Acta Botanica Neerlandica **8** (1959) 449–472

SOME NOTES ON SKALLINGENS SALT MARSH VEGETATION AND ITS HABITAT

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(*received March 3rd,* 1959)

1. Introduction

From 1–7 July 1956 an excursion was organized through Schleswig and Jutland by the International Society for Plant Geography and Ecology. The objects were salt marshes and dunes along the coasts of the Wadden Sea and the North Sea. During this excursion Dr. J. Iversen invited the author kindly to stay some days (5–8 July) at Skalling-Laboratory, situated in the northern part of the Danish peninsula Skallingen near the village Ho. The author is greatly indebted to Dr. Iversen for his kind invitation, which enabled him to carry out the present work.

The Skalling Peninsula — about 3 × 10 km large — forms the northern barrier of the Danish Wadden Sea, which ends in the Ho Bugt. The narrow but deep channel Graadyb separates it from the isle of Fanø. Skallingen is one of the most northern regions with salt marshes on the west coast of Denmark and therefore it is of major importance for the study of the Westeuropean halophytic biocenoses.

On the side of the North Sea the peninsula consists of dunes with beaches. These dunes form the southern continuation of the chains along the west coast of Jutland. Behind the dunes a sandy and hilly landscape is found, for the greater part situated at an altitude fairly high above MHW-level. The more clayey salt marshes are found further on to the east along the Wadden Sea, largely overgrown with a closed vegetation which is flooded by spring-tides and storm floods.

It was not possible to study the whole salt marshes in the few days available. Therefore a rather small region was chosen, which, apparently, never had been grazen by cattle. This region forms a strip going from the Wadden Sea to the west overlapping both clayey and sandy soils (Fig. 1).

2. Environment and geomorphological development

The foundation on which the marshes have been formed is a sand flat of higher level than normal tidal flats (Jakobsen, 1952/53). Through several gaps in the dunes the sea deposited a great deal of sand behind the coastline. In the beginning of this century, however, the gaps were closed by dams and since the salt marshes and their vegetation have developed. The first marshes were formed as small islands along the Wadden Sea. About 1931–1934, when Iversen (1936) investigated the vegetation of Skallingen, the area was divided

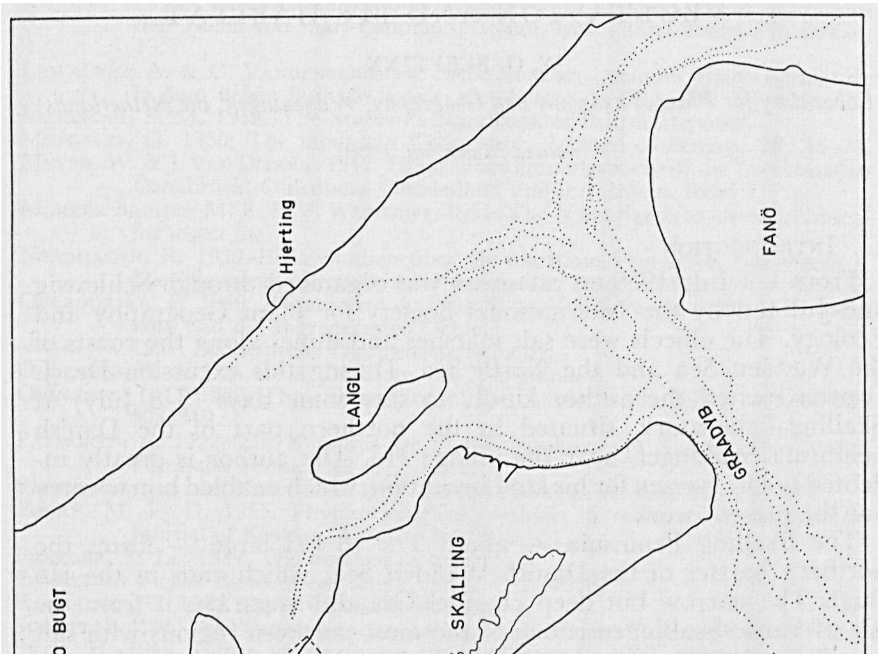

Fig. 1. Sketch map of Skallingen. (scale 1: 120.000). The area studied has been marked with a rectangle.

into so-called "outer salt marshes" situated on the Wadden Sea coast, and "inner salt marshes" near the dunes, which were separated by "a large sandplain nearly barren except for scattered *Salicornia*, often submerged by salt water for considerable periods" (IVERSEN, 1952/53). Nowadays the sandplain is silted up entirely and the outer and inner marshes overlap. This phenomenon of sedimentation of silt after closing gaps in the range of dunes is not restricted to Skallingen. It is observed, too, on the Dutch isles of Texel and Terschelling (WESTHOFF, 1947 manuscript).

On Skallingens salt marshes sedimentation from the Wadden Sea did not take place over the whole area. The inner marshes have only occasionly been silted up on a few localities, as a result of the fairly high elevation above MHW-level. This circumstance combined with the effect of a small number of tidal creeks and of the large distance to the sea results in inundations by storm floods only. In those circumstances the possibilities for sedimentation of silt are limited. For this reason the greater part of the area will have obtained its present condition, during the period that gaps in the dune ranges still existed. The outer marshes are younger and have been silted up recently. Locally, some sandhills emerge out of the clayey soil. They are probably high parts of the underlying sand flat. The formation of many tidal creeks with their banks and basins between them results in a landscape characteristic for such salt marshes. It may be called a bank-and-basin-landscape (Fig. 2). The tidal creeks are not so deep as those in the southwestern part of the Netherlands. Doubtless this phenomenon is related to the difference in tide-level (near Skallingen average about 1.35 m, in the S.W.-Netherlands 3.— till 4.50 m).

Except for the mud flats along the Wadden Sea the outer marshes are silted up to a height exceeding average high tide level. The rate of sedimentation was about 3,6 mm p.a. in the years 1931–1933 as stated by NIELSEN (1935), but according to JAKOBSEN (1952/53) the real accretion was only some 2 mm due to settling in young deposits. However, the above mentioned authors have made no distinction

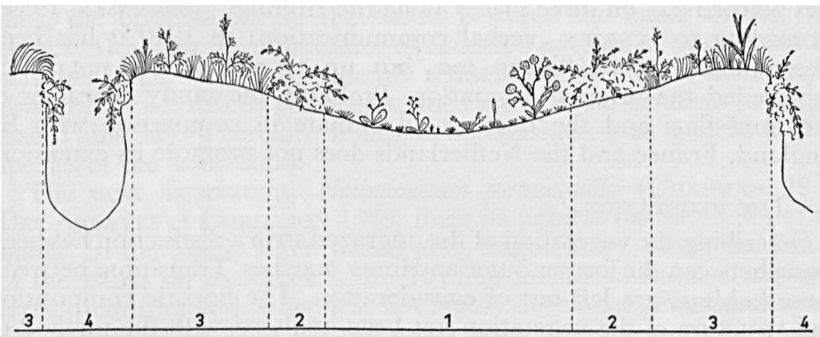

Fig. 2. Cross-section of the bank-and-basin-landscape with vegetation zones. 1 = *Puccinellietum maritimae;* 2 = *Halimionetum portulacoidis;* 3 = *Artemisietum maritimae;* 4 = Creeks with individuals of *Halimione portulacoides* on the walls along the inside of the banks.

between the difference of accretion in basins and that on banks a result of the difference in distance from the water-supplying creeks, for according to VERHOEVEN (1954) accretion on the banks is generally larger than in the basins, and, moreover, deposits were found to settle on banks to a lower degree.

On account of the sandy character of the inner marshes and their less frequent floods the soil moisture and its salt content are on an average lower compared with the outer marshes. The floristic composition and structure of the vegetation presents evident consequences of these differences in soil and water conditions.

The lime content of the soil is very low. According to SANDERS and VERHOEVEN (1956) it decreases regularly on the salt marshes from Bretagne till Denmark. The soil of Skallingen still contains some lime, in contrast to some soils along the coast near Skaerbaek and Ribe which contain practically no lime (VERHOEVEN, verbal communication). According to Verhoeven, in 8 samples the content varies from 0,36 till 1,46 % $CaCO_3$ with a variation from 0 till 32,5 % silt $< 16\ \mu$.

Probably this difference between Skallingen and the above mentioned Danish salt marshes is due to a complex of factors of which the following may be important: (1) the origin and age of sedimentation materials; (2) a difference in sedimentation velocity which may be directly proportional to the lime content; (3) locally, mixing of seawater with the acid, or at least less calcareous, water of small rivers (see also the view of DE SMET, 1954) or (4) perhaps difference in withdrawal of $CaCO_3$ from the sediments as an additional effect of oxydation of iron sulphide (VAN DER SPEK, 1952) and of oxydation and hydrolization of iron compounds (RIVIÈRE, 1942). It is uncertain which factor prevails, the first two being generally perhaps the most common as a cause of local differences. On Skallingen the rather high sedimentation rate might be the primary cause of the relative high lime content.

Spartina townsendii promoting sedimentation along the European coasts, has not acted such a part here. In 1931 and 1932 the species was planted a.o. on three places along the Ho Bugt (JØRGENSEN, 1934). According to IVERSEN (verbal communication) in 1940 it has been disseminated on Skallingen too, but up to now it has not much superseded the original vegetation. Probably the sandy character of the mud flats and the rather cold climate in comparison with S.-England, France and the Netherlands does not promote its extension.

3. THE VEGETATION

Describing the vegetation of the ungrazed strip a distinction has been made between the former outer and inner marshes. Transitions between those habitats are left out of consideration. The floristic composition and structure of the vegetation has been analysed with the method of BRAUN-BLANQUET (1951). The sample plot analyses (BECKING, 1957) — Fr.: relevés, Ge.: Aufnahmen — have been assembled in the Tables I and II. In order to ensure as objective a survey as possible most analyses have been taken in transects perpendicular to the contour lines in the landscape. From low to high the transects consist of the following sample plot analyses:

Outer marshes	Inner marshes
56022–56023–56024–56025	56057–56058–56059–56060–56061
56027–56028–56029	56063–56064–56065–56066–56067–56068
56030–56031–56032–56033	56069–56070–56071–56072–56073
56034–56035	56075–56076–56078–56079–56080
56037–56038–56039	56082–56081
56045–56044	56084–56085
56046–56047–56048	56086–56087
56055–56054	

3.1 *The outer salt marshes*

On the mud flats along the Wadden Sea *Zostera nana* grows locally (*Zosteretum nanae* HARMSEN 1936). The mud flats are mostly bare, but *Spartina townsendii* establishes itself gradually. Near the closed vegetation of the higher marshes the flats are overgrown with a vegetation almost entirely consisting of *Salicornia europaea* scattered with clumps of *Spartina townsendii* (*Salicornietum europaeae* (WARMING 1906) HOCQUETTE 1927, see Table I). The abundance of the *Salicornia*-individuals was not large, but it increased on the higher parts being the largest in the transition to the next association, *Puccinellietum maritimae* (WARMING 1890) BRAUN-BLANQUET et DE LEEUW 1936. However, vitality decreased in this association.

As a result of the sod-forming properties of *Puccinellia maritima* the transition from *Salicornietum europaeae* to *Puccinellietum maritimae* is rather distinct. The latter association appears at first in an initial phase, which may be distinguished from the optimal one by a more open turf (cover 20–40 % in contrast with 40–80 % in the optimal phase) and the lower frequency of individuals of *Halimione portulacoides* with reduced vitality. Moreover, *Spartina townsendii* occurs only in the initial phase up to now. The initial phase is found mainly along the mud flats, the optimal one in the basins between the banks of the tidal creeks. Although the abundance of *Salicornia europaea* in this association is rather large, vitality is evidently reduced. According to the analyses *Aster tripolium* is strictly confined to the *Puccinellietum maritimae* (compare also Table II). Therefore it might be considered as a local faithful species of the association.

The next association, *Halimionetum portulacoidis* (CHAPMAN 1934) DES ABBAYES et CORILLION 1949, finds its habitat on the slopes of the banks, in the highly silted basins and, fragmentary, along the insides of the banks on the creek walls. It often includes *Limonium vulgare* in large quantities and, when it is not highly developed, *Plantago maritima var. dentata* Bl. et Fing. In the upper part *Artemisia maritima* appears locally, sometimes in large quantities (analyse 56051), perhaps due to favourable circumstances influencing the competition between *Artemisia maritima* on the one side and *Halimione portulacoides* and *Festuca rubra* on the other side. Other species such as *Aster tripolium*, *Triglochin*

TABLE I

Vegetation of the outer

		Salicornietum europaeae						
Sample plot analyse nr.	56027	56026	56019	56030	56028	56018	56062	56020
Surface in m²	4×5	8×10	8×50	25×30	5×15	15×30	4	8×15
Cover in %	20	1	1	1	1	1	1	1
Faithful taxa of the associations and sociation								
Salicornia europaea	+.1	1.1	1.1	1.1	1.1	1.1	2.1	1–2.1
Puccinellia maritima	—	—	—	—	—	—	+.1	+.1–3
Aster tripolium	—	—	—	—	—	—	—	—
Halimione portulacoides	—	—	—	—	—	—	—	—
Artemisia maritima	—	—	—	—	—	—	—	—
Agropyron litorale	—	—	—	—	—	—	—	—
Faithful taxa of the Puccinellion maritimae								
Spartina townsendii	2.5	+.1	+.2–3	1.2–3	+.1–2	1.1–3	—	+.1–3
Suaeda maritima	—	—	—	—	—	+.1	—	—
Spergularia marginata	—	—	—	—	—	—	—	—
Faithful taxa of the Puccinellion maritimae and Armerion maritimae together								
Triglochin maritimum	—	—	—	—	—	—	—	—
Limonium vulgare	—	—	—	—	—	—	—	—
Plantago maritima typicum and var. dentata	—	—	—	—	—	—	—	—
Festuca rubra f. litoralis	—	—	—	—	—	—	—	—

Salt Marshes of Skallingen

Transition		Puccinellietum maritimae										
		initial phase						optimal phase				
56029	56031	56034	56022	56021	56023	56032	56036	56024	56033	56025	56037	56035
6×25	8×20	3×12	5×10	5×12	6×20	5×10	8×10	5×10	5×15	10×20	12×20	4×12
3	3	20	25	25	25	40	25	40	65	60	70	80
2.5	2.5	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	1.1	2.1
1.1–2	1.1–2	2.4	2–3.5	2–3.5	2–3.5	3.5	2.5	3.5	3.4	4.5	4.5	3.3
—	—	+.1	+.1	1.1–2	1.1–2	1.1–2	+.1	1.1–2	+.1–2	1.1–2	1.1–2	1.1–2
—	—	+.1°	+.1°	+.1°	+.1	+.1°	+.1–2	1.1–2	2.1–3	2.1–3	2.2–3	2–3.2–3
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
+.1–3	—	+.1–2	1.1–2	1.2–3	+.1–2	1.2	+.2	—	+.2	—	—	—
+.1	+.1	2.1	1.1	1.1	1–2.1	2.1	1.1	1.1	1–2.1	1.1	2.1	1.1
—	—	—	—	—	—	+.1	—	—	—	—	—	+.1
—	—	—	—	+.2	1.2–3	1–2.2	1–2.2	+.1–3	+.2	+.1–2	+.2	1.2
+.1–2	+.2	—	—	+.1	+.2	1.2	1–2.2	+.1–2	+.2	+.1–2	+.2	1–2.2–3
—	—	—	—	—	—	—	—	—	—	—	—	+.2
—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE I

"/egetation of the outer

	Transition		Halimionetum optimal phase			
Sample plot analyse nr.	56053	56055	56045	56038	56050	56044
Surface in m²	4×15	4×6	5×6	3×20	3×7	6×15
Cover in %	90	90	80	85	85	80
Faithful taxa of the associations and sociation						
Salicornia europaea	+.1°	+.1°	+.1°	+.1°	+.1°	+.1°
Puccinellia maritima	2.1–2	2.2	2.2	+.2	+.1–2	1.2
Aster tripolium	+.1	+.1	—	+.1–2	—	—
Halimione portulacoides	2–3.2–3	3.2–3	4.3	5.5	4.3	4.3
Artemisia maritima	—	—	—	—	+.1	+.1
Agropyron litorale	—	—	—	—	—	—
Faithful taxa of the Puccinellion maritimae						
Spartina townsendii	—	—	—	—	—	—
Suaeda maritima	1.1	+.1	+.1	—	+.1°	+.1
Spergularia marginata	—	+.1	—	—	—	—
Faithful taxa of the Puccinellion maritimae and Armerion maritimae together						
Triglochin maritimum	+.2	—	+.2	+.2	—	—
Limonium vulgare	3.2–3	3.3	3.2–3	+.2	3.2	3.2–3
Plantago maritima typicum and var. dentata	2–3.2	2–3.2	1.2	1.2	2.2	1.2
Festuca rubra f. litoralis	—	—	—	—	—	+.2–3

(*continued*)

Salt Marshes of Skallingen

portulacoidis			Artemisietum maritimae								Sociation with Agropyron litorale
terminal phase with Artemisia			initial phase		optimal phase						
56052	56051	56049	56054	56046	56039	56047	56042	56040	56043	56048	56041
4×10	3×5	5×6	3×10	5×15	8×12	6×20	6×30	3×8	3×5	8×15	4×6
>95	100	90	100	>95	100	100	100	100	100	100	100
+.1°	+.1°	—	—	+.1°	+.1°	—	—	—	—	—	—
+–1.2	+.1–2	1.2	1.2–3	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
4.3	4.4	5.5	3.3	3–4.2–3	1–2.2–3	1.1–3	+.1–3	+.1–2	+.2	+.1°	—
2.1	3.5	1–2.1	2.1–2	1–2.1	2.1	1.1	1.1–2	+–1.1	3.5	1.1	+.1
—	—	—	—	—	—	—	—	—	—	—	5.5
—	—	—	—	—	—	—	—	—	—	—	—
+.1°	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
+.1	—	—	—	—	—	—	+.2	—	—	—	—
3.1–2	1–2.2	2.2	2.1–2	2.2–3	1.1–2	2.1–2	1–2.2	+–1.1–2	2.4	2.1–2	—
2.2	1.2	+–1.2	+.2	1.2	+.1	+.2	+.2	—	+.2	+.1	—
+.2	—	1.2	4.4	4.4	5.5	5.5	5.5	5.5	4.5	5.5	+.2

TABLE II

Vegetation of the inner

	Salicornietum europaeae		phase	
Sample plot analyse nr.	56062	56063	56056	56057
Surface in m²	4	5×15	2×3	4×6
Cover in %	1	<1	35	30
Faithful taxa of the associations				
Salicornia europaea	2.1	1.1	2.1	2.1
Puccinellia maritima	+.1	+.1	3.5	3.5
Aster tripolium	—	—	+.1	+.1
Juncus gerardi	—	—	—	—
Sagina maritima	—	—	—	—
Plantago maritima var. leptophylla	—	—	—	—
Faithful taxa of the Puccinellion maritimae				
Halimione portulacoides	—	—	+.1°	+.1°
Artemisia maritima	—	—	—	—
Suaeda maritima	—	+.1	1.1	1.1
Spergularia marginata	—	—	—	+.1
Faithful taxa of the Armerion maritimae				
Armeria maritima	—	—	—	—
Parapholis strigosa	—	—	—	—
Glaux maritima	—	—	—	—
Carex extensa	—	—	—	—
Euphrasia litoralis	—	—	—	—
Faithful taxa of the Puccinellion maritimae and Armerion maritimae together				
Triglochin maritimum	—	—	+.1	—
Limonium vulgare	—	—	+.1	+.1
Plantago maritima typicum and var. dentata	—	—	—	—
Festuca rubra f. litoralis	—	—	—	—
Other taxa				
Agrostis stolonifera var. stricta	—	—	—	—
Phragmites communis	—	—	—	—
Bryum sp.	—	—	—	—
Dianthus deltoides	—	—	—	—
Juncus anceps	—	—	—	—
Lyngbya digueti Gom.	—	—	—	—
Elymus arenarius	—	—	—	—
Poa annua	—	—	—	—
Poa pratensis	—	—	—	—
Plantago coronopus	—	—	—	—
Sagina procumbens	—	—	—	—
Sedum acre	—	—	—	—
Empetrum nigrum	—	—	—	—
Sonchus arvensis	—	—	—	—
Leontodon autumnalis	—	—	—	—

Salt Marshes of Skallingen

Puccinellietum maritimae											
rich in therophytes					phase with Limonium vulgare and Plantago maritima						
56064	56075	56069	56058	56083	56076	56065	56070	56077	56066	56059	56060
4×10	4×6	3×5	10×20	2×4	3×5	3×8	3×5	2×8	5×10	8×10	6×12
60	70	60	55	90	70	60	75	40	70	25	65
2.1	1.1	2.1	2.1°	+.1	1.1	2.1	1.1	2.1	+.1	2.1°	+.1°
4.5	4.5	4.5	4.5	5.5	3.5	3–4.5	3.5	2.2–3	3.5	2.2–3	2.2
+.1	+.1	+.1	1.1	2.1–2	1–2.1	1.1	2.1–2	1.1	2.1	1.1	1.1
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
+.1°	+.1°	+.1°	+.1°	+.1	+–1.1	1.1°	1–2.1	+.1°	1.1	+.1	1.1–2
—	—	—	—	—	—	—	—	—	—	—	+.1
+.1	2.1	2.1	+.1°	+.1	+.1	+.1	+.1	+.1	—	+.1	+.1°
+–1.1	—	+.1	1.1	1.1	+.1	1.1	+.1	—	+.1	1.1	1.1
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	+.1	—	+.1	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	+.2	+.2	+.2	+–1.1–2	+–1.1	+–1.2	+.2	2.2	+.2	+.2	+.1
+.1	—	+.1–2	1.1–2	+.1	2–3.2	2.1–2	2–3.2	1–2.2	2–3.2	2.2	2–3.2
—	—	+.2	—	+–1.2	+.1–2	+.1–2	2.1–2	1–2.1–2	2.1–2	2.2	3.2
—	—	—	—	—	—	—	—	—	—	+.2	+.2
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
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—	—	—	—	—	—	—	—	—	—	—	—

TABLE II

Vegetation of the inner

	Juncetum				
Sample plot analyse nr.	56061	56071	56078	56067	56072
Surface in m²	3×8	2×10	3×8	2×10	2×10
Cover in %	100	100	100	100	>95
Faithful taxa of the associations					
Salicornia europaea	—	—	—	—	—
Puccinellia maritima	—	—	—	—	—
Aster tripolium	—	—	+.1	—	—
Juncus gerardi	+.1-2	+.1-2	1.2	1.1-2	1-2.1-2
Sagina maritima	—	—	—	—	—
Plantago maritima var. leptophylla	—	—	—	—	—
Faithful taxa of the Puccinellion maritimae					
Halimione portulacoides	+.1	+.1°	—	+.1°	+.1°
Artemisia maritima	+.1	—	—	—	+.1°
Suaeda maritima	—	—	—	—	—
Spergularia marginata	—	—	—	—	—
Faithful taxa of the Armerion maritimae					
Armeria maritima	+.1-2	+.1	+.1	+.1-2	+.1
Parapholis strigosa	—	—	—	—	—
Glaux maritima	—	—	—	—	—
Carex extensa	—	+.1	+.1	+.1	—
Euphrasia litoralis	—	—	—	—	—
Faithful taxa of the Puccinellion maritimae and Armerion maritimae together					
Triglochin maritimum	+.1	+.1	+-1.1-2	+.1	—
Limonium vulgare	2.1-2	1-2.1-2	+-1.1	1.1	+.1
Plantago maritima typicum and var. dentata	+-1.1-2	1.1-2	+.1	+-1.1	+-1.1
Festuca rubra f. litoralis	5.5	5.5	5.5	5.5	5.5
Other taxa					
Agrostis stolonifera var. stricta	—	—	—	+.1	+.1
Phragmites communis	—	—	—	—	—
Bryum sp.	—	—	—	—	—
Dianthus deltoides	—	—	—	—	—
Juncus anceps	—	—	—	—	—
Lyngbya digueti Gom.	—	—	—	—	—
Elymus arenarius	—	—	—	—	—
Poa annua	—	—	—	—	—
Poa pratensis	—	—	—	—	—
Plantago coronopus	—	—	—	—	—
Sagina procumbens	—	—	—	—	—
Sedum acre	—	—	—	—	—
Empetrum nigrum	—	—	—	—	—
Sonchus arvensis	—	—	—	—	—
Leontodon autumnalis	—	—	—	—	—

(*continued*)

Salt Marshes of Skallingen

gerardi			Saginetum maritimae								
56079	56084	56086	56074	56068	56082	56080	56073	56087	56085	56081	56088
2×8	2×8	2×6	3×5	3×6	4×6	8×12	3×6	3×4	3×5	3×6	4×8
100	100	100	95	90	80	70	45	35	20	15	10
—	—	—	—	+.1°	—	+.1°	+.1°	—	—	+.1°	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
1–2.2	+.2	—	1.2	+.1	+.1–2	—	—	—	—	—	—
—	—	—	1.1–2	1.1–2	2.2	1.1–2	2.2	+–1.1	+.1–2	+–1.1–2	—
—	—	—	—	+.1	1–2.1	+.1	—	+–1.1	+.1	2.1–2	+.1
+.1°	—	—	+.1°	+.1°	+.1°	+.1°	+.1°	—	—	+.1°	—
—	—	—	—	+.1°	—	+.1°	1.1°	—	—	—	—
—	—	—	—	—	—	+.1°	+.1°	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
+.1	—	+.1	+.1–2	+–1.1	2.1	2.1–2	1–2.1–2	2.1–2	2.1–2	1.1–2	1–2.1–2
—	—	—	—	—	—	—	+.1	+.1	+.1	—	—
—	—	—	—	—	—	—	—	—	—	—	—
+.1	+.1	1.1–2	—	—	+.1	—	—	—	—	—	—
—	—	+.1	—	—	+.1	—	—	—	—	—	+.1
—	+.1	+.1	—	—	—	—	—	—	—	—	—
+.1	+.1	+.1	+.1°	+.1°	+.1°	+.1°	+.1°	—	—	—	—
1–2.1–2	+.1	+.1	1.1	2.1–2	+.1	2.1	1–2.1–2	1.1	1.1–2	1.1	+–1.1
5.5	5.5	5.5	5.5	5.5	4.5	4.5	3.5	2–3.5	2.2	2.2	2.1–2
+.1	+.1	+.2	+.1–2	+.2	+.2	1–2.2	1.1–2	+.1	+.2	+–1.1–2	+.2
—	+.1	+.1	—	—	—	—	—	—	—	—	—
—	—	—	—	+–1.2	+.2	1–2.2	1.2	—	—	—	—
—	—	—	—	—	+.1	—	—	—	—	+.1	+.1
—	—	—	—	—	+.2	—	—	—	—	—	—
—	—	—	—	—	1.2	—	—	2.2	1.2	1–2.2	—
—	—	—	—	—	—	+.1	—	—	—	—	1.1
—	—	—	—	—	—	—	—	2.1–2	—	—	—
—	—	—	—	—	—	—	—	+–1.1	—	—	—
—	—	—	—	—	—	—	—	+.1	—	—	—
—	—	—	—	—	—	—	—	+–1.1	+.1	—	—
—	—	—	—	—	—	—	—	—	+–1.2	—	+.2
—	—	—	—	—	—	—	—	—	—	+.1	—
—	—	—	—	—	—	—	—	—	—	—	+.1
—	—	—	—	—	—	—	—	—	—	—	+.1

maritimum, *Suaeda maritima* and *Spergularia marginata* are very sparse or entirely lacking.

On the banks a *Festuca rubra* sward is found with scattered individuals of *Artemisia maritima*, *Halimione portulacoides*, *Limonium vulgare* and *Plantago maritima*. Of the latter both the *var. dentata* and the typical form occur. This vegetation belongs to the *Artemisietum maritimae* (HOCQUETTE 1927) BRAUN-BLANQUET et DE LEEUW 1936 em. WEEVERS 1940.

The synsystematics of the *Artemisietum maritimae* offer interesting problems. CHRISTIANSEN (1927) has described the association without giving it a name; VAN LANGENDONCK (1931, 1933) distinguished the "association à *Artemisia maritima* et *Statice Limonium*"; BRAUN-BLANQUET and DE LEEUW (1936) and afterwards TÜXEN (1937) the "*Artemisia maritima-Obione portulacoides* Assoziation (*Artemisietum maritimae*)" with *Artemisia maritima*, *Obione portulacoides*, *Parapholis strigosa* and *Limonium vulgare* as supposed faithful species; VLIEGER and ADRIANI (1938), ADRIANI (1945) and WESTHOFF (1947) reduced the faithful species to three, viz. *Artemisia*, *Halimione* and *Limonium*. The first who broke with this view was WEEVERS (1940), considering *Halimione* and *Limonium* faithful species of the *Puccinellietum maritimae*. Afterwards, TÜXEN (1957) goes in this direction, however considering *Halimione* a species characteristic for the order *Juncetalia maritimi*. The author sides with WEEVERS taking only *Artemisia* as faithful species of the association.

Essentially the cause of this misunderstanding may be the poor development of the *Artemisietum maritimae* in the Wadden Sea area. This poor development is due (1) to the chiefly very sandy character of the soil and (2) on those localities where more fine material was deposited, to the absence of tidal creeks with banks, usually offering well-aerated soil conditions and a slightly clayish character of the soil. If the association occurs it has often a floristic composition related to the *Armerion maritimae* (CHRISTIANSEN, 1927; BRAUN-BLANQUET and DE LEEUW, 1936; TÜXEN, 1937; WESTHOFF, 1947; TÜXEN, 1957). However, Skallingen shows that in the Wadden Sea area the association can develop completely under favourable sedimentation conditions and along well-evolved tidal creeks. On that marsh it resembles the corresponding phytocenoses in the S.W.-Netherlands to a high degree: it lacks elements of the *Armerion maritimae* and therefore it belongs to the alliance *Puccinellion maritimae*.

Table I shows the ecological amplitudes of the three above mentioned species in the series of the outer salt marshes. *Limonium vulgare* has its optimum in the transition of *Puccinellietum maritimae* to *Halimionetum portulacidis* and in the lower parts of the latter. The character of its amplitude — the height and range of a constructed bell-shaped curve along the environmental gradients — accounts for its position of faithful species of the alliance *Puccinellion maritimae*. (Compare also table II). Under well-aerated soil conditions mainly involved in the development of banks along tidal creeks *Halimione portulacoides* forms a zone above the *Puccinellietum maritimae* and below the *Festuca rubra*-

sward. According to its high optimum in comparison with the range of its amplitude it seems better to segregate the *Halimionetum portulacoidis* like English and French authors do (CHAPMAN, 1934; TANSLEY, 1939, 1949; DES ABBAYES and CORILLON, 1949; CORILLON, 1953). According to these references and the present data of Skallingen the *Halimionetum* has a wide distribution occurring from Denmark southwards perhaps to the coast of Spain and, fragmentary (?), to Portugal (FONTES, 1945). Finally, the optimum of *Artemisia maritima* is found in the *Festuca rubra*-sward on the banks along the tidal creeks and, locally, in the upper part of the *Halimionetum portulacoidis*. The range of its amplitude is very small. Therefore it seems better to consider only that species as faithful to the *Artemisietum maritimae* following the above discussed view of WEEVERS (1940). Local occurrence of *Artemisia maritima* in the upper part of the *Halimionetum* may then lead to distinction of a terminal phase with *Artemisia* in this association. Likewise in the *Artemisietum maritimae* an initial phase with co-dominance of *Halimione* may be distinguished.

Besides the *Artemisietum maritimae* a vegetation with *Agropyron litorale* (Host.) Dum. 1823 (= *Agropyron pycnanthum* (Godr.) Gren. et Godr. 1855/56 = *Elytrigia litoralis* (Dum.) Hyl. 1945) as dominant species may be found on the banks (leg. W. G. Beeftink, Herb. Hydrobiol. Inst. afd. Delta-onderzoek nr 244). According to HANSEN (1945, 1958), discussing its systematics and distribution along the German North Sea coast, the most northern record was from the isle of Fanø. During the present investigation of Skallingen one well-developed phytocenose has been found in which this species is dominant (analyse 56041, Table I). On another bank a few individuals of the species have been discovered occurring in the *Artemisietum maritimae*. This phytocenose, which here may be considered provisionally as a sociation with *Agropyron litorale* of the alliance *Puccinellion maritimae* occurring southwards to the west coast of France, is also an important indicator of the abiotic environmental processes at work on the peninsula. In section 4 the interpretation of this phenomenon will be discussed.

Concerning the classification of the associations into higher floristically defined vegetation units the author agrees with the view of TÜXEN (1937, 1952) who separates the *Salicornia*-associations from the proper salt marsh vegetations. Therefore the distinction of the alliances *Thero-Salicornion* BRAUN-BLANQUET 1930 and *Puccinellion maritimae* (CHRISTIANSEN 1927 p.p.) TÜXEN 1937 is preferred to the *Puccinellio-Salicornion* BRAUN-BLANQUET et DE LEEUW 1936. However, the assertion of BRAUN-BLANQUET and TÜXEN (1952, p. 273) that these alliances can be separated completely according to ecological factors except the salt factor, cannot be accepted. Typical differences in floristic composition should be considered here and other criteria than the fidelity of species ought to be involved.

3.2. *The inner salt marshes*

The lower places of the inner marshes do either not bear any vegetation of Phanerogams or they are covered with scattered individuals of *Salicornia europaea*, perhaps presenting another form than those of the outer marshes (compare KÖNIG, 1939 and CHRISTIANSEN, 1955). The adjacent *Puccinellietum maritimae*, here too, may be divided into two phases (Table II): the lower one linking with the *Salicornietum europeae* and rich in the therophytes *Suaeda maritima* and *Salicornia europaea*, the higher phase with optimal development of *Limonium vulgare* and *Plantago maritima* (the typical form and the *var. dentata* Bl. et Fing.). Therefore the character of the phytocenoses differs from that of the *Puccinellietum maritimae* of the outer marshes. Moreover, *Spergularia marginata* has a greater presence and *Aster tripolium* a greater cover in the first mentioned habitat. On the other hand *Halimione portulacoides* occurs with a smaller cover and, generally, it has a rather more reduced vitality. Finally, physiognomically the association of the inner marshes stands out owing to the reddish colour of *Puccinellia maritima*. All those differences and also the occurrence of *Festuca rubra* and *Glaux maritima* in the high parts of the inner salt marsh association are connected with diversities in soil conditions, particularly the granular composition related to water and salt properties.

The *Puccinellietum maritimae* extends up to the foot of the sandhills. The frequently steep slopes of these hills are covered with a dense turf of *Festuca rubra* sometimes preceeded by a zone — up to about 25 cm — where *Juncus gerardi* is dominant or co-dominant. This narrow *Juncus*-strip of which no analyses has been made, is only found where stagnating water can occur in the *Salicornia* and *Puccinellia* vegetation. The rainspell combined with a storm flood of the preceding days showed this relation very clearly.

In the *Festuca* vegetation *Armeria maritima* is found very sparsely and in the upper zone only. In the whole country of Denmark the species has been observed on higher localities, mostly in and above the storm flood zone. Moreover, in the interior of Jutland it grows rather frequently in habitats, such as sandy areas with heath vegetation (IVERSEN, 1936). This phenomenon is one of the arguments why the name of *Armerieto-Festucetum* BRAUN-BLANQUET et DE LEEUW 1936 does not suit this most important association of the spring-tide zone. Westhoff also pointed to the necessity of re-interpretation of the alliance *Armerion maritimae* (WESTHOFF and VAN LEEUWEN, 1958). Therefore it seems preferable to use the older name of *Juncetum gerardi* (WARMING 1906), TÜXEN 1957. On Skallingen the association shows an affinity to the *Junceto-Caricetum extensae* BRAUN-BLANQUET et DE LEEUW 1936 because of the presence of *Carex extensa*.

In the above mentioned *Festuca* vegetation, in the following *Saginetum maritimae* and in the *Artemisietum maritimae* of the outer marshes *Festuca rubra* (leg. W. G. Beeftink, Herb. Hydrobiol. Inst. afd. Delta-onderzoek nr 226) conforms to the description of *f. litoralis* given by HACKEL (1882, p. 139) and WEBER (1892, p. 212). Although concise the description of Hackel[1]) is clear, consequently the author's name of

[1]) HACKEL (1882, p. 139): forma litoralis humilis, valde repens, panicula brevi (2–4 cm lg.) compacta.

C. A. Weber given by WESTHOFF (1947, manuscript) and TÜXEN (1957), ought to be replaced by Hackel. According to Ir R. DUYVENDAK (verbal communication) who studied the systematics of *Festuca* species, *Festuca rubra f. litoralis* Hack. 1882 clearly differs from *var. genuina* Hack. *subvar. vulgaris* (Gaud.) Hack. and *subvar. arenaria* (Osb.) Hack. Therefore it is justified to maintain the distinction which has been drawn by Hackel and Weber.

Finally the open vegetation at the top of the sandhills belongs to the *Saginetum maritimae* WESTHOFF 1947. From the three faithful species, *Sagina maritima, Plantago maritima var. leptophylla* M. et K. and *Pottia heimii*, only the first two were observed. However, according to ROMOSE (1938), *Pottia heimii* does occur in this association on Skallingen. Probably its occurrence in the analysed vegetations was prevented by high winds blowing away the sand. In the *Saginetum maritimae* a very outstanding form of *Agrostis stolonifera* was observed (leg. W. G. Beeftink, Herb. Hydrobiol. Inst. afd. Delta-onderzoek nr 245). Its stiff shoots and leaves are erect. The plants form little tufts of characteristic withered appearence. The most striking feature however, is the missing of rhizomes and stolons. It is not sure whether the form has a genetic status. Perhaps the, above mentioned, high winds, blowing away the dry sand, may have been instrumental in creating this modification. Probably this form is not found in the Netherlands up to now. IVERSEN (1936) has described it under the name *A. stolonifera var. stricta.* It is doubtful whether this name can be maintained for it was often used previously in the systematic literature on *Agrostis stolonifera.*

4. DYNAMICS OF THE VEGETATION IN CONNECTION WITH ENVIRONMENTAL DEVELOPMENT

The thorough investigation of Skallingens salt marsh vegetation by IVERSEN (1936) in 1931–'34, his comparison of the vegetation at this time with that of 20 years later (IVERSEN, 1952/53), together with the author's investigations, offer a good base for some conclusions about its dynamics in relation to environmental changes in this century and for a prognosis about its future development. However, it is necessary to make restrictions: The investigations of Iversen refer to the vegetation of the whole peninsula and those of the present author only to a part of it. Moreover, the investigation methods of Iversen and the present author are different. Therefore it seems indicated to simplify the data so that a rough classification into three groups of combined cover degree-abundance (BECKING, 1957) — Fr.: dominance-abundance, Ge.: Dominanz-Abundanz — may be made. The author's classification is as follows:

(1) combined cover degree-abundance + and 1, the latter only when presence is evidently smaller than 100 % (dotted lines in Table III);
(2) combined cover degree-abundance 1 and 2 (drawn lines) and
(3) combined cover degree-abundance 3, 4 and 5 (cross-striped lines).

Likewise the data of IVERSEN (1936, 1952/53) from the years 1931–'34 are fitted in these groups by estimation as best as possible.

TABLE II

The halophytic vegetrtion of Skallingen i

The outer salt marshes

Associations in 1931–'34	Salicornietum europaeae	Puccinellietum maritimae variant with Halimione pedunculata: initial phase	Puccinellietum maritimae variant with Halimione pedunculata: phase with Suaeda and Aster	Puccinellietum maritimae variant with Halimione pedunculata: phase with Limonium and Plantago
Associations in 1956	**Salicornietum europaeae**	**Puccinellietum maritimae: initial phase**	**Puccinellietum maritimae: optimal phase**	**Halimionetum portulacoidis**
Salicornia europaea	—++++++++	+++++++++	+++— — — —	— — — — — —
	——————+++	+++++++++	+++++++—	— — — — — —
Puccinellia maritima	—	—++++++++	+++++++++	+++++++—
	—	———++++++	+++++++++	— — — — — —
Halimione pedunculata		— — — — —	————	— — — — — —
Halimione portulacoides		— — — — — —	——————+	+++++++++
Artemisia maritima				— — ——
				— — ++
Agropyron litorale				
Spartina townsendii	———— ——— — —	— ———— —— —	— —	
Aster tripolium		— — ————	+++++++++	———— —
		— — ————	————	—
Suaeda maritima		— ———+++	+++++++++	++— — — —
	—	——++—+++—	—++—++—++	— — — —
Spergularia marginata		— —	— — ————	———— —
		— —	— — —	
Triglochin maritimum			— — — — —	— — — — —
		— ————	— — — — —	— — — —
Limonium vulgare			— — — ——	————
		— — — — ——	— — — — —+	+++++———
Plantago maritima			— — — — — —	—++++++++
			— —	———— —
Festuca rubra				— — ——
				— — ——
Glaux maritima			— — —	— — — — — —
Juncus gerardi				
Armeria maritima				

1931-'34 *(the upper lines)* 1956 *(the lover lines)*.

	The inner salt marshes				
Artemisietum maritimae	Salicornietum europaeae	Puccinellietum maritimae: phase rich in therophytes	Puccinellietum maritimae: phase with Aster and Plantago	Juncetum gerardi	Saginetum maritimae
Artemisietum maritimae	Salicornietum europaeae	Puccinellietum maritimae: phase rich in therophytes	Puccinellietum maritimae: phase with Limonium and Plantago	Juncetum gerardi	Saginetum maritimae
—	——+++++++	+++++++++	+++—— — —	— —	—
- —	——+++++++	+++++++++	+++—— — — -		— — — — —
— —	— — —	+++++++++	+++++++——	—	
—	— — —	+++++++++	+++++++——		
— — —	— —	— — — — — —	— — —	— —	—
+++— — — —		— — — — — —	————	— — — — —	— — — — —
————				— — — — —	— — — — —
—++—++——			—	— —	— — —
— +++					
— —		— — — — ——	++++++++—	———— — —	
		— — — — ——	————	— —	
- — —	— —	———— —	— — — —	— —	—
	— —	———— —	— — — — — —		— —
— —		— — — ——	————	—	
		— — — ——	— — — —		
—		— — — ——	————	———— — —	—
		— — — — — —	— — — — — —	— — — — —	
——— — —		— — — — —	— — ——— —	— — — — —	
————		— — — — ——	——++——+++	———— — —	— — — —
+++++++++		— —	— — — ——++	——— — — —	————
— — — — — —		— —	— — ——++	——— — — —	————
+++++++++			— — —	+++++++++	+++++++——
+++++++++			— — —	+++++++++	+++++++——
— — — — — —			— — — — —	— — — — — —	— — — —
			— — —		
— — — — —			—	++— — — — —	— — — —
				++— — — —	— — — —
— — —				— —	— — ———
				— —	— — ———

The changes in the abiotic environment discussed in the second section induce the vegetation to react: (1) with extension or shrinking of the potential ecological amplitudes of taxa directly consequent on changes of abiotic habitat factors in favourable resp. unfavourable sense; (2) with disturbing the equilibrium in the mutual influences of individual organisms and taxa due to changes in competition power in consequence of (1) and resulting in shifting the actual ecological amplitudes. Without experiments these two aspects cannot be distinguished in vegetational changes and therefore we are now only able to make some suppositions.

In Table III the most important halophytes have been assembled with their actual ecological amplitudes and optima in 1931–'34 (the upper lines) and in 1956 (the lower lines). The most striking feature is the invasion of *Halimione portulacoides*. According to GABRIELSEN and IVERSEN (1933) in 1909, when Raunkiaer studied the vegetation of Skallingen, this species was not observed. In 1931 a few specimens were discovered and in the following years the number greatly increased (GABRIELSEN and IVERSEN, 1933). Nowadays *Halimione* is very abundant, especially in a zone between *Puccinellia maritima* and *Festuca rubra*. According to HULTÉN (1950) it reaches its northern limit on Skallingen and consequently it might be supposed that its area had extended in the last decennia as a consequence of climatic factors. Yet the author is inclined to attribute its extension on the outer marshes mainly to favourable conditions of sedimentation. The study of salt marsh vegetation in the S.W.-Netherlands indicated that *H. portulacoides* prefers well-aerated silty banks along tidal creeks. In the Wadden Sea from the Netherlands till Denmark these banks are generally rare and so the species is but sparsely presented there. Once established it is able to endure accumulation of sand very well (CHAPMAN, 1934 and the author's experience). Its extension in the inner marshes might be connected with sedimentation also, but probably the actual presence of an important centre of diaspores in the outer marshes preponderates here while sedimentation of silt is insignificant.

Halimione pedunculata — another "halophyte pur sang" — has its optimal development in the salt steppes of Central Europe, especially those of Germany (WESTHOFF, 1947 manuscript; WENDELBERGER, 1950). The western and northern limit of its geographical area is reached on the Atlantic and Baltic coasts. On Skallingen it had its optimum in the *Puccinellietum maritimae*, while it also regularly occurred in the *Artemisietum maritimae*, *Juncetum gerardi*, *Junceto-Caricetum extensae* and *Saginetum maritimae* but with very little frequency (IVERSEN, 1936 p. 187–193). Its coastal occurrence depends on the presence of an open vegetation which is often connected with a sandy substratum. It is not sure which factor preponderates but according to WESTHOFF (1947, manuscript) it may be the first one. Sedimentation of silt promotes a dense growth of *Puccinellia maritima*, especially when there is no intensive grazing. This phenomenon combined with the increased competition power of *H. portulacoides* may have caused the disappearance of *H. pedunculata* in the investigated strip.

Next to *H. portulacoides Limonium vulgare* has spread very much. Its favourable reaction on sedimentation of silt seems evident on the outer marshes but does not give a sufficient explanation of the extension on the inner marshes. The creation of a centre of diaspores on the first ones may be a factor but its effect is perhaps not as marked as in the case of *H. portulacoides* owing to the fact that the initial population of 1931–'34 was only slightly smaller than the present one. The competition power of *Limonium vulgare* is large, for it was able to extend having an optimum which strongly coincides with that of *H. portulacoides*. However, the analyses 56053 and 56055 ought to be considered as transitions in time and not geographically, starting from a terminal phase with *Limonium* and *Plantago* of the *Puccinelietum maritimae* to the *Halimionetum portulacoidis*. The third species which prefers silty soils is *Artemisia maritima* but only to a certain extend as will be pointed out further on.

The extension of *Halimione portulacoides* and *Limonium vulgare* may result in a shrinking of the ecological amplitude of *Puccinellia maritima, Aster tripolium, Suaeda maritima, Spergularia marginata* and *Plantago maritima* on the outer marshes and of *Aster tripolium, Spergularia marginata* and *Triglochin maritimum* on the inner marshes. Except for *Plantago maritima* probably the changed soil texture conditions are not important, for these species seem to be fairly indifferent in this respect (for *Aster* compare CLAPHAM, PEARSALL and RICHARDS, 1942). The large frequency of *Triglochin maritimum* in 1931–'34 on the inner marshes compared with that on the outer marshes points to local stagnant water in the first mentioned marshes, a phenomenon already indicated in section 3.2 in connection with *Juncus gerardi*. Therefore it is possible that the ecological amplitude of *Triglochin* on the inner marshes was more influenced by those soil water conditions than by the increased competition power of *Halimione* and *Limonium*. Likewise the extension of *Triglochin* on the outer marshes may be explained by the larger water content of the soil, a result of the more clayey character. Compared with the situation in 1931–'34 *Salicornia europaea* has extended on somewhat higher levels. This phenomenon, too, may be connected with progressive sedimentation during the last decennia, the result of this proces being a changed granular composition of the upper soil layers promoting a slightly higher salt content of the soil-liquid, owing to reduced leeching of salts in the, now heavier, soils.

In 1931–'34 the *Artemisietum maritimae* showed a floristic composition related to the *Armerion maritimae* on account of the occurrence of *Glaux maritima, Juncus gerardi* and *Armeria maritima*, which last three species are absent today in the investigated part of the outer marshes. At present, on isolated localities, *Agropyron litorale* is superseding the *Artemisietum maritimae*. In the S.W.-Netherlands the author encountered *Agropyron litorale* ousting the *Artemisietum maritimae* on localities, where the banks were silted up with much fine material. These floristic changes may therefore be regarded as results of the heavier character of the soils along the banks of the tidal creeks, as described earlier.

On the outer marshes the following synecological trends may be considered as a reaction on environmental development: (1) A transition of the final phase of the *Puccinellietum maritimae* with *Limonium* and *Plantago* as co-dominants into the *Halimionetum portulacoidis*. (2) A more optimal development of the *Artemisietum maritimae* on account of the disappearance of elements of the *Armerion maritimae*. (3) At a few localities the establishing of a sociation with *Agropyron litorale* from the *Artemisietum maritimae*.

On the outer marshes sedimentation of silt has already made great progress. Owing to the relatively high position of the marshes related to MHW-level only high floods mostly combined with storms are able to cover the marshes. The feature of these floods is a mostly very turbulent condition of the water. Therefore the proportion between sand and silt of the material deposited will shift in favour of the sand fraction the higher the marshes have been built up, for silt is only able to settle in relatively calm water. For this reason it is to be expected that on the outer marshes of Skallingen in the future the material deposited will increase its sandier character once more in some degree. The expansion of *Agropyron litorale*, depending to a great extend on a relatively high silt content of the banks, will therefore probably remain confined to a few banks unless the existence of centres of diaspores enables the species to conquer the banks in spite of the *Artemisietum maritimae*. The latter progress, however, depends on the granular composition of the bank soils which was not studied. Finally, we may expect the *Halimionetum portulacoidis* to develop still further especially at the cost of the *Puccinellietum maritimae*, at present in the basins growing in its optimal phase.

On the inner marshes the modification of the floristic composition of the associations is less spectacular than on the outer marshes. Possibly only the increase of *Limonium vulgare* and the decrease of *Aster tripolium* will necessitate a change in the denomination of the highest situated phase of the *Puccinellietum maritimae*. Owing to the limited extend of these changes it is not to be expected that the vegetation of the inner marshes will change much in the future.

SUMMARY

During the excursion of the International Society for Plant Geography and Ecology in 1956 the author was in a position to stay some days at Skalling-Laboratory to study the salt marsh vegetation of the Peninsula (Fig. 1). In the past 25 years silt has been deposited mainly on a strip along the Wadden Sea coast, the so-called outer marshes. These sedimentation conditions have created a bank-and-basin-landscape (Fig. 2). The inner marshes have been modificated only slightly in this respect.

The vegetation of an ungrazed strip overlapping both outer and inner salt marshes is described in detail. On the outer marshes the following communities are distinguished: *Zosteretum nanae* (fragmentary), *Salicornietum europaeae*, *Puccinellietum maritimae* divided into an initial and an optimal phase, *Halimionetum portulacoidis*, *Artemisietum maritimae* and very scarcely, a sociation with *Agropyron litorale*, a species which is new for Skallingen. The different views about synsystematic limitation of the *Artemisietum maritimae* are discussed in detail; the author agrees with the view of Weevers (1940). From the inner marshes are described: *Salicornietum europaeae*, *Puccinellietum maritimae* divided into a phase rich in therophytes and a phase with *Limonium vulgare* and *Plantago maritima*, *Juncetum gerardi* and *Saginetum maritimae*. The taxonomy of the forms of *Festuca rubra* and *Agrostis stolonifera* occurring on these

marshes is discussed briefly. Arguments for a change of the association's name from *Armerieto-Festucetum* to the older name of *Juncetum gerardi* are tentatively proposed. A separation of the *Puccinellio-Salicornion* into the alliances *Thero-Salicornion* and *Puccinellion maritimae* is preferred and discussed briefly.

The vegetation was found to react to changes in the environment with the establishment and extension of *Halimione portulacoides* and the extension of *Limonium vulgare* and *Artemisia maritima*. *Halimione pedunculata* disappeared as well as *Glaux maritima*, *Juncus gerardi* and *Armeria maritima* in the *Artemisietum maritimae*. On the outer marshes species decreasing their ecologic amplitude and partly their cover are *Puccinellia maritima*, *Aster tripolium*, *Suaeda maritima*, *Spergularia marginata* and *Plantago maritima*. Contrary to the above mentioned species *Salicornia europaea* and *Triglochin maritimum* have extended on the outer marshes in consequence of progressive sedimentation resp. changed soil water conditions.

Finally synecological trends have been discussed. The most important ones are the development of the *Halimionetum portulacoidis* and the establishment of a sociation with *Agropyron litorale* on the outer salt marshes. It is expected that these trends will proceed on a limited scale in the future.

ACKNOWLEDGMENTS

The author wishes to express his sincere gratitude to the direction of the Skalling-Laboratory for its hospitality. His further indebtedness goes to Dr J. Iversen (Charlottenlund) for much information on the history of Skallingens vegetation and landscape; to Dr Ir B. Verhoeven (Kampen) for placing at his disposal some data about soil-properties; to Ir R. Duyvendak (Wageningen) for assistance in taxonomic problems of *Agrostis stolonifera* and *Festuca rubra;* to Mr A. Hansen (Copenhagen) for the identification of *Agropyron litorale;* to Miss Dr J. Th. Koster (Leiden) for the identification of Lyngbya digueti; to Dr V. Westhoff (Bilthoven) for the loan of the manuscript of his thesis; and to Dr K. F. Vaas (Yerseke) who kindly corrected the English text.

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Acta Botanica Neerlandica **8** *(1959)*

ERRATUM

SOME NOTES ON SKALLINGENS SALT MARSH VEGETATION AND ITS HABITAT

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RECTIFICATION of the publication in the Acta Botanica Neerlandica **8** (4), 1959: 449-472.

Owing to an oversight Table III of the above article, on p. 466-467, was wrongly composed, and does not correspond with the text of Section 4 of the article.

It was decided to reprint the table and the reader is requested to ignore p. 466 and 467 of the original text.

The halophytic vegetation of Skallingen in

The outer salt marshes

Associations in 1931–'34	Salicornietum europaeae	Puccinellietum maritimae variant with Halimione pedunculata: initial phase	Puccinellietum maritimae variant with Halimione pedunculata: phase with Suaeda and Aster	Puccinellietum maritimae variant with Halimione pedunculata: phase with Limonium and Plantago
Associations in 1956	**Salicornietum europaeae**	**Puccinellietum maritimae: initial phase**	**Puccinellietum maritimae: optimal phase**	**Halimionetum portulacoidis**
Salicornia europaea	—+++++++++	+++++++++	+++— — — —	— — — — — — —
	————+++	+++++++++	+++++++—	— — — — — —
Puccinellia maritima	—	—++++++++	+++++++++	++++++++—
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Halimione pedunculata		— — — — —	————	— — — — — —
Halimione portulacoides				— — —
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Artemisia maritima				— — —
				— — ++
Agropyron litorale				
Spartina townsendii				
	——— — — —	——— — —	— —	
Aster tripolium		— — ————	+++++++++	———— —
		— — ————	————	—
Suaeda maritima		— ——+++	+++++++++	++— — — — —
	—	——++—+++—	—++—++—++	— — — —
Spergularia marginata		— —	— — ———	——— — —
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Triglochin maritimum			— — — — —	— — — — — —
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Limonium vulgare			— — — ——	————
		— — — — —	— — — — —+	+++++———
Plantago maritima			— — — — — —	—+++++++++
			— —	——— —
Festuca rubra				— — —
				— — —
Glaux maritima			— — — —	— — — — — — —
Juncus gerardi				
Armeria maritima				

TABLE III

1931-'34 *(the upper lines)* and in 1956 *(the lower lines)*.

	The inner salt marshes				
Artemisietum maritimae	Salicornietum europaeae	Puccinellietum maritimae: phase rich in therophytes	Puccinellietum maritimae: phase with Aster and Plantago	Juncetum gerardi	Saginetum maritimae
Artemisietum maritimae	Salicornietum europaeae	Puccinellietum maritimae: phase rich in therophytes	Puccinellietum maritimae: phase with Limonium and Plantago	Juncetum gerardi	Saginetum maritimae
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