

The Zonation of the Salt Marsh Vegetation of Skallingen in 1931-34 and in 1952.

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The salt marsh vegetation on the leeseide of the Danish peninsula Skallingen in SW Jutland is one of the very few areas in our country, the vegetation of which may be called virgin.

This applies to the so-called "outer salt marshes" of Skallingen which were divided from the "inner salt marshes" by a large sand-plain nearly barren except for scattered *Salicornia*, often submerged by salt water for considerable periods. In later years this "middle plain" has, to a large extent, been invaded by *Puccinellia maritima* and other pioner plants, and a rapid tidal silting is in progress. The distinction between the inner and the outer marshes, therefore, will soon be obliterated. The "inner salt marshes" are appreciably effected by grazing and, in some cases, also by grass-cutting. On the other hand, the major part of the salt marsh area, despite occasional grazing of straying flocks of sheep and cattle, is only slightly effected. For once it may be said, that the zonation and succession of the plant communities on these vast areas are governed by natural factors only.

In the years 1931, 1933 and 1934 I have spent a good deal of time investigating the vegetation of Skallingen; the first year I worked together with E. K. Gabrielsen, D. Sc. The major part of this work has been published in my dissertation (1936), but an account of the zonation of the salt marsh vegetation was not included. In the 20 years that have passed since my investigation was carried out, great vegetational changes have occurred in the salt marshes of Skallingen. I regret that I had no opportunity to follow the details of this development, but I think it of some importance

to give information about the conditions 20 years ago, to provide a background for future investigations. Here I shall, in addition, just give a rough outline of the zonation today; but this scheme is only based on a short visit (6/8—7/8 1952), and does not claim to be precise. The principal changes will, however, be apparent when the two figures in the plate are compared.

I am indebted to Mrs. E. Bro Larsen, D. Sc., for valuable information and discussion.

Zonation of the salt marsh vegetation in 1931-34.

Fig. 1 in the plate shows the zonation of the vegetation in 1931—33. The ranges of the principal species are given by silhouettes based on a comprehensive statistical material (cf. Iversen 1936). It must be stressed that the actual zonation varied from place to place; the figures represent averages, and they are, therefore, rather schematical.

The series begins, where *Salicornia* colonizes the bare ground. Several species of *Salicornia* contribute to this Salicornietum (Danish: Kveller-vade); *S. strictissima* is usually the first to appear.

The next zone is characterized by *Puccinellia maritima* (Danish: Annel-marsk). To begin with, *Salicornia herbacea*, later *Aster tripolium*, may be co-dominants. Also *Suaeda maritima*, *Obione pedunculata*, and *Spergularia marginata* occur in this zone, while *Triglochin maritima* is extremely rare, curiously enough.

In the period in question, a well defined *Plantago maritima*-*Puccinellia* zone always follows, at a slightly higher level (the "middle marsh" of Tansley 1949). Both *Plantago* and *Puccinellia* grow vigorously, especially the former, which is here found in a broad-leaved, very succulent ecotype. *Salicornia* is suppressed in this zone. *Limonium vulgare* and *Glaux maritima* appear, but rather sparsely.

In the upper marsh *Puccinellia* is replaced by *Festuca rubra*, which forms a dense carpet. Most of the succulents are now suppressed, only *Plantago* appears fairly to resist. *Artemisia maritima* is a conspicuous but rather sparse element of the *Festuca* sward. *Glaux maritima* is rarely absent, and *Armeria maritima* appears, especially at the highest level, where silting is replaced by erosion.

The succession of the plant communities in the inner marshes differs from the above mentioned principally by the insertion of a *Juncus gerardi* zone between the *Puccinellia maritima* zone and the *Festuca rubra* zone. In the outer marshes *Juncus gerardi* is only

found in the *Festuca rubra* zone and it is sparse at that. In the inner marshes, however, it is the most important constituent on the middle level. Later *Festuca* immigrates, but even then *Juncus gerardi* maintains its preponderance. This difference is explained by the fact that the deeply rooting *Juncus gerardi* demands brackish ground water. This is found in the inner marshes of Skallingen, as normally in Danish salt marshes, as a result of an influx of fresh ground water; which, on the other hand, does not extend so far as to the outer salt marshes of Skallingen. In 1934 the salt concentration in the ground water of the *Juncus gerardi* zone was found to be up to 14‰, while in the *Festuca rubra* zone of the outer marshes it was about 20‰, and even in excess of that, at lower levels. *Juncus gerardi* cannot tolerate such high salt concentrations in the ground water.

Also *Agrostis stolonifera* is found at lower levels in the inner marshes than in the outer marshes; in the latter it occurs at highest level only, and very sparsely here. Where the salt concentrations are only very low, *Agrostis* descends into the lowest levels and replaces *Puccinellia maritima*, and here we have an *Agrostis stolonifera* zone below the *Juncus gerardi* zone, which latter is then associated with oligohalobious species as *Carex distans*, *Trifolium repens*, *T. fragiferum*, *Leontodon autumnalis*, *Potentilla anserina* a. o. (cf. Iversen 1936).

Zonation of the salt marsh vegetation in 1952.

Since my first investigation was carried out important vegetational changes have taken place in the salt marshes, as mentioned above. In the first place, *Spartina townsendi* has immigrated to Skallingen by natural means from sites in the Ho Bugt outside Skallingen, where planted. Still the occurrences on Skallingen are somewhat scattered, but it grows well in the outer marshes where it colonizes the bare ground of the lowest levels, indeed earlier than the *Salicornietum*. Possibly its further spreading will completely alter the vegetational development in the outer marshes of Skallingen.

Another remarkable fact is the spreading of *Obione portulacoides*. This succulent bush has always been considered a very rare plant in Denmark; and in 1909, when Raunkjær studied the vegetation of Skallingen, this plant was not found there. In 1931 we discovered a few specimens of it on Skallingen, and in the following years the number was multiplied (Gabrielsen & Iversen 1934). To-day

it is perhaps the most abundant plant of the outer marshes. Also *Limonium vulgare* and *Triglochin maritima* have spread very much, while most other plants have receded; this is especially true of *Plantago maritima* and *Obione pedunculata*. Instead of the former *Plantago-Puccinellia* zone we have now an *Obione portulacoides-Limonium vulgare* zone, which, in addition, has a wider vertical range than the former. At higher levels *Artemisia* has become more widespread.

Another great change concerns the large sand plain, which formerly divided the outer salt marshes from the inner salt marshes. Now this plain is covered for miles by beautiful, strange looking, mats of *Limonium vulgare*, *Obione portulacoides*, and even *Artemisia*, where bordering on creeks; while the *Salicornietum* is split up into small patches.

Large areas of this plain now belong to the inner marshes and they are, as formerly mentioned, characterized by the invasion of *Limonium* and *Obione portulacoides*. Apart from this area the vegetational changes are less conspicuous in the inner salt marshes, and my visit in 1952 was too short to enable me to make precise statements.

Comparison with other regions.

Vegetational zonation and successions different from those described above are, on Skallingen, found on pure sand where the soil is not stabilized (*Agrostis stolonifera* var. *maritima*, *Carex extensa*, *Armeria maritima*, *Sagina nodosa*, *Plantago coronopus* and many annuals as *Lepturus filiformis*, *Sagina maritima*, *Centaurium erythraea* and others occur here). I have in this survey only described the principal types of vegetational zonation found in those areas, which are within the reach of the tides and where silting is in progress. Briefly we shall now make comparisons with other regions.

The zonation of the vegetation as it is found today in the outer marshes of Skallingen is not known from any other place in the Scandinavian countries, but similar conditions are described from The British Isles (Yapp and Johns 1917, Chapman 1934). The following general zonation for The British Isles is given by Tansley (1949)¹); one or more of the zones may be absent. To the right corresponding zones in the outer marshes of Skallingen.

¹) The *Suaedetum fruticosae* (4 b) has been left out, since the Mediterranean species *Suaeda fruticosa* does not occur in Denmark.

The British Isles (Tansley 1949)	Skallingen outer marshes	
	1952	1931-33
(1) <i>Salicornietum herbaceae</i>	(1)	(1)
(1a) <i>Spartinetum townsendii</i>	(1a)	—
(2a) <i>Glycerietum maritimae</i>	(2a)	(2a)
(2b) <i>Asteretum tripolii</i>	(2b)	(2b)
(3) <i>Limonietum vulgaris</i>	(3)	—
(4) <i>Armerietum vulgaris</i>	—	—
(4a) <i>Obionetum portulacoidis</i>	(4)	—
(5) <i>Festucetum rubrae</i> (sandy marshes)	(5)	(5)
(6) <i>Juncetum maritimi</i>	—	—

It appears from the comparison, that there is very good agreement between the zonation of the outer salt marshes in Skallingen and the general zonation in The British Isles as described by Tansley. There is only one striking difference: Nothing corresponding to Tansley's *Armerietum vulgaris* is known from Skallingen, nor from any other part of Denmark. *Armeria maritima* (= *A. vulgaris*) occurs abundantly in Skallingen, but always at a much higher level, and, especially, on pure sand where erosion takes place. In an earlier paper (1936) I have discussed this discrepancy; it is, I think, due to the fact, that the British ecotype (the *A. vulgaris* var. *maritima* of Willy Christiansen), which is able to tolerate submersion by seawater, does not occur in Denmark, even if specimens of *Armeria* may be found, which, morphologically, are very similar. In the Frisian area of Germany (Willy Christiansen 1927), and in the Netherlands (Meltzer, J. en Westhoff, W. 1944), conditions are similar; scattered specimens of *Armeria* may, however, be found at lower levels than *Festuca rubra*.

The great vegetational changes in the salt marshes of Skallingen are, first and foremost, due to the fact that the outer marshes of Skallingen are a very recent formation, still in progress. Nielsen has proved in his substantial investigation of 1935 that the process of silting on Skallingen began as late as about 1900. It is not until now that the formation of salt marshes, on a great scale, has commenced, and that ideal conditions for exclusive clayey salt marsh plants such as *Obione portulacoides* have been established.

On Skallingen, edaphic factors, and accordingly, also vegetation and animal life, are subject to constant changes (cf. E. Bro Larsen 1953). The region, therefore, affords an eminent opportunity to study ecological development.

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