SD19

Phleum arenarium-Arenaria serpyllifolia dune annual community

Tortulo-Phleetum arenariae (Massart 1908) Br.-Bl & De Leeuw 1936

Constant species

Ammophila arenaria, Arenaria serpyllifolia, Carex arenaria, Festuca rubra, Phleum arenarium.

Rare species

Mibora minima, Vulpia membranacea.

Physiognomy

The *Tortulo-Phleetum* comprises generally open assemblages of ephemerals which make a brief appearance in the dampness of spring and early summer among gaps in a cover of perennial grasses and dicotyledonous herbs of semi-fixed to fixed dunes.

The most distinctive species of the community are the annual grass *Phleum arenarium* with *Arenaria serpyllifola, Cerastium diffusum* ssp. *diffusum, Aira praecox* and *Viola tricolor* ssp. *curtisii* and the moss *Tortula ruralis* ssp. *ruraliformis. Ammophila arenaria, Festuca rubra* and *Carex arenaria* are consistently represented in the grassland matrix in which this vegetation makes its appearance, together with *Ononis repens, Lotus corniculatus, Senecio jacobaea* and, more occasionally, *Poa pratensis.*

Light-demanding mat plants like *Thymus praecox* and *Sedum acre* figure quite commonly and there are occasional records for *Cerastium semidecandrum, Desmazeria marina, Euphorbia paralias, Logfia minima, Erophila verna, Trifolium dubium, T. campestre, Erodium cicutarium, Geranium molle* and *Centaurium erythraea.* This community also provides a locus for the nationally rare *Mibora minima* and *Vulpia membranacea.*

In addition to *T. ruralis* ssp. *ruraliformis, Hypnum cupressiforme* is frequent, *Homalothececium lutescens, Brachythecium albicans* and *Tortella flavovirens* occasional. *Peltigera canina* can also occur with some local abundance.

Habitat

The *Tortulo-Phleetum* is a community that capitalises on the appearance of gaps with essentially stable sand that develop where semi-fixed and fixed dune swards are opened up by drought or locally disturbed, often by rabbits or modest anthropogenic activity.

The distinctive annuals of the community, being small, are unable to establish themselves on shifting sand or in closed swards of perennials, so the patchwork of open but stabilising ground characteristic of maturing stands of the *Ammophila-Festuca* community offers a very congenial habitat. Wind can play some part in the dispersal of seed or fruits in the plants, though usually only over very short distances because of their low flowering stems (Pemadasa et al. 1974, Pemadasa & Lovell 1974*a*, Watkinson 1978*b*, *c*), but burial of seed under just a few centimetres of sand has been shown to be highly inimical to germination in *Aira praecox, Cerastium diffusum* ssp. *diffusum, Erophila verna* and *Mibora minima* (Pemadasa & Lovell 1975), and wind-drag is very destructive of seedling establishment in *Vulpia fasciculata* (Watkinson 1978*a*). This grass can actually grow quite bulky and will tolerate a modest amount of accretion, putting out short underground stems if its tussocks bases get covered (Watkinson 1978*c*), but this is unusual and most of the annuals remain vulnerable to being overwhelmed or uprooted throughout their life cycle. They thus play little part in this vegetation until the dune surface has become more or less fixed with the drop in sand supply or the provision of local shelter.

The establishment of patches of the mosses upon which the annuals can germinate in the *Turtulo-Phleetum* may be of very considerable importance. At the same time, however, conditions must remain such as to hinder the development of a continuous cover of taller perennial plants among the marram tussocks if the annuals are not to be crowded out. This is especially true of potentially vigorous associates like *Festuca rubra* which is a constant feature of the vegetation of semi-fixed and fixed dunes: indeed, in the study of Pemadasa *et al.* (1974), the distribution of annuals in this community was essentially the inverse of the patterning in this grass in the dune sward around. At this stage of dune growth, mobility of the sand is of much reduced consequence in keeping the

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cover open, and it is shortage of water and nutrients that now play the leading role. The amounts of moisture, nitrogen and phosphorus may be little higher here than in the raw sands of more mobile dunes and remain strongly limiting to plant growth (Willis & Yemm 1961, Pemadasa & Lovell 1974*b*, Noble 1982), there being little return as yet of decaying organic matter to the soils, and probably only a small contribution from nitrogen-fixing plants like *Ononis repens* and *Lotus corniculatus* which can improve their local edaphic environment and eventually benefit the surrounding vegetation (Willis 1985*a*, Jones & Turkington 1986). Death of perennials in more severe summer droughts, and the annual die-back of deciduous plants like *O. repens* and *Anthyllis*, can also make room for the establishment of annuals (Watkinson 1978*c*), and trampling and grazing may assist by scuffing the sand surface and keeping down the height of the herbage. Grazing, though, can be highly deleterious to the annuals themselves because, when flowering or fruiting shoots are devoured, this effectively prevents re-establishment of a population in the following season unless there are some seed stores in the sand (Watkinson & Harper 1978, Watkinson 1978*c*). With *V. fasciculata*, for example, which is selectively grazed by rabbits, particularly in its reproductive phase, there was a very dramatic spread on some dune systems after myxomatosis (Willis 1967, Watkinson 1978*c*).

Nutrient shortage is also limiting to the growth of the annuals themselves (Willis & Yemm 1961, Willis 1963, Pemadasa & Lovell 1974*b*) though, with the sub-optimal light and temperatures of autumn, when germination in these plants charactericaly takes place (Ratcliffe 1961, Pemadasa & Lovell 1975), this may be less critical: even with the addition of balanced nutrients, these climatic factors continue to control growth in the short period before the onset of virtual dormancy in the winter months (Pemadasa & Lovell 1974*a*, 1976). However, this timing of the life-cycle is of crucial importance to the success of these plants because it enables them to complete most of their growth while the perennials are least active (Pemadasa & Lovell 1974*a*, 1975) and, with flowering complete by summer, to avoid the worst effects of water shortage by passing the driest part of the year as seed (Ratcliffe 1961, Pemadasa & Lovell 1976, Rozijn & van der Werf 1986).

Germination in these winter annuals is, in fact, controlled by complex interactions between innate dormancy and the need for after-ripening, characteristics which vary considerably from species to species, and climatic and soil conditions, which can be very variable from one year to the next (Ratcliffe 1961, Pemadasa & Lovell 1975). Generally speaking, however, germination is timed to take advantage of rains which moisten the dune surface in autumn. The overall distribution of some of these plants has been correlated with a minimum level of precipitation through the autumn and winter months (Watkinson 1978*c*) and for unimpeded germination an adequate and continuous supply of moisture is needed. Both viability and germination rate have been shown to decline markedly in a number of species with decreasing soil moisture, desiccation often arresting establishment (Pemadasa & Lovell 1975).

Seedlings of winter annuals and maturing plants are often resistant to the short periods of drought which can characterise these dunes through the winter and particularly in spring (Pemadasa & Lovell 1975, Watkinson 1978*c*) and this may be critical for their survival. With the two *Aira* spp., for example, which are both drought-avoiders in their life-cycles, it may be the poorer drought-resistance of *A. caryophyllea* as compared with *A. praecox*, that largely excludes it from this community (Pemadasa & Lovell 1974*a*, Rozijn & van der Werf 1986). In general, however, supplies of soil moisture continue to be important for growth and reproduction (Newman 1967, Pemadasa & Lovell 1974*a*, Ernst 1981, Watkinson 1982) though, despite the coming of more favourable light and temperature regimes in spring, vegetative activity often shows a sharp decline with the initiation of flower primordia as the season advances (Pemadasa & Lovell 1976). Survival through the driest months is then assured by adequate seed-set, high summer temperatures imposing dormancy and a need for prolonged hydration before germination can take place (Newman 1963, Pemadasa & Lovell 1975).

Translocation of nitrogen and phosphorus from ageing vegetative tissues to generative organs during this final phase of growth is sometimes very striking and interactions between water and nutrient supplies as the time for reproduction approaches can be sharply contrasting. With *Erodium cicutarium* for example, Ernst (1983) showed that shortage of major nutrients delayed fruiting, whereas in *Phleum arenarium* the process was accelerated, perhaps because the shallower rooting system of this grass rendered it additionally more susceptible to drought (Ernst 1981). In this species, too, fewer nutrients made for larger numbers of lighter fruits, propagules which have a higher degree of dormancy and offered a better chance of contributing to a modest seed-bank and so enhancing the possibility of survival into future seasons (Ernst 1981). Differences such as these among the annuals make a further contribution to their varied representation from one year to the next.

Zonation and succession

The *Tortulo-Phleetum* is characteristically a minor and local element within stretches of more stable dune grasslands. Its distinctive contingent of ephemerals comes and goes as particular locations become congenial and it can be rapidly overwhelmed in any one place by renewed vigour among the perennials in the surrounding swards.

Zonations to the *Ammophila-Festuca* and *Festuca-Galium* grasslands, the two communities that generally provide the context for this assemblage, involve a thickening up of the perennial grasses and recolonisation by dicotyledonous herbs. Where local disturbance becomes more acute, however, for example where rabbit activity loosens the sand surface, there can be renewed erosion and a spread of *Carex arenaria* or *Ammophila* vegetation which rapidly overwhelms the *Tortulo-Phleetum*.

Distribution

The community is widespread but local on dune systems in England and Wales, more scarce in Scotland.

Affinities

Phytosociological investigations have characterised a number of syntaxa from among assemblages of dune annuals, locating them in the Sedo-Scleranthetea, the class of largely ephemeral vegetation of dry, sandy soils (or the Koelerio-Cornephoretea as Westhoff & den Held (1969) have it). The commonest association of this kind along warmer coasts in north-west Europe is this *Tortulo-Phleetum arenarii*, which Moore (1977) and Schouten & Nooren (1977) recorded from Eire. From cooler, oceanic seaboards, Braun-Blanquet & Tüxen proposed recognising a *Viola curtisii-Tortuletum ruraliformis* and this was subsequently recorded from Eire by Ivimey-Cook & Proctor (1966), Beckers *et al.* (1976) and Ni Lamhna (1982), and from Scottish dunes by Birse (1980, 1984). However, the distinction between this and the *Tortulo-Phleetum* is often slim (White & Doyle 1982) and the available data do not reveal much consistent variety among the assemblages of annuals encountered. Irish workers and Birse (1980, 1984) locate these associations in the Koelerion (or Galio-Koelerion as it was renamed by Westhoff).

Floristic table SD19

Phleum arenarium	V (1–5)
Arenaria serpyllifolia	IV (2–4)
Festuca rubra	IV (1–7)
Ammophila arenaria	IV (1–8)
Carex arenaria	IV (2–5)
Tortula ruralis ruraliformis	III (2-7)
Cerastium diffusum diffusum	III (1–4)
Aira praecox	III (1–4)
Ononis repens	III (1–5)
Viola tricolor curtisii	III (1–7)
Hypnum cupressiforme	III (2–5)
Lotus corniculatus	III (1–5)
Sedum acre	III (1–5)
Senecio jacobaea	III (1–5)
Thymus praecox	II (2–8)
Galium verum	II (1–5)
Trifolium arvense	II (1–3)
Anthyllis vulneraria	II (1–3)
Homalothecium lutescens	II (1–5)
Cerastium semidecandrum	II (2–6)
Crepis capillaris	II (1–3)
Poa pratensis	II (2–4)
Vulpia membranacea	II (1–5)
Brachythecium albicans	II (1–4)
Desmazeria marina	I (1–5)
Hypochoeris glabra	I (1–3)
Euphorbia paralias	I (1–4)
Aira caryophyllea	I (2–4)
Tortella flavovirens	I (1–3)
Cirsium arvense	I (1–2)
Logfia minima	I (1–2)
Mibora minima	I (1–3)
Erophila verna	I (1–2)
Trifolium dubium	I (1–3)
Trifolium campestre	I (1–3)
Plantago lanceolata	I (1–3)
Peltigera canina	I (1–5)
Anthoxanthum odoratum	I (1–5)
Erodium cicutarium	I (1–3)
Geranium molle	I (1–4)
Plantago coronopus	I (2–4)
Trifolium repens	I (1–6)
Centaurium erythraea	I (3–4)
Luzula campestris	I (2–4)
Tortella tortuossa	I (2–6)
Number of samples	28
Number of species/sample	19 (8–33)
Herb height (cm)	15 (2–50)
Herb cover (%)	76 (40–100)
Ground height (mm)	14 (3–30)
Ground cover (%)	23 (1–60)

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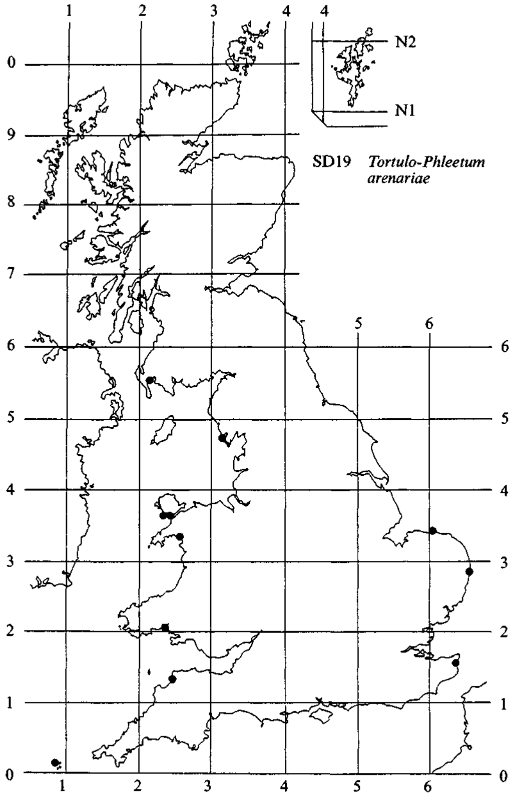

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