internodes on the shoots elongate, effectively converting them into vertical rhizomes which are able to maintain upward growth through 1 m or so of sand a year (Grieg-Smith *et al.* 1947, Ranwell 1972). By producing more daughter tillers and horizontal rhizomes, the plant can thus re-establish dominance on the upbuilding surface it has helped to create. Conversely, where erosion strips back the substrate or where whole sections of dune shift to expose deeper layers of sand, dormant buds on buried rhizomes can regenerate a cover of tillers on the freshly-exposed surface.

Accretion and ablation on the scale characteristic of mobile dunes are inimical to most potential competitors of *Ammophila* and help maintain the sands in a raw and uncongenial state. The material freshly blown from the beach is of varying composition, though often very calcareous where the proportion of shell fragments is high: pH is generally within the range 6–9 and, with any tendency to leaching outpaced by fresh deposition, fairly constant with depth (Willis *et al.*, 1959*b*, Marshall 1967, Huiskes 1979). In fact, although *Ammophila* itself is reported as absent from soils with a pH below 4.5 or so (Lux 1964, 1966) and shows depressed shoot densities where this vegetation occurs on more acid dunes, as at Winterton in Norfolk (Boorman in Huiskes 1979), its growth seems to be little affected by differences above neutral, and the community associates rarely reflect variations in this factor.

More limiting to the character and vigour of the vegetation is the impoverished nutrient content of the mobile sands, whether these are alkaline or acidic (Willis *et al.* 1959*a*, Wilson 1960, Willis & Yemm 1961). Away from the foot of foredune stands, where more nitrophilous herbs can still capitalise on flushing from strandline debris in the *Elymus* and *Elymus-Leymus* sub-communities, organic carbon is in extremely short supply, with very low amounts, too, of total nitrogen and available N, P and K. The growth of *Ammophila* itself is markedly affected by such deficiences and much stimulated by experimental additions of mineral nutrients (Lux 1964, Willis, 1965). After a two-year period of additions at Braunton Burrows in Devon, for example, marram showed a three-fold increase in fresh weight of the shoot system with enhanced tillering, taller shoots and wider leaves, and a four-fold increase in the root systems, with dense mats of fine roots developing. Glasshouse sand culture revealed here that nitrogen shortage was the major limitation and also that adding purified sand to the established cultures continued to promote growth by providing an opportunity for new root formation by the buried nodes. Other authors, like Hassouna & Wareing (1964) have suggested that *Ammophila* may be able to avoid some of the effects of nitrogen-limitation by capitalising on the activity of non-symbiotic nitrogen-fixers in the rhizosphere, and it is known that *Azotobacter* occurs in mobile dune sand (Géhu 1960). Abdel-Wahab (1969, 1975) found that *Bacillus* spp. also played a role in nitrogen-fixation in mobile dunes, although Pegtel (1976) and Woldendorp (in Huiskes 1979) have expressed doubts about the contribution of this process, dependent as it is on organic carbon, itself in very short supply in this habitat.

The second important factor limiting the cover and composition of this vegetation on mobile sand is water, particularly as the dune surface and the rooting zone of the plants are raised by accretion to what is often a very considerable distance above the ground water-table, over 26 m at Braunton, for example (Willis *et al.* 1959*a*). Most of the water available to the community comes from rain and the level of the water-table is strongly dependent on the amount of precipitation in the preceding period. Where dunes develop on an elevated rocky base and where there is substantial drainage in from the surrounding area, the water regime can be very complex. If they accumulate on low ground with its own catchment, then the hydrology is that of a virtually isolated granular deposit, the water-table is domed and there is an essentially rectilinear relationship between its level and rainfall (Willis *et al.* 1959*b*, Willis 1985*a*). Close to the water-table, the sand is maintained near saturation capacity but capillary rise is poor in dune sand, reaching only 30–50 cm at Braunton, for example (Willis *et al.* 1959*b*; see also Olsson-Seffer 1909, Ranwell 1959). Thus, although *Ammophila* regularly puts down roots below 2 m depth (Salisbury 1952, Willis in Huiskes 1979), with other associates like *Euphorbia portlandica* and *Hypochoeris radicata* often reaching 50 cm below the surface (Willis 1985*a*), the free water-table can be of little significance for growth on even moderately high dunes.

Much of the available water is thus probably intercepted as it drains through the sand after episodes of rain which can temporarily increase the moisture content tenfold. But drainage is generally very sharp, especially through the superficial layers, even in finer sands, because the amount of retentive organic matter is so small, less than 1% among mobile dunes under this vegetation at Braunton, for example (Willis & Jefferies 1963). Field moisture capacity here may thus be less than one-quarter of that in fixed dune sand (Salisbury 1952) and much lower than that of most other kinds of soil (Willis 1985*a*). In summer in particular, when the water-table is lower (Ranwell 1959, Willis *et al.* 1959*b*) and the climate generally drier and warmer, drought can be severe, with sand more than 50 cm or so above the water-table having a water-content of less than 5%. *Ammophila*, however, is strongly drought-tolerant: it transpires at a comparatively low rate, protecting itself by inrolling of the leaves and wilts only when water is in extremely short supply, below 0.5% (Salisbury 1952, Willis & Jefferies 1963). In the exceptionally dry summer of 1976, for example, Huiskes (1979) detected only a slight decrease in the rate of leaf production in the field, a marked contrast with *Festuca rubra* where growth ceased completely. These plants showed the same contrast in their tolerance of high temperatures in greenhouse experiments, and these different responses probably contribute to the restricted role which *F. rubra* has even on somewhat more stable sands here in the *Festuca* sub-community. Probably, too, the occurrence of *Poa pratensis* in the *Ammophila* vegetation is related to the sand moisture, the *Poa* sub-community becoming common on less mobile dunes only around our northern coasts, where potential water deficits are smaller and where the summers especially are wetter and cooler than further south (*Climatological Atlas* 1952, Chandler & Gregory 1976).

Particular episodes of rainfall and, in periods of drier weather, the formation of dew, are likely to be also of considerable significance for the establishment of the various associates able to find a limited place on the somewhat more stable sands typical of the *Festuca* and *Poa* sub-communities. Wide diurnal fluctuations in soil temperatures, from over 40 °C at midday in summer to only 10 °C in the night, are a striking feature of the more open dune environment (Willis *et al.* 1959*b*, Stoutjesdijk 1961) and the moist air of onshore breezes may condense in appreciable amounts on the surfaces of sand-grains and herbage. Willis (1985*a*) drew attention to the dew that can be seen running down marram leaves at dawn after clear summer nights, and Salisbury (1952) recorded a nightly increase in water content of almost 1 ml per 10 ml soil in cloudless summer weather. More important perhaps than this advective humidity is the redistribution of moisture that may occur within the sand from deeper warmed levels to cooling superficial layers (Willis *et al.* 1959*b*), thus bringing water within the reach of more shallow-rooted plants. Even this moisture, though, may be largely lost as the sand surface warms up during the day (Huiskes 1979).

The *Ammophila* community maintains its ascendancy among mobile coastal sands until accretion slows enough for associates to compete more effectively for water and nutrients in the stabilising environment. The marram itself can retain spatial dominance for some time in the vegetation that succeeds the community and, where erosion strips back more consolidated sand surfaces, releasing material for renewed bouts of local accretion in blow-outs or precipitating more catastrophic shifts of entire tracts of dune, *Ammophila* vegetation can be found reinvigorated on the mobilising sand. Such stands are usually of the species-poor *Ammophila* sub-community, but the *Carex* sub-community is also characteristically associated with newly-deposited sand, particularly where the ground is a little moister, as around slacks and pools.

The impressive sand-binding ability of *Ammophila* has led to its being widely planted around the British coast, as elsewhere in Europe, to stabilise eroding stretches of dune, something which is especially important where dunes form an integral part of soft sea-defences (Kidson & Carr 1960, Lux 1964, 1966). Cuttings are used, often in conjunction with some kind of brushwood thatch or fencing to help arrest sand movement, and can quickly take a hold to form the basis of stands of this vegetation soon indistinguishable from those of natural origin. Remedial action of this kind may also be necessary where disturbance by visitors damages the vegetation cover, whether in young stands along the beach top, where trampling may open up the foredunes to destruction in winter gales, or further in the dune hinterland, where camping or picnicking are commonplace. Enclosure is often necessary to ensure the re-establishment of the community in such circumstances.

Zonation and succession

Where there is little opportunity for accretion of wind-blown sand above the tidal limit, fragmentary stands of

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the *Ammophila* community may be the only kind of vegetation maintaining itself on a narrow and ill-defined zone of low dunes exposed to the constant threat of erosion. In more extensive systems, though, this community can occupy wide tracts of mobile sand accumulating behind strandline and foredunes, and giving way inland to stretches of more stable material deposited in fixed dunes or on sand plains. The zonations of vegetation types across such landscapes have a generalised form in which the *Ammophila* community represents an immature phase between the pioneer foreshore assemblages and the more permanent products of succession on ground where accretion and erosion have come to a halt. However, the dynamics of dune development, and the accompanying vegetation changes, are often complex and the communities represented in the sequences also vary considerably according to the phytogeographic influence of regional climate on the dune flora. Later stages in the successions are increasingly affected, too, by biotic factors like grazing and land treatment, which is often intensive and destructive of natural patterns. Throughout, there may be additional variation in the vegetation types related to the hydrology of the dune system, slacks or pools interrupting the basic zonation.

The *Ammophila* sub-community itself sometimes comprises the pioneer zone of vegetation on sand deposited above the tidal limit, helping to build up foredunes set back a little way from some kind of assemblage on the strandline and usually clearly marked off from it floristically. Along many shores around Britain, however, the *Elymus farctus* community precedes *Ammophila* vegetation, establishing itself within the zone of periodic tidal inundation, colonising the strandline itself and then stimulating modest accretion of wind-blown sand. Where this raises the beach level sufficiently, it can be instrumental in allowing *Ammophila* to invade, such that the low foredunes are occupied by the transitional *Elymus* sub-community, with its strandline survivors. Particularly down the eastern coast as far as Norfolk, *Leymus arenarius* complicates this basic zonation, being able to colonise a little further down the beach than *Ammophila*, sometimes invading an *Elymus* zone or coming to dominate in virtually pure stands on young dunes, when the *Elymus-Leymus* or *Leymus* sub-communities form a transition to the *Ammophila* sub-community on the bigger dunes behind. The Lincolnshire and Humberside coasts have some complex zonations in which all three of these grasses play a part.

Except locally in Northumberland and parts of north-east Scotland, Orkney and Shetland, it is the *Ammophila* community rather than the *Leymus* vegetation which is the more important on younger mobile dunes and, even there, the latter begins to be excluded with accretion above a certain speed and height. Around the whole coast, the species-poor *Ammophila* sub-community is the usual vegetation type where sand mobility is at its peak closer to the coastline or in the recolonisation of more catastrophic blow-outs in the dune hinterland, with the *Carex* sub-community figuring very locally on freshly-stabilised sand or where bared ground is a little moister. Further back in the dunes, where accretion has begun to slow down, the *Ammophila* sub-community typically gives way to the slightly richer and more varied *Festuca* sub-community or, increasingly towards the moister and cooler north of Britain, the *Poa* sub-community.

On dune systems where there is a more extended gradation from mobile to fixed sand, one or other of these latter kinds of *Ammophila* vegetation generally forms a transition to the *Ammophila-Festuca* community on dunes where accretion is appreciably slower and erosion increasingly rare (Figure 12). Here in addition to constant *P. pratensis* and *F. rubra*, which can increase their cover appreciably among the *Ammophila*, species such as *Senecio jacobaea*, *Hypochoeris radicata*, *Taraxacum officinale* agg., *Galium verum* and *Lotus corniculatus*, at most only moderately frequent in the *Ammophila* community, become very common. In addition, *Carex arenaria* and *Hieracium pilosella* are often found, while there are many occasional associates, including numerous plants hardly ever found on mobile dunes, such as *Plantago lanceolata*, *Leontodon taraxacoides*, *Luzula campestris* and *Cerastium fontanum*. A number of bryophytes, too, increase their frequency and cover, with *Brachythecium albicans*, *Tortula ruralis* ssp. *ruraliformis* and *Hypnum cupressiforme s.l.* becoming especially important, while on more open patches of the essentially stable surface, a variety of diminutive annuals come and go. Around our more southerly shores, *Ononis repens* is a further distinctive newcomer with the shift from what is usually the *Festuca* sub-community of the *Ammophila* vegetation to the *Ononis* or *Viola* sub-communities of *Ammophila-Festuca* vegetation. North of the Solway–Forth line, it is the *Poa* type of *Ammophila* dune which generally passes behind to the Typical or *Hypnum* sub-communities of the *Ammophila-Festuca* dune.

In its turn, the *Ammophila-Festuca* dune can grade on fixed sand where the surface pH is often a little below neutral, though less drought-prone, to the *Festuca-Galium* community, a vegetation type widely distributed on older dunes all around the British coast, though especially extensive on the sand-plains of the machair along the north-west Scottish seaboard. Bouts of erosion in both the *Ammophila-Festuca* community and, less commonly, in the *Festuca-Galium* vegetation can lead to a local regeneration of the *Ammophila* community with sharper floristic boundaries at the switch to the newly mobile sand and, where there are more substantial shifts

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in dune dynamics, whole areas of partly stabilised dune may be overtaken by freshly deposited sand on which the more immature vegetation gains a hold again. In this way, stands of the *Ammophila* community can be found developing next to calcifugous grassland, heath or other vegetation types of the dune hinterland before the sand finally comes to a halt.

Other variations on the basic zonation reflect edaphic and treatment differences. Where the sands are somewhat more fixed, and particularly where there is little grazing, the *Ammophila* community may give way inland, not to the *Ammophila-Festuca* vegetation, but to the *Ammophila-Arrhenatherum* community, the *Geranium sanguineum* sub-community of warm, south-facing dune slopes being particularly distinctive with its mixtures of *Arrhenatherum*, *G. sanguineum*, *Ononis repens*, *Dactylis glomerata*, *Galium verum* and *Veronica chamaedrys*, together with occasional low bushes of *Rosa pimpinellifolia*, among the *Ammophila*, *P. pratensis* and *F. rubra*. Especially good examples of this kind of pattern can be seen on the Northumbrian dune systems. More species-poor rank mesophytic swards of the *Ammophila-Arrhenatherum* type can also sometimes form an intermediate zone between the *Ammophila* community and dune-slack surrounds but these wetter areas more often occur in depressions among more stable dune ridges where *Ammophila-Poa* or *Festuca-Galium* vegetation covers the surrounding slopes.

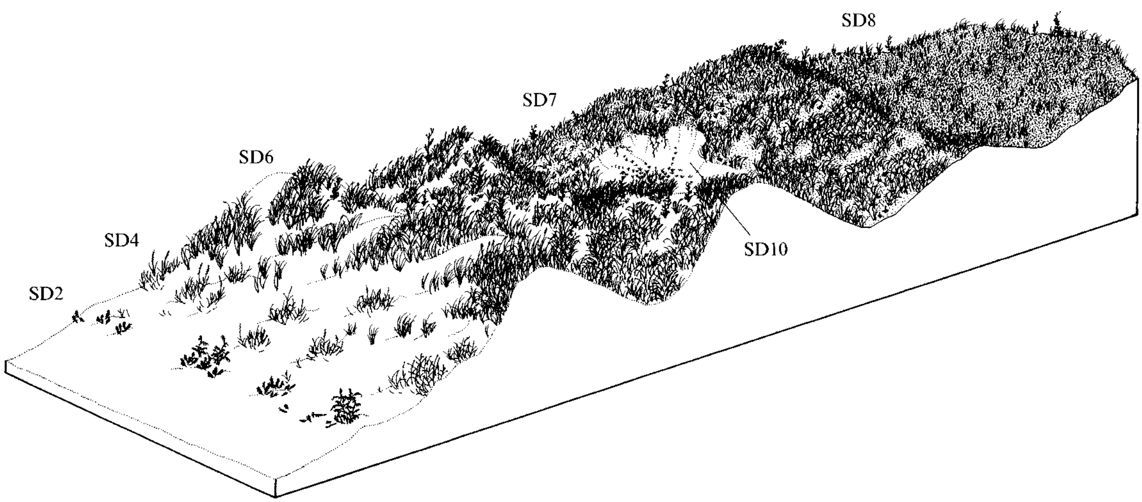
Figure 12. Simplified zonation of vegetation types on strandline, embryo, semi-fixed and fixed dunes in southern Britain.
The strandline has fragmentary SD2 *Honkenya-Cakile* vegetation with embryo dunes building around SD4 *Elymys farctus* community behind. Then, there are mobile dunes with SD6 *Ammophila* vegetation and, behind, semi-fixed dunes with the SD7 *Ammophila-Festuca* community. A large blow-out on one ridge has the SD10 *Carex arenaria* community. To the rear, the fixed dunes have SD8 *Festuca-Galium* grassland.

Distribution

The *Ammophila* community occurs widely on suitably mobile sands in dune systems all around the British coast. *Leymus* figures most prominently in the younger stands of the *Leymus* and *Elymus-Leymus* sub-communities on the east coast, with the *Poa* sub-community much more common north of the Solway–Forth line, but otherwise the presence of the different kinds of *Ammophila* vegetation is a reflection of the local stability of the dune sands.

Affinities

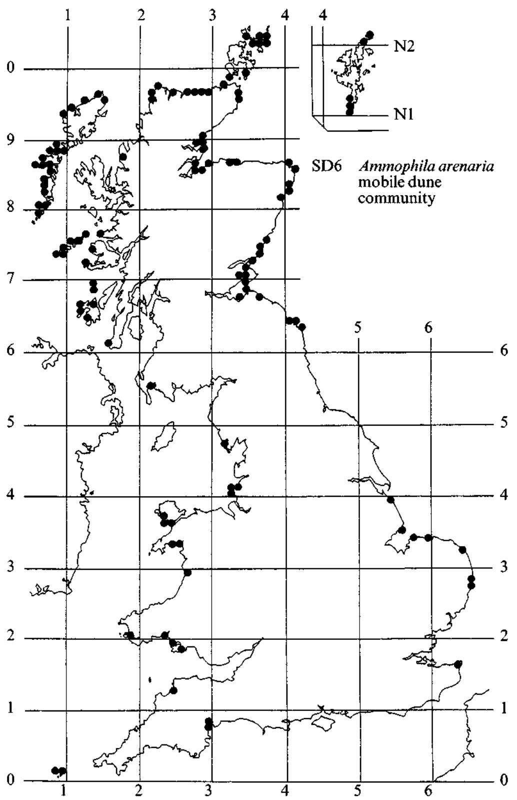
As defined here, the *Ammophila* community represents the younger vegetation among that generally subsumed in a broadly-defined *Ammophiletum* in British descriptive schemes (Moss 1906, Tansley 1911, 1939), a category which also takes in much of what we have separated off as the *Ammophila-Festuca* community, an assemblage of less mobile sands, and even on occasion some of our *Festuca-Galium* vegetation where marram can remain of high cover, though much reduced vitality. As Birse (1980, 1984) proposed, this kind of vegetation is best seen as equivalent to part of the *Elymo-Ammophiletum* which Braun-Blanquet & De Leeuw (1936) characterised as the major association of more mobile sands around the seaboard of north-west Europe, and which has since been described from Belgium (LeBrun *et al.* 1949), The Netherlands (Westhoff & den Held 1969), France (Géhu & Géhu 1969) and Ireland (Braun-Blanquet & Tüxen 1952, Ivimey-Cook & Proctor 1966, Beckers *et al.* 1976, Schouten & Nooren 1977 and Ni Lamhna 1982).



Floristic table SD6

	a	b	c	d	e	f	g	6
Ammophila arenaria	V (4–10)	V (2–8)	V (4–8)	V (3–10)	V (3–8)	V (2–9)	V (2–10)	
Elymus farctus	V (1–7)	V (2–5)			I (2–4)	I (2–4)	I (2–4)	II (1–7)
Honkenya peploides	II (3–4)	II (1–6)		I (3)	I (1–4)	I (2–4)		I (1–6)
Leymus arenarius		V (2–7)	V (1–7)		II (2–5)	II (1–5)		II (1–7)
Atriplex glabriuscula		I (3)						I (3)
Atriplex laciniata		I (1)						I (1)
Carex arenaria	I (1–3)				I (1–4)	I (1–4)	V (2–5)	I (1–5)
Festuca rubra		I (3)		I (1)	V (2–9)	V (1–7)	I (5)	III (1–9)
Senecio jacobaea	I (2–3)	I (1)		II (1–5)	II (1–3)	II (1–3)		II (1–5)
Cirsium arvense	I (1–4)	I (1–3)		I (1–3)	II (1–4)	II (1–6)		II (1–6)
Hypochoeris radicata	I (1–2)	I (1–3)	I (1)	I (2–4)	II (1–5)	I (1–5)	I (3)	I (1–5)
Trifolium arvense					I (3–5)			I (3–5)
Agrostis capillaris					I (2–5)			I (2–5)
Desmazeria marina					I (1–2)			I (1–2)
Urtica dioica					I (2–3)			I (2–3)
Poa pratensis					I (3)	V (1–7)		II (1–7)
Elymus repens			I (1)	I (3)	I (1–5)	II (2–3)		I (1–5)
Heracleum sphondylium		I (2)			I (1–4)	II (1–6)	I (3)	I (1–6)
Sonchus arvensis	I (3–4)	I (1–3)			I (1–4)	II (1–6)		I (1–6)
Sonchus asper	I (4)	I (1)	I (3)	I (2–3)	I (1–3)	I (1)		I (1–4)
Rumex crispus	I (2)	I (1)		I (2–3)	I (1–3)	I (1–5)		I (1–5)
Senecio vulgaris	I (1)	I (1–2)	I (1)		I (2–3)	I (3)		I (1–3)
Calystegia soldanella	I (3–5)		I (4)	I (3–4)	I (2–5)			I (2–5)
Cakile maritima	I (3)			I (3)	I (1–6)	I (1)		I (1–6)
Eryngium maritimum	I (2–4)			I (3)	I (3–5)			I (2–5)
Cirsium vulgare	I (4)			I (1)	I (1)			I (1–4)
Ceratodon purpureus	I (6)			I (1–3)	I (1–9)	I (2–5)		I (1–9)
Tortula ruralis ruraliformis		I (5)		I (1–3)	I (3–6)	I (1–5)		I (1–6)
Elymus pycnanthus		I (2–7)		I (2–4)	I (3–8)			I (2–8)
Brachythecium albicans				I (2)	I (1–6)	I (2–6)		I (1–6)
Holcus lanatus			I (1)		I (1–6)	I (2–5)	I (2)	I (1–6)
Euphorbia paralias			I (1)	I (1–3)	I (2–7)			I (1–7)
Euphorbia portlandica			I (3)	I (1–4)	I (4)	I (3)		I (1–4)
Taraxacum officinale agg.				I (2)	I (1–7)	I (1–5)		I (1–7)
Senecio squalidus			I (3)		I (1–2)	I (1)		I (1–3)
Tussilago farfara	I (5)		I (4)		I (2–5)	I (1–4)		I (1–5)
Cynoglossum officinale			I (3)		I (2)	I (2–3)		I (2–3)
Ranunculus repens			I (3)		I (3–5)	I (2–3)		I (2–5)
Rubus fruticosus agg.			I (3)	I (2)	I (2–4)		I (4)	I (2–4)
Lupinus arboreus				I (2–3)	I (4–9)			I (2–9)
Epilobium angustifolium					I (2–8)	I (2–4)	I (4)	I (2–8)
Agrostis stolonifera					I (3)	I (1)		I (1–3)
Galium verum					I (2–4)	I (1–4)		I (1–4)
Linaria vulgaris					I (1–3)	I (3–5)		I (1–5)
Angelica sylvestris					I (2–3)	I (1–3)		I (1–3)
Dactylis glomerata					I (3–4)	I (3)		I (3–4)
Erodium cicutarium					I (1–3)	I (4)		I (1–4)
Poa annua					I (2–3)	I (2)		I (2–3)
Trifolium repens					I (2–5)	I (2–3)		I (2–5)
Number of samples	28	18	10	35	62	36	10	199
Number of species/sample	4 (2–10)	5 (3–10)	3 (2–7)	3 (1–9)	7 (4–14)	9 (5–15)	3 (2–7)	5 (1–15)

a *Elymus farctus* sub-community
b *Elymus farctus-Leymus arenarius* sub-community
c *Leymus arenarius* sub-community
d Typical sub-community
e *Festuca rubra* sub-community
f *Poa pratensis* sub-community
g *Carex arenaria* sub-community
6 *Ammophila arenaria* mobile dune community (total)



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