
SM13

Puccinellia maritima salt-marsh community *Puccinellietum maritimae* (Warming 1906) Christiansen 1927

Synonymy

The *Puccinellietum maritimae* includes a considerable range of closely-related vegetation types. The limits of the association as a whole are similar to those adopted in recent Continental accounts (e.g. Beetsink 1965, Westhoff & den Held 1969) and, as such, would include all or part of a variety of salt-marsh types in earlier British descriptions. The synonymy of the communities is complex and, as many synonyms would be partial, a complete list is not attempted here. Where a particular sub-community has a clear counterpart *in litt.* a note is given below.

Constant species

Puccinellia maritima.

Rare species

The association does not provide the sole, or even major, context for any national rarity but the following occur occasionally: *Arthrocnemum perenne*, *Limonium bellidifolium*, *L. binervosum*, *Salicornia pusilla*, *Spartina maritima* and *Suaeda vera*.

Physiognomy

Mostly, the association occurs as a closed species-poor grassland but the complete range includes very open pioneer vegetation and herb-dominated stands in which *Puccinellia maritima* is of minor importance or even absent. The sward varies from a tight low turf 1–2 cm high to a rank mattress up to 50 cm tall. Although grazing is important in controlling the physiognomy (see below), a considerable range of genetically determined morphotypes of *P. maritima* is present in Britain (Gray & Scott 1977a; 1980). Although species from low- and high-marsh communities occur as associates, the *Puccinellietum maritimae* as a whole is differentiated from the low-marsh communities by the reduced frequency and cover/abundance of annual *Salicornia* species and *Spartina anglica* and from the high marsh by low levels of *Festuca rubra*, *Agrostis stolonifera* and *Juncus gerardii*.

The most common associates throughout are *Triglochin maritima*, *Plantago maritima* and *Armeria maritima* and there is frequently an algal mat, often floristically varied and comprising a number of distinct species assemblages (Carter 1932, 1933a, b; Chapman 1934, 1937; Polderman 1979).

Sub-communities

Although the association is of widespread occurrence and individual stands are often great in extent and highly distinctive, the general species-poverty of the vegetation and the site-specific nature of much variation makes it difficult to attain an entirely satisfactory national subdivision. The sub-communities described below should be regarded as provisional and independent local schemes may sometimes be preferable. Alternative national classifications would also be possible: the scheme of Beetsink (1962, 1965) could, for example, be applied here with the addition of units to accommodate communities of northern and western Britain.

Sub-community with *Puccinellia maritima* dominant:

Puccinellietum (Glycerietum) maritimae Tansley 1911. This is the most extensive and widespread perennial community of the lower salt-marsh in the British Isles. *P. maritima* is constant and dominant throughout forming a fairly closed sward in which other species are generally poorly represented. Adam (1976) recognised two nodes, making a distinction between samples which are less and more species-rich but such a division is somewhat arbitrary and it is probably preferable to recognise a single rather diverse unit. The associate species vary with the level in the marsh and the geographical locality of the sub-community. At the lowest levels, annual *Salicornia* spp. and *Suaeda maritima* are most frequent: at higher levels, *Triglochin maritima*, *Plantago maritima* and *Aster tripolium* are found. *Limonium vulgare* is more frequent in the south and east and *Armeria maritima* in the west. *Glaux maritima* is virtually absent from this vegetation in south-east England. Locally, very dense stands of tall

Puccinellia maritima occur at relatively high levels in the marsh, most notably around The Wash; these stands are often monospecific but may have *Atriplex hastata*.

***Glaux maritima* sub-community:** *Glaucetum maritimae* Dahl & Hadač 1941; *Glaux maritima* isozion Dahlbeck 1945; *Glaux maritima* sociatie Beeftink 1962. Although *G. maritima* occurs at varying levels throughout the association, it is here constant and co-dominant with *Puccinellia maritima* in a low generally species-poor sward. The frequency and cover/abundance of *Triglochin maritima*, *Plantago maritima* and *Armeria maritima* stand between their low levels in the *Puccinellia*-dominated sub-community and the high values they attain in the *Limonium-Armeria* sub-community. *L. vulgare* itself and *Halimione portulacoides* are rare. Stands of this sub-community are often small and fragmentary but at some sites cover large areas. During hot dry summers, the shoots of *Glaux maritima* may become shrivelled by late July in upper-marsh sites. Further, although *G. maritima* is a perennial, its aerial parts die back completely in the winter when stands may appear virtually devoid of vegetation.

***Limonium vulgare-Armeria maritima* sub-community:** General Salt Marsh Tansley 1911 & Chapman 1934 (but not Chapman 1960); *Puccinellietum (Glycerietum) maritimae* Tansley 1911 p.p.; *Statice & Armeria* societies Marsh 1915; *Plantag(in)etum* Chapman 1934 p.p.; *Limonietum & Armerietum* Tansley 1939 (but not *Armerietum* Yapp & Johns 1917); *Plantagini-Limonietum* Westhoff & Segal 1961; forb salt marsh Dalby 1970. This is one of the most distinctive communities of British salt-marshes with a varied sward dominated by herbaceous dicotyledons which present a colourful spectacle when flowering. *Limonium vulgare*, *Armeria maritima*, *Triglochin maritima*, *Plantago maritima*, *Halimione portulacoides* and annual *Salicornia* spp. (including locally the uncommon *S. pusilla*) are all constant and can be abundant. *Puccinellia maritima*, though also constant, rarely comprises more than 10% of the sward. There is often an algal mat and frequent scattered plants of *Spergularia media* and *Suaeda maritima*. *Limonium humile*, though of only occasional occurrence in this sub-community in south-east England, sometimes replaces *Limonium vulgare*, as in Milford Haven (Dalby 1970) and, to a lesser extent, in south-west Scotland. At the highest levels to which the sub-community extends, *Festuca rubra* and *Juncus gerardii* may occur.

The vitality of the common species is variable. Both *Limonium vulgare* and *Armeria maritima* flower profusely but *Aster tripolium* and, at some sites, *Plantago maritima* flower infrequently. *Halimione portulacoides* occurs not in shrubby form but as scattered prostrate shoots with small fleshy leaves which tend to be shed in late summer. Annuals, such as the *Salicornia* spp. and

Suaeda maritima, persist as small plants which often turn red in early summer, possibly reflecting their inability to compete with established perennials for nutrients, particularly nitrogen.

***Plantago maritima-Armeria maritima* sub-community:** *Armerietum* Yapp & Johns 1917 p.p.; *Plantag(in)etum* Chapman 1934 p.p.; *Plantago maritima* isozion Dahlbeck 1945. This resembles the *Limonium-Armeria* sub-community in being dominated by herbaceous dicotyledons. *Plantago maritima*, *Armeria maritima* and *Triglochin maritima* are again constant and abundant and *Puccinellia maritima* is, as there, a relatively inconspicuous contributor to the sward. Here, however, *Halimione portulacoides* is rare and *Limonium vulgare* absent while *Glaux maritima* and rayed *Aster tripolium* are constant. Although always virtually closed, the vegetation exists in two physiognomic forms based on variation in *Plantago maritima* which sometimes has long leaves and an upright habit (Chapman 1934), sometimes short leaves appressed to the soil surface.

***Puccinellia maritima-turf fucoid* sub-community.** Turf fucoids occur at low levels in various types of *P. maritima* salt-marsh, but here they comprise an extensive dense understorey of diminutive plants beneath a sward often dominated by *Plantago maritima* but also with constant and abundant *Puccinellia maritima*, *Glaux maritima* and *Armeria maritima*. *Fucus vesiculosus* *ecad muscoides* is the principal fucoid and Cotton (1912) and Polderman & Polderman-Hall (1980) have both described the understorey as a discrete algal assemblage.

***Puccinellia maritima-Spartina maritima* sub-community:** *Puccinellietum maritimae* typicum, phase with *Spartina maritima* Beeftink 1962. Here, *P. maritima* dominates with variable amounts of *Spartina maritima*, annual *Salicornia* spp., *Limonium vulgare*, *Suaeda maritima* and *Aster tripolium* var. *discoideus*. Stands of this sub-community are generally a few tens of square metres in extent.

Habitat

The *Puccinellietum maritimae* is the most widespread and extensive perennial community of the lower salt-marsh in Britain. It occurs both as a discontinuous pioneer zone and as a continuous sward in the zonation above the pioneer vegetation. It is also common on slumped creek-sides, in old pans and on disturbed sites in the upper marsh. Fragmentary stands of the association are found infrequently on very exposed maritime cliffs, for example on the Butt of Lewis, Outer Hebrides. (see also Praeger 1911).

The association occurs on a wide range of substrates including various clays and silts, highly calcareous sands

and soils of high organic content; more rarely, it is found on gravel and shingle. Its importance as a colonising community is very much increased on sandier substrates: it is the most frequent pioneer on the sandy marshes of western England and Wales and commoner, for example, on the north-west as against the south-east shore of The Wash (Anon. 1976). The pH is usually basic with most soils in the range 6.0–8.5 (Adam 1976, Bridges 1977, Gray & Scott 1977a). Sediments in pioneer and lower marsh zones are generally higher in calcium content and lower in organic matter than those higher up the marsh (Gray & Bunce 1972, Adam 1976). Soils are often intermittently waterlogged and poorly aerated and share a moderate to high submergence rate and salinity. Data on submergence are limited but suggest that the lower limit of the *Puccinellietum* may experience more than 350 submergences/year; Gray & Scott (1977b) recorded a mean rate for their Morecambe Bay samples with *Puccinellia maritima* of 220 submergences/year while on Scolt Head, Norfolk, Chapman's General Salt Marsh extended from 150 to 225 submergences/year (Chapman 1960b). Proctor (1980) measured salinities of 12–30 g l⁻¹ for *Puccinellia maritima* in the Exe estuary, Devon, but levels well in excess of those of sea-water may develop in the higher marsh because of evaporation in the absence of submersion.

Grazing is of undoubted importance in the maintenance of the association though its effect is complex and there is evidence that the response of species varies between sites. Many marshes are heavily used for pasturing stock, most frequently sheep but also cattle and horses; wildfowl, rabbit, hare and vole grazing may also be intensive. Grazing affects the species composition of the sward. It may be important in maintaining the dominance of perennial grasses as against herbaceous dicotyledons (Gray 1972) or in controlling the balance between *Puccinellia maritima* and *Festuca rubra* (Gray & Scott 1977b): *P. maritima* responds to grazing by the production of small, prostrate, short-leaved and rapidly tillering forms (Gray & Scott 1977a, 1980). With intensive grazing *Limonium* spp. and *Halimione portulacoides* may be reduced in abundance (Boorman 1967, Ranwell 1968, Rojanavipart & Kay 1977). On silt and clay marshes heavy cattle-trampling can lead to widespread poaching.

Moderate grazing helps maintain a sward which can support considerable populations of wintering wildfowl. There is evidence of a preference for *Puccinellia maritima* as against rank swards, such as those of the *Juncetum gerardi*, in wigeon (Cadwalladr *et al.* 1972, Cadwalladr & Morley 1974) and the brent goose (Charman & Macey 1978). For brent, the *Puccinellietum* provides a valuable food source after *Zostera* and *Enteromorpha* and there is heavy use in January–March (Ranwell & Downing 1959; Charman 1975, 1977b, 1979; Charman & Macey 1978).

Some of the species in the association are resistant to oil spillage by virtue of their underground storage organs, e.g. *Plantago maritima*, *Armeria maritima* and *Triglochin maritima*, but *Puccinellia maritima* itself declines rapidly with repeated oiling (Baker 1979).

The particular environmental relationships of the sub-communities are as follows. The *Puccinellia-Glaux* sub-community occurs in a number of different habitats all of which are open to rapid disturbance: old turf-cuttings, former pans, creeks, old cart tracks. It is also found in situations where the boundary between salt-marsh and dune becomes blurred: where sand is blown on to the upper marsh, where dune lows are subject to tidal flooding (see Lambert & Davis 1940) and where salt-marsh/dune interfaces are subject to disturbance by trampling or car-parking. There are small stands on gravel and shingle on the upper marsh at some sites and, at others, large stands in the open areas behind sea walls.

The *Limonium-Armeria* sub-community is found at relatively high levels in the salt-marsh zonation. Frequently it does not form a continuous belt but occurs as a series of small discrete stands separated from each other by creek levees. The soil in these inter-creek basins is normally a heavy clay with a considerable quantity of organic matter (loss on ignition >30%) in the upper few centimetres of the profile. The development of creek levees restricts the drainage in the basins (the concave stage of marsh development after Beetsink 1966): water may be retained there after submergence (Perraton 1953) and the soils are often strongly gleyed. On many salt-marshes in south-east England such stands have the maximum pan density within the sites (Pethwick 1974). The pan edges are often marked by a narrow fringe of more vigorous vegetation in which *Triglochin maritima* is particularly prominent.

At some sites, where salt-marsh abuts onto dunes, there is an unbroken zone of this sub-community. Here the sediments are sands or alternating bands of sand and clay and pans and creeks are relatively few; such creeks as do occur lack pronounced levees. At the higher parts of such stands *Festuca rubra* and *Juncus gerardii* occur. This habitat seems to be that described for the *Plantagini-Limonietum* Westhoff & Segal 1961.

The *Plantago-Armeria* sub-community is also found at comparatively high levels. The form with tall *Plantago maritima* occurs above the *Limonium-Armeria* sub-community and the form with short *P. maritima* in shallow depressions throughout the upper *Puccinellietum* and sometimes in the higher *Juncetum gerardi* of grazed salt-marshes. Extensive stands are found in some re-vegetated turf-cuttings in Morecambe Bay.

The *Puccinellia*-turf fucoid sub-community is rare or absent from sandy salt-marshes and is especially characteristic of loch-head sites in west Scotland where shallow soils (20–30 cm deep) develop over rock or shingle. Such

soils tend to have a high organic content, to be reddish in colour and to contain coarse gravel throughout the profile. Although high salinities can be attained during drought (Gillham 1957b), *Festuca rubra* may occur even at the lowest levels attained by this sub-community, perhaps reflecting the influence of high regional rainfall. Small stands of the sub-community are also widespread among coastal rocks in the lower splash zone.

The *Puccinellia-Spartina maritima* sub-community is very local but it has been recorded from mid-marsh depressions and upper-marsh borrow pits with soft mud. Beeftink (1962) considered the vegetation characteristic of mud-flat/salt-marsh transitions.

Zonation and succession

Where the *Puccinellietum* is a pioneer community, as on sandier substrates, it appears to establish itself mainly by the rooting of vegetative fragments of *P. maritima* uprooted from existing swards by grazing stock and carried by tides (Ranwell 1961, Brereton 1971, Adam 1976, Gray & Scott 1977a). *P. maritima* can set abundant seed (Gray & Scott 1977a) but it has no special dispersal mechanism and, though caryopses can be washed away, seedling establishment in the pioneer zone seems uncommon.

Once established, the scattered plants produce numerous radiating stolons and accrete sediment into a series of hummocks (see Plate 3 in Ranwell 1972). Hummock size varies from shore to shore: some hummocks never exceed 50 cm in height but others are taller and attain a diameter of several metres. The hummock tops may carry the transitional *Puccinellia-Salicornia-Suaeda* community. Yapp & Johns (1917) postulated that the intervening hollows developed into pans but Pethwick (1974) showed that such a model could not account for the majority of upper-marsh pans.

At some sites a narrow zone of very scattered hummocks gives way quickly to a continuous sward of the *Puccinellia*-dominated sub-community. In other cases the hummocky topography persists much higher upshore (see the striking photographs in Yapp & Johns 1917) and eventually passes to fairly smooth swards of some *Puccinellietum* vegetation or, in the mid- and upper marsh, to *Juncetum gerardi* which is the usual high level vegetation of the grazed marshes of the west coast (Figure 8). On ungrazed west coast sites, the *Limonium-Armeria* sub-community may occur in the upper marsh.

In the south-east, the *Puccinellietum* is rarely a pioneer community. Its position in the zonation varies, the *Puccinellia*-dominated sub-community appearing either below or above the *Halimionetum portulacoidis*. In this region, the *Puccinellietum* can be found right up to the tidal limit, either as the *Puccinellia*-dominated sub-community, as around The Wash, or as the very

characteristic high marsh *Limonium-Armeria* sub-community.

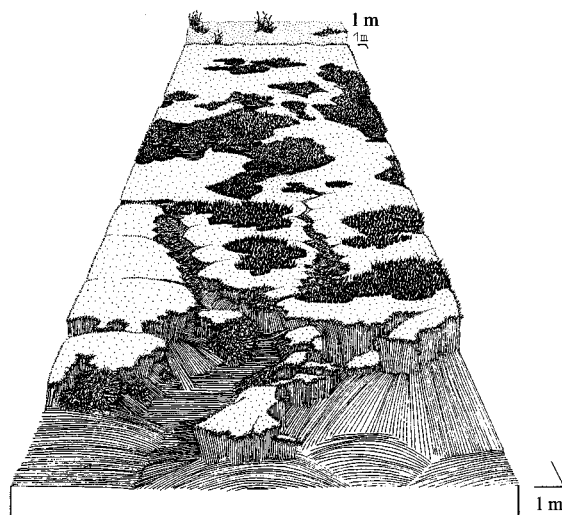
In the upper reaches of estuaries, where the soil salinity in the lower marsh is kept constantly low by freshwater dilution, an inversion of the normal zonation may be found with the *Puccinellietum* in upper marsh depressions where evaporation produces high salinities (Gillham 1957a, Adam 1976). Disturbance of upper marsh sites frequently results in the association appearing as a secondary pioneer, especially in the form of the *Puccinellia-Glaux* sub-community (cf. Beeftink 1962).

In the loch-head sites where the *Puccinellia*-turf fucoid sub-community is characteristic, it is frequently the lowest vegetation but it seems only rarely to be actively expanding. To seaward, there is usually a very low cliff or the vegetation cover is discontinuous with discrete patches on isolated rock or gravel plinths.

Distribution

The association is the most widespread community on British salt-marshes and probably no site lacks at least a fragmentary stand. The *Puccinellia*-dominated sub-community is the most widespread of the types, being frequent on all coasts except those of west Scotland and

Figure 8. Zonation on an eroding salt-marsh. The intact marsh carries various kinds of SM16 *Juncetum gerardi*, a ground of the *Armeria* variant of the *Festuca-Glaux* sub-community with patches of the *Juncus gerardii* sub-community. Running down below, on material slumped from the sides of the simple 'herring-bone' creeks, is a narrow zone of the SM13 *Puccinellietum maritimae*. The sequence terminates above in fragmentary SM24 *Atriplici-Elymetum pycnanthi*.



the northern Isles where it is largely replaced by the *Puccinellia*-turf furoid sub-community. The *Plantago-Armeria* sub-community is also widespread, though local, and the *Puccinellia-Glaux* sub-community is commoner on the west coast. The *Limonium-Armeria* sub-community is widespread in the south-east but much less frequent on the west coast where it is confined to lightly grazed and ungrazed sites. *Spartina maritima* is declining throughout northern Europe and the *Puccinellia-S. maritima* sub-community is restricted to Essex (and perhaps north Kent?).

Affinities

The vegetation types within the *Puccinellietum maritimae* can be seen as a floristic transition between the open annual communities of the lower marsh dominated by *Salicornia* spp. and *Suaeda maritima* and the *Juncetum gerardi* swards of the mid- and high marsh. The association grades floristically to the former through the more species-poor forms of the *Puccinellia*-dominated sub-community and the transitional *Puccinellia-Salicornia-Suaeda* vegetation.

Floristic table SM13

	a	b	c	d	e	f	13
<i>Puccinellia maritima</i>	V (4–10)	V (2–10)	V (1–8)	III (2–7)	V (4–9)	V (9–10)	V (1–10)
<i>Glaux maritima</i>	II (1–7)	V (5–9)	I (2–5)	V (2–5)	V (3–6)		II (1–9)
<i>Armeria maritima</i>	II (1–7)	III (2–7)	IV (3–8)	V (3–8)	IV (2–8)	I (1–5)	II (1–8)
<i>Plantago maritima</i>	II (1–7)	III (2–5)	IV (3–9)	V (5–9)	V (4–7)		II (1–9)
<i>Salicornia</i> agg.	III (2–6)	III (2–6)	IV (2–8)	II (2–3)	II (2–4)	V (4–10)	II (2–10)
Algal mat	II (3–10)	II (5–8)	IV (3–9)	II (4–8)	IV (4–7)		II (3–10)
<i>Triglochin maritima</i>	II (1–8)	III (2–4)	V (2–8)	IV (2–7)	II (1–3)	II (1–6)	II (1–8)
<i>Aster tripolium</i> (rayed)	III (1–8)	II (2–6)	II (2–7)	IV (2–7)	II (2–3)		II (1–8)
<i>Suaeda maritima</i>	III (1–6)	I (1–3)	III (1–3)	I (2–3)		IV (1–10)	II (1–10)
<i>Halimione portulacoides</i>	II (1–5)	I (2)	IV (1–6)	I (2–4)		III (4–10)	II (1–10)
<i>Limonium</i> cf. <i>L. vulgare</i>	II (1–8)	I (3)	V (2–8)			V (1–10)	II (1–10)
Turf fucoids*	I (2–3)		I (3)		V (4–9)		I (2–9)
<i>Spartina maritima</i>						V (1–10)	I (1–10)
<i>Aster tripolium</i> var. <i>discoideus</i>	I (1–5)					IV (1–8)	I (1–8)
<i>Spergularia media</i>	II (1–5)	II (2–3)	III (1–4)	III (1–3)	II (2–4)	I (3–5)	II (1–5)
<i>Spartina anglica</i>	I (1–7)	I (3)	I (2)	I (1–2)		I (5)	I (1–7)
<i>Festuca rubra</i>	I (2–5)	II (2–5)	II (2–6)	III (2–6)	II (2–4)		I (2–6)
<i>Agrostis stolonifera</i>	I (3–5)	I (2–3)	I (3–4)	II (3–6)	I (3–4)		I (2–6)
<i>Limonium humile</i>	I (2–5)	I (1–3)	I (1–8)	I (1–3)		I (4)	I (1–8)
<i>Cochlearia officinalis</i>	I (1–3)	I (2)	I (1–4)		I (3)		I (1–4)
<i>Juncus gerardii</i>	I (2–3)		I (2–6)	II (2–6)	I (3–4)		I (2–6)
<i>Bostrychia scorpioides</i>	I (4–7)		I (3–8)	I (6)	I (3)	I (8)	I (3–8)
<i>Arthrocnemum perenne</i>	I (1–3)		I (1–4)			II (1–6)	I (1–6)
<i>Aster tripolium</i>	I (1–6)		II (1–5)	I (3–4)			I (1–6)
<i>Cochlearia anglica</i>	I (1–6)		I (1–4)	I (2–3)			I (1–6)
<i>Atriplex prostrata</i>	I (1–7)						I (1–7)
Number of samples	319	23	89	26	17	20	494
Mean number of species/sample	6 (1–13)	6 (3–12)	9 (3–14)	8 (5–11)	7 (5–12)	7 (4–10)	7 (1–14)
Mean vegetation height (cm)	11 (2–50)	6 (2–15)	11 (3–25)	6 (2–15)	5 (2–15)	no data	6 (2–50)
Mean total cover (%)	88 (20–100)	85 (45–100)	91 (50–100)	96 (90–100)	91 (75–100)	no data	90 (20–100)

* Includes *Ascophyllum nodosum* ecad *mackaii*, *Fucus vesiculosus* ecad *caespitosus* and ecad *volubilis* and *Pelvetia canaliculata*.

a Sub-community with *Puccinellia maritima* dominant

b *Glaux maritima* sub-community

c *Limonium vulgare*-*Armeria maritima* sub-community

d *Plantago maritima*-*Armeria maritima* sub-community

e *Puccinellia maritima*-turf fucoid sub-community

f *Puccinellia maritima*-*Spartina maritima* sub-community

13 *Puccinellietum maritimae* (total)

