Effects of five years of grazing on a salt-marsh vegetation

*A study with sequential mapping**

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Abstract

In a salt-marsh, which was ungrazed from 1958 to 1971, grazing was reintroduced in 24 out of 32 ha from 1972 onwards. Vegetation changes under these conditions were investigated. The area studied is part of a larger grazed area of ca. 110 ha, grazed with a stocking rate of 1.3–1.7 cattle, ha. from May to October. This allowed a comparison between vegetation development under continued ungrazed conditions and under the reintroduction of grazing. A quantitative comparison has been made, based on sequential detailed mapping in 1971 and 1976.

The ungrazed area shows a progressive succesion. Because of the erosive coast this is not the succession of a developing salt-marsh but rather a 'recovery' succession, after grazing was stopped in 1958. Drift deposits appear to play an important role.

The grazed marsh shows successional trends in some areas, but in others signs of retrogressive succession were seen. The vegetation becomes more open, alpha- and beta-diversity increase and the vegetation develops in a more intricate pattern while some vegetation boundaries seem to become more distinct, especially on the higher salt-marsh. The large extension of *Saginion maritimae* types is remarkable and is probably caused by a combined effect of warm, dry summers and grazing. Further investigation is required to test whether local qualitatively different changes in communities are caused by different grazing intensities. The ungrazed area becomes more rugged, a process that can be effectively reversed by grazing.

Introduction

Comparisons between grazed and ungrazed salt-marshes are usually made at one point in time (Beeftink, 1965, 1977a; Schmeisky, 1974) and in such studies descriptions of the vegetation successions are often speculative. Long term and detailed (permanent quadrat (p.q.)) observations are a prerequisite for understanding and eventually predicting successions (Beeftink, 1965, 1977a). Westhoff (1969) and Westhoff & Sykora (1979) studied the effect of desalinization on the *Juncetum gerardii*, one p.q. being enclosed against grazing and mowing, which continued in the other. The enclosed area became rugged due to litter accumulation. A similar result following the cessation of grazing was reported by Schmeisky (1974), and Bakker (1978). The traditional practice of grazing salt-marshes is being discontinued throughout Western Europe (Beeftink, 1977b).

Grime's (1978) general assertion that a high standing crop (including litter) is related to a small number of species, suggests that discontinuing

* Nomenclature of taxa follows Heukels & Van Ooststroom (1977), that of syntaxa Westhoff & Den Held (1969).

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grazing will lead to a diminished species diversity.

In a previous paper (Bakker, 1978) a comparison of grazing and mowing, based upon p.q.'s, was published for five plant communities. As the number of communities in the study area was rather high and it was difficult to foresee where interesting and/or representative changes would take place, a complementary study to the p.q. data is necessary. The best method for the investigation of succession is a combination of a restricted number of p.q.'s and successive mapping (Londo, 1974). Moreover, successive mapping enables vegetation changes to be followed in specific areas and these changes to be related to differences in grazing intensity.

The main objective of the study was to obtain data on vegetation dynamics resulting from renewed grazing. Special attention will be given to successions and the time required to reach some state of equilibrium. The results based on five year's measurements must be regarded as preliminary.

Methods

The study area of 32 ha is part of the Oosterkwelder of Schiermonnikoog, one of the Dutch Frisian Islands (53°30′N, 6°10′E). The study area has a cliffed, eroding coast. The lower salt-marsh occurs behind the levees bordering the tidal flats and creekbanks. The mid- and upper salt-marsh, including depressions with poor drainage, occur inland from the lower salt-marsh and contain low dunes with gradients to the creekbank levees. The study area had been grazed by young cattle up to 1958 when it was stopped. It was reintroduced in 1972 in such a way that 8 ha remained ungrazed, enabling a comparative study of the vegetation response to grazing (see Bakker, 1978 for further details).

A vegetation map at scale 1 : 1000 was made of the study area before grazing in 1971 (Prins, 1976). For the present study the area was remapped in 1976 (Norder & Ruyter, 1977). The different communities were characterized in 1971 from 150 relevés, according to the Braun-Blanquet approach, at places with a deviating species composition and/or physiognomy of the vegetation. Several communities were dominated by a single species which probably strongly influenced the structure and species composition of the community. Grazing may have affected the dominant species, enhancing already existent, but masked vegetation differences. Hence certain communities are best mapped on the basis of the dominance of a single species or a few species, whereas in others the entire species composition plays a more important role (cf. Londo, 1974).

In 1976 about 200 relevés were made. Those who mapped in 1971 verified the description of the communities. All relevés were arranged in synoptic tables from which community types (coena) are derived (cf. Westhoff & van der Maarel, 1978 for method and terms). For a comparison the 1976 map was overlaid with a transparancy of the 1971 map. The distribution of the communities in 1971 and 1976 was worked out for each separate point by means of a dot grid with a dot spacing of 0.5 cm. This enabled a study of changes in communities and the areas of the different communities to be calculated (400 points equals 1 ha).

An area ca. 2 ha (the *Juncus maritimus*/*Elytrigia* spp.* complex in 1971) was not included in the calculations because it had not been mapped in sufficient detail in 1971. Corrections had to be made for bias resulting from difficulties in field orientation, a problem inherent in repeated mapping. Such corrections are indicated as F-changes (F = False). Sometimes a community was found in 1976 within a larger area of an unrelated one. Such 'changes' are characterized as D-changes (D = Detail) based on the assumption that these communities already existed in 1971 but were too small to map at that time.

In order to locate the changes, the study area was subdivided by a 50 × 50 m grid. The percentage change, based on the dot grid points with a different community in 1976 compared to 1971, was calculated for each grid cell. (Since there are 100 points per 50 × 50 m cell the number of such points gives the required percentage).

The change in number of vegetation boundaries in relation to the 1971 number, per grid cell (as a measure for the coarseness of vegetation pattern) is calculated for the two maps. For clarity's sake

* *Elytrigia* spp. means *Elytrigia pungens* incl. *Elytrigia x obtusiuscula* both are met with and often mixed. *E. x obtusiuscula* seems to have its optimum somewhat higher with respect to Above Ordnance Date (A.O.D.) on the salt-marsh than *E. pungens*.

aerial photographs (taken in 1976) of parts of the salt-marsh, as well as vegetation maps of the same areas are given.

Besides effects of grazing on the vegetation as a whole an attempt is made to summarize the effect of grazing (combination of selective removal of the above ground parts, trampling, manuring) on single species. Criteria for positive, negative, indifferent and local disparities are defined in terms of cover and area.

Results

Communities

The coena of the lower salt-marsh (Table 1, Fig. 1)

On the lower salt-marsh (1.20–1.30 m A.O.D.) the alliance *Puccinellion maritimae* is represented in the coena 1b, 1c, 1d and 1e.

Coenon 1a. Comm. of *Puccinellia maritima* and *Spartina anglica.*

This coenon can be regarded as a degeneration phase (Beeftink 1965) of the *Salicornietum strictae* of the alliance *Thero-Salicornion* with elements of the *Suaedetum maritimae* of the *Thero-Suaedion* probably due to drift material of dead algae. It can be observed on creek sides and in small creeks which are regularly flooded and continuously accreting sediments. On the grazed area the *Suaeda maritima* cover is very small, while *Aster tripolium, Halimione portulacoides* and *Spartina anglica* are absent.

Coenon 1b. Comm. of *Puccinellia maritima* and *Aster tripolium*

Coenon 1c. Comm. of *Puccinellia maritima* and *Limonium vulgare*

Coenon 1d. Comm. of *Puccinellia maritima* and *Plantago maritima*

These three coena often occur on gradients in depressions, coenon 1b can be observed on the lowest places, coenon 1c is found somewhat higher and coenon 1d occurs slightly higher again. Coenon 1b can be assigned to the *Puccinellietum maritimae typicum.* It occurs on creek sides and in small irregularly flooded creeks. The cover of *Suaeda maritima, Puccinellia maritima, Aster tripolium, Spartina anglica* and *Spergularia media* is small on the grazed area. According to Beeftink (1965) coenon 1c should be classified as *Puccinellietum maritimae* variant with *Limonium vulgare.* Coenon 1d can be

Table 1. Synoptic table of the lower salt-marsh.

Coenon	1 a	1 b	1 c	1 d	1 e
	Community of Puccinellia maritima and Spartina anglica	Community of Puccinellia maritima and Aster tripolium	Community of Puccinellia maritima and Limonium vulgare	Community of Puccinellia maritima and Plantago maritima	Community of Puccinellia maritima and Halimione portulacoides
No. of relevés	7	13	3	15	2
Spartina anglica	58(+ - 1)	22(r - 2)	.	26(+ - 1)	50(+)
Suaeda maritima	100(1 - 4)	78(r - 5)	100(2 - 4)	65(+ - 2)	100(+ - 1)
Salicornia europaea	86(+ - 2)	78(+ - 2)	100(+ - 1)	65(+ - 2)	100(+)
Puccinellia maritima	100(1 - 2)	100(1 - 3)	100(+ - 2)	100(+ - 3)	100(2)
Aster tripolium	72(+ - 1)	85(r - 2)	33 (r)	65 (+ - 2)	50 (+)
Glaux maritima	14(+)	62(1 - 2)	100(+ - 2)	81(r - 2)	.
Juncus gerardii	14(+)	18(2)	.	59(+ - 3)	.
Atriplex hastata	58(r - 1)	38(+ - 1)	.	43(+ - 1)	.
Halimione portulacoides	42(r - 1)	46(+ - 2)	.	39(r - 1)	100(5)
Triglochin maritima	14(r)	78(+ - 2)	100(1 - 2)	100(+ - 2)	.
Spergularia media	58(r - 1)	53(r - 1)	33(1)	87(+ - 2)	50(+)
Plantago maritima	14(r)	46(+ - 2)	67(+ - 2)	100(+ - 2)	50(1)
Artemisia maritima	14(r)	38(r - 1)	33(r)	93(r - 2)	100(r - 2)
Spergularia marina	.	18(+ - 1)	67(+ - 1)	13(+)	.
Limonium vulgare	.	78(r - 2)	100(2 - 3)	87(+ - 3)	.
Elytrigia spp.	.	8(1)	.	.	.
Cochleraria danica	.	.	.	19(r - +)	.
Agrostis stolonifera	.	.	.	19(r - +)	.
Armeria maritima	.	.	.	19(r - +)	.
Festuca rubra	.	.	.	52(r)	50(1)

assigned to the *Plantagini-Limonietum. Halimione portulacoides* is restricted to the ungrazed area.

Coenon 1e. Comm. of *Puccinellia maritima* and *Halimione portulacoides.*

This coenon is identical with the *Halimionetum portulacoidis.* It can be observed on creek sides and small silted creeks and is restricted to the ungrazed area.

The coena of the mid and the upper salt-marsh (Table 2, Fig. 1)

The coena of the mid and upper salt-marsh comprise representatives of the alliances *Puccinellion maritimae,* of the *Armerion maritimae* and of the *Agropyro-Rumicion crispi.* Gradients from a depression or silted up creek on the lower salt-marsh to a creek bank levee often occur producing a zonation of comm. 1b, 1c, 1d, 6a, 6b, 3a. On the higher salt-marsh gradients from a depression to a low dune can be observed producing a zonation of comm. 2, 6d, 6f, 6g, 7, 8a, 8b.

Coenon 2. Comm. of *Juncus gerardii* and *Glaux maritima.*

This coenon can be assigned to the *Juncetum gerardii typicum* of the *Armerion maritimae.* It can be observed in hollows between the low dunes and in a depression (1.50 m A.O.D.) with often stagnant salt water or fresh water. On the ungrazed area the *Juncus gerardii* cover is large and *Plantago maritima* is often absent, whilst the cover of *Glaux maritima, Triglochin maritima* and *Puccinellia maritima* is large on the grazed area.

Coenon 3a. Comm. of *Artemisia maritima* and Puccinellia maritima.

Coenon 3b. Comm. of *Artemisia maritima* and *Juncus maritimus.*

These two coena represent the *Artemisietum maritimae* of the *Armerion maritimae.* Coenon 3a can be considered as *Artemisietum maritimae typicum.* It occurs on the levee along the tidal flats (1.30–1.60 m A.O.D.). On the grazed area *Juncus gerardii* and *Triglochin maritima* are found, while the *Plantago maritima* cover is larger on the grazed area. Coenon 3b occurs on the gradient of the lower salt-marsh to the creek bank levees (1.40 – 1.80 m A.O.D.). *Poa pratensis, Glaux maritima,*

Table 2. Synoptic table of the mid- and upper salt-marsh.

Coenon	2	3a	3b	4a	4b	4c	5a	5b	6a	6b	6c	6d	6e	6f	6g
	Community of Juncus gerardii and Glaux maritima	Community of Artemisia maritima and Puccinellia maritima	Community of Artemisia maritima and Juncus maritimus	Community of Juncus maritimus and Puccinellia maritima	Community of Juncus maritimus and Potentilla anserina	Community of Juncus maritimus and Elytrigia spp.	Community of Elytrigia spp. and Artemisia maritima	Community of Elytrigia spp. and Halimione portulacoides	Community of Festuca rubra and Puccinellia maritima	Community of Festuca rubra and Glaux maritima	Community of Festuca rubra and Agrostis stolonifera	Community of Festuca rubra and Juncus gerardii	Community of Festuca rubra and Artemisia maritima	Community of Festuca rubra and Carex distans	Community of Festuca rubra and Elytrigia spp.
No. of relevés	15	17	9	12	20	6	12	17	20	15	9	18	4	28	18
Festuca rubra	80(1-2)	100(1-4)	100(1-3)	100(1-2)	100(1-4)	100(2-3)	85(2-3)	77(+-3)	100(2-4)	100(2-5)	100(2-4)	100(1-3)	100(2-4)	100(2-5)	100(1-3)
Agrostis stolonifera	93(+-2)	12(+-1)	67(+-2)	50(1-2)	85(+-2)	83(r-2)	26(1-2)	12(1)	10(1-2)	52(r-2)	77(+-2)	100(1-3)	100(+-2)	89(+-2)	44(+-2)
Plantago maritima	77(+-3)	42(r-2)	17(1)	25(r-+)	70(+-1)	50(+-2)	17(+1)	12(r-+)	100(+-2)	93(1-2)	100(1-2)	94(1-2)	25(1)	100(1-2)	66(+-2)
Atriplex hastata	75(+-1)	94(r-2)	100(+-2)	100(r-2)	85(r-2)	83(+-1)	100(+-2)	88(r-2)	90(r-1)	80(r-2)	33(r-2)	61(r-1)	.	64(r-+)	33(+-1)
Artemisia maritima	33(r-1)	100(2-5)	100(2-4)	100(r-2)	40(r-1)	34(+-1)	68(r-1)	29(r-2)	100(1-4)	100(r-2)	100(r-+)	50(r-+)	100(1-2)	45(r-1)	28(r-+)
Aster tripolium	.	6(r)	.	17(+)	.	.	.	12(r-+)	10(+)	13(r)	11(r)	.	.	.	.
Puccinellia maritima	45(+-2)	36(1-2)	11(1)	25(r-2)	.	.	.	.	50(+-3)	26(1-2)	11(r)	.	.	.	.
Triglochin maritima	87(+-2)	30(r-2)	17(1)	25(+-2)	10(+-1)	.	.	.	70(r-2)	67(+-2)	33(+-1)	17(r-1)	.	14(r-1)	.
Limonium vulgare	7(r)	18(r-+)	.	9(r)	5(1)	17(r)	.	.	100(+-2)	93(+-2)	100(+-2)	6(+)	50(r-+)	4(1)	.
Spergularia media	20(r-1)	30(r-1)	.	17(r)	5(r)	.	.	12(r-+)	30(r-1)	13(+-1)	.	17(+-1)	.	7(r)	6(r)
Suaeda maritima	.	12(r-1)	.	17(r-+)	5(r)	.	.	6(+)	40(r-+)	19(r-+)	.	.	25(r)	.	6(r)
Salicornia europaea	7(r)	18(r-+)	.	17(r-+)	5(+)	17(r)	9(+)	6(r)	55(r-+)	40(r-1)	11(r)	17(r)	25(r)	4(r)	.
Halimione portulacoides	.	30(r-1)	22(r)	.	.	.	9(r)	83(+-3)	25(r-+)	7(r)	.	.	25(r)	.	.
Juncus gerardii	100(2-4)	18(+-2)	.	9(2)	10(1-2)	.	.	.	55(+-2)	67(+-3)	66(+-2)	100(1-2)	.	43(+-2)	6(+)
Glaux maritima	100(+-2)	18(r-+)	33(1)	59(r-1)	70(+-2)	83(r-1)	9(1)	6(+)	70(r-2)	80(r-2)	44(1)	50(r-2)	.	39(+-2)	.
Potentilla anserina	.	.	.	17(+-1)	85(r-2)	83(1-2)	.	6(+)	.	7(1)	.	72(r-2)	75(+-1)	36(r-2)	39(r-+)
Elytrigia spp.	.	.	11(1)	42(+-2)	20(1-2)	83(+-2)	100(2-4)	100(2-5)	15(+-1)	7(+)	11(1)	11(+-1)	100(+-2)	7(+-1)	100(+-3)
Juncus maritimus	.	.	100(2-3)	100(2-4)	100(2-3)	100(1-2)	100(1-3)	12(+-2)	.	.	.	.	.	4(+)	.
Poa pratensis	.	.	11(1)	17(r-+)	40(+-2)	67(+-3)	51(r-2)	12(+)	.	.	.	44(+-2)	25(2)	68(r-2)	100(+-2)
Armeria maritima	26(r-2)	.	.	.	15(r-+)	17(1)	.	.	40(r-+)	67(r-1)	100(+-2)	94(1-2)	25(2)	96(r-2)	89(+-2)
Cerastium semidecandrum	.	.	17(r)	.	.	.	.	.	.	.	.	.	.	4(r)	17(r)
Spergularia marina	.	.	.	9(r)	5(r)	.	.	12(r-+)	5(+)	17(r-+)	.	.	25(r)	.	.
Polygonum aviculare	.	.	.	.	.	.	.	6(+)	.	.	.	11(+)	.	.	.
Stellaria graminea	.	.	.	.	.	17(+)	.	.	.	.	.	.	.	4(1)	.
Odontites verna	.	.	.	.	.	.	.	.	.	.	.	7(1)	.	4(r)	.
Carex distans	.	.	.	.	.	.	.	.	.	.	22(+-1)	22(r-1)	.	50(+-1)	11(r)
Trifolium repens	.	.	.	.	.	.	.	.	.	.	.	22(1-2)	25(+)	25(r-2)	11(r-+)
Plantago coronopus	.	.	.	.	.	.	.	.	.	.	.	.	25(r)	7(r-+)	17(r-1)
Lotus corniculatus	.	.	.	.	.	33(+)	.	.	.	.	11(r)	6(2)	.	14(+-2)	50(r-1)

Addenda:

Spartina anglica	3a	(6,r)	Sagina maritima	5b	(6,1)	Holcus lanatus	6f	(4,+)
Vicia cracca	4b	(5,1)	Atriplex littoralis	5b	(6,r)	Ononis spinosa	6f	(4,1)
Cochlearia danica	4b	(5,r)	Carex extensa	6c	(4,r)	Agrostis tenuis	6f	(4,+)
Phragmites australis	4c	(17,r)	Leontodon autumnalis	6f	(4,r)	Plantago lanceolata	6g	(7,r)
Bupleurum tenuissimum	5a	(9,r)	Sonchus arvensis	6f	(4,r)	Festuca ovina	6g	(7,+)
Cerastium holosteoides	5b	(6,r)	Stellaria media	6f	(4,r)	Elytrigia repens	6g	(14,+-2)

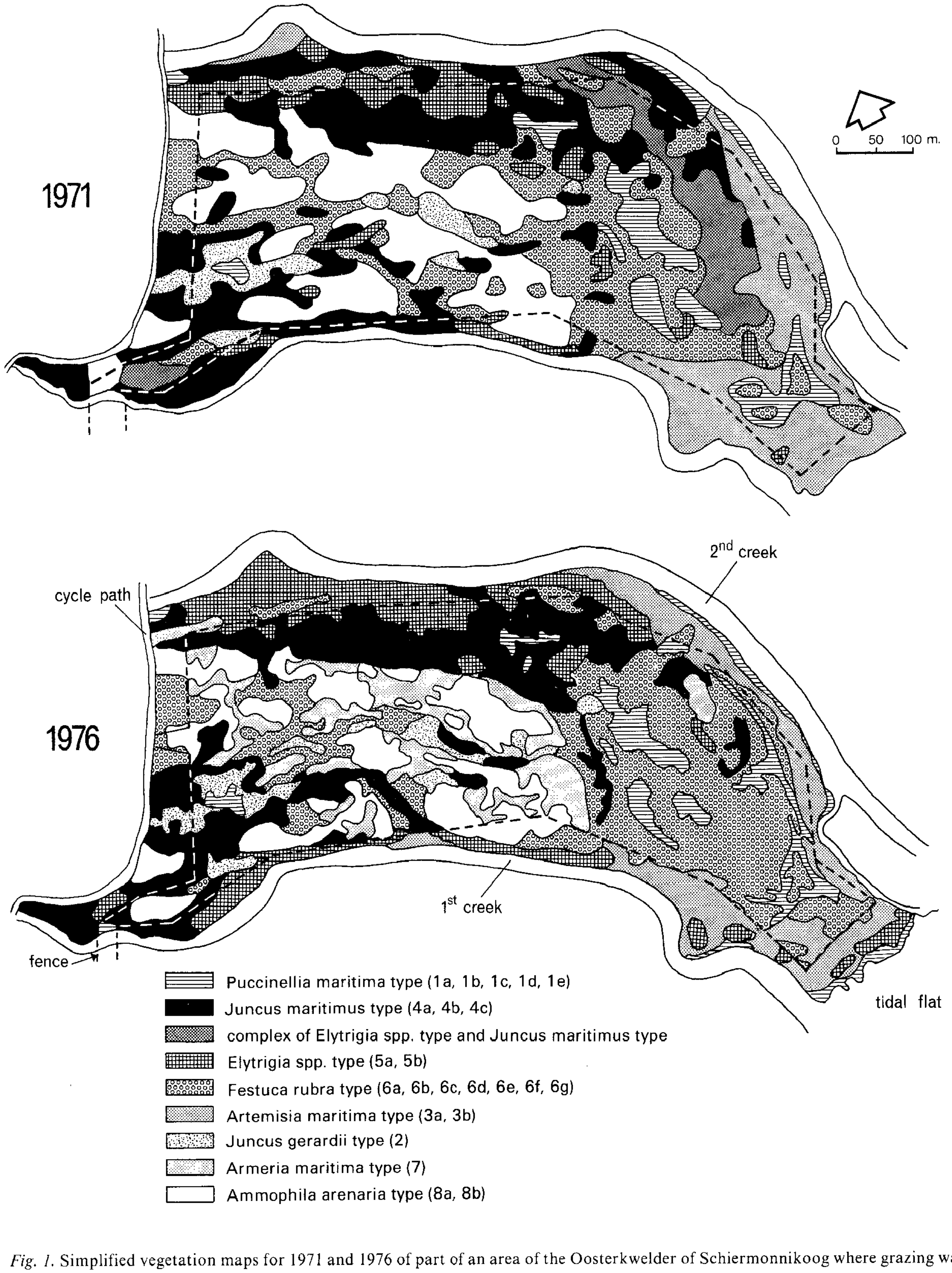


Fig. 1. Simplified vegetation maps for 1971 and 1976 of part of an area of the Oosterkwelder of Schiermonnikoog where grazing was reintroduced in 1972.
Communities are characterized by dominant species according to Prins (1976) and Norder & Ruyter (1977), resp.

Triglochin maritima and *Puccinellia maritima* are restricted to the grazed area.

Coenon 4a. Comm. of *Juncus maritimus* and *Puccinellia maritima*

Coenon 4b. Comm. of *Juncus maritimus* and *Potentilla anserina*

Coenon 4c. Comm. of *Juncus maritimus* and *Elytrigia* spp.

These three coena have representatives both of the *Armerion maritimae* and of the *Agropyro-Rumicion crispi*. In coenon 4a *Artemisia maritima* is a differential species. Coenon 4a differs from coenon 3b by the small *Artemisia maritima* cover and occurs on low parts of the higher salt-marsh and on the gradient of the creek bank levees to the low dunes (1.40 - 1.80 m A.O.D.). *Puccinellia maritima, Salicornia europaea, Suaeda maritima* and *Spergularia media* occur only on the grazed area. Coenon 4b can be considered as a typical variant (no differential species). It occurs on the gradient of the higher salt-marsh to the low dunes and in depressions (1.50 - 1.70 m A.O.D.). The cover of *Juncus maritimus* and *Atriplex hastata* is large on the ungrazed area. Coenon 4c is a transition to the alliance *Angelicion litoralis* with *Elytrigia* spp. as differential species. This coenon can be observed on the gradient of the creekbank levees to the low dunes (1.60–1.90 m A.O.D.).

Coenon 5a. Comm. of *Elytrigia* spp. and *Artemisia maritima*.

Coenon 5b. Comm. of *Elytrigia* spp. and *Halimione portulacoides*.

These coena represent the *Atriplici-Agropyretum pungentis* of the *Angelicion litoralis*. In coenon 5a *Juncus maritimus* is a differential species. Coenon 5a differs from coenon 4c by the denser canopy of *Elytrigia* spp. and the absence of *Potentilla anserina*. It occurs on the creekbank levees and in depressions (1.50–1.70 m A.O.D.). Coenon 5b can be considered as a typical variant (no differential species), and is restricted to the creekbank levees (1.50–1.70 m A.O.D.). The *Elytrigia* spp. cover is large on the ungrazed area whilst *Festuca rubra* cover is large on the grazed area.

Coenon 6a. Comm. of *Festuca rubra* and *Puccinellia maritima*.

Coenon 6b. Comm. of *Festuca rubra* and *Glaux maritima*.

Coenon 6c. Comm. of *Festuca rubra* and *Agrostis stolonifera*.

In these three coena representatives both of *Puccinellion maritimae* and *Armerion maritimae* viz. *Juncetum gerardii typicum* and *Artemisietum maritimae armerietosum* can be observed. These communities occur on gradients from the lower to the mid salt-marsh and on gradients from depressions to creekbank levees (1.20–1.70 m A.O.D.). In coenon 6a the *Festuca rubra* cover is large on the ungrazed area. The cover of *Juncus gerardii*, however, is large on the grazed area. Coenon 6b differs from coenon 6a by the smaller cover of *Artemisia maritima*. *Puccinellia maritima, Suaeda maritima, Salicornia europaea* and *Spergularia media* are restricted to the grazed area. In coenon 6c a small abundance of representatives of the *Puccinellion maritimae* can be observed. The presence of *Carex distans* and *Lotus corniculatus* as representatives of the *Agropyro-Rumicion crispi* indicate a transition to the next group of coena. *Agrostis stolonifera, Juncus gerardii* and *Carex distans* are found particularly on the grazed area.

Coenon 6d. Comm. of *Festuca rubra* and *Juncus gerardii*.

Coenon 6e. Comm. of *Festuca rubra* and *Artemisia maritima*.

Coenon 6f. Comm. of *Festuca rubra* and *Carex distans*.

Coenon 6g. Comm. of *Festuca rubra* and *Elytrigia* spp.

These four coena both have representatives of the *Armerion maritimae, Juncetum gerardii leontodontetosum autumnalis* and *Agropyro-Rumicion crispi* viz. comm. of *Agrostis stolonifera* and *Trifolium fragiferum*, comm. of *Ononis spinosa* and *Carex distans*. These communities most frequently occur on the gradients from depressions to the low dunes (1.70–1.90 m A.O.D.). Coenon 6d is identical with the *Juncetum gerardii leontodontetosum autumnalis*. *Poa pratensis, Carex distans* and *Triglochin maritima* are more abundant on the grazed area than on the ungrazed area. Coenon 6e, characterized by the differential species *Artemisia maritima*, is restricted to the grazed area. Coenon 6f is characterized by the differential species *Carex distans* and the low abundance of *Juncus gerardii* and *Potentilla anserina*. The *Festuca* cover is large on the ungrazed are whereas that of *Agrostis stolonifera* is large on the grazed area. Coenon 6g differs by a larger cover of *Elytrigia* spp. and a small cover of *Agrostis stolonifera*. The cover of *Festuca rubra* and *Elytrigia* spp. is larger on the ungrazed than on the grazed area.

The coena of (the slopes of) the low dunes (Table 3, Fig. 1)

Coenon 7. Comm. of *Armeria maritima* and *Plantago coronopus*.

In this coenon representatives of the *Armerion maritimae*, of the *Agropyro-Rumicion crispi* (comm. of *Ononis spinosa* and *Carex distans)* and of the alliance *Saginion maritimae* can be observed. This community is characterized by the differential species *Cochlearia danica, Sagina procumbens* and *Cerastium holosteoides*. It occurs on the slopes of the low dunes (1.90–2.20 m A.O.D.) and is freely restricted to the grazed area.

Coenon 8a. Comm. of *Ammophila arenaria* and *Elytrigia* spp.

Coenon 8b. Comm. of *Ammophila arenaria* and *Galium verum*.

These two coena represent the transition between the *Armerion maritimae* and the *Galio-Koelerion* and can be observed on the low dunes (1.80–2.50 m A.O.D.). Coenon 8a can be considered as a typical variant (no differential species). *Lotus corniculatus, Carex arenaria* and *Bromus mollis* are nearly completely restricted to the grazed area. Coenon 8b is characterized by the differential species *Galium verum, Holcus lanatus* and *Rumex acetosella*. The cover of *Ammophila arenaria, Festuca rubra* and *Elytrigia* spp. is larger on the grazed than on the ungrazed area.

Changes on the grazed salt-marsh

A comparison of the generalized vegetation maps (Fig. 1) and the areas under the different coena in Table 4 clearly shows that on the grazed area some communities with a large cover of *Elytrigia* spp. (coena 5b and 6g), the comm. with *Ammophila arenaria* (coena 8a and 8b) and a comm. with *Artemisia maritima* (coenon 3a) decrease. By contrast comm. with a large *Juncus gerardii* cover (coena 2 and 6d), comm. with a large *Juncus* *maritimus* cover (coena 4b and 5a) and the *Armeria maritima* comm. and the comm. with a large *Limonium vulgare* cover (coena 1d and 6c) can be seen to have increased.

Fig. 2 shows the large variation in structural characteristics. This might be expected because different communities have been lumped together. Differences can be seen between 1976 grazed and ungrazed relevés as compared with 1971 relevés. Although it would be more correct to use p.q. information, some general structural changes can be discerned in the same communities in which p.q.'s are situated after reintroduction of grazing. There is a decrease in mean height, in mean herb cover, and probably in mean litter cover resulting in a low cover and more open canopy and an increase

Table 3. Synoptic table of (the feet) of low dunes.

Coenon	7	8 a	8 b
	Community of Armeria maritima and Plantago coronopus	Community of Ammophila arenaria and Elytrigia spp.	Community of Ammophila arenaria and Galium verum
No. of relevés	17	21	21
Festuca rubra	100 (1 - 3)	100 (2 - 3)	95 (1 - 2)
Elytrigia spp.	100 (+ - 2)	100 (r - 2)	76 (+ - 2)
Poa pratensis	100 (1 - 2)	100 (+ - 2)	86 (+ - 2)
Stellaria graminea	36 (+ - 2)	14 (1 - 2)	45 (+ - 2)
Bromus mollis	54 (+ - 2)	29 (+ - 2)	43 (r - 2)
Atriplex hastata	6 (+)	34 (r - +)	34 (+ - 1)
Cerastium semidecandrum	12 (+)	14 (r)	14 (r - 1)
Trifolium arvense	6 (r)	.	14 (r - 1)
Cochleraria danica	36 (r - +)	.	.
Sagina procumbens	24 (r - +)	.	.
Artemisia maritima	12 (r - +)	14 (r)	.
Leontodon autumnalis	6 (r)	5 (r)	.
Plantago coronopus	48 (+ - 2)	19 (r - 1)	.
Agrostis stolonifera	82 (+ - 2)	29 (+ - 1)	29 (+ - 1)
Plantago maritima	82 (+ - 2)	76 (r - 2)	10 (+ - 1)
Cerastium holosteoides	82 (+ - 2)	14 (r - 1)	29 (+)
Armeria maritima	94 (1 - 2)	86 (r - 2)	53 (r - 1)
Trifolium repens	54 (+ - 1)	14 (r - +)	19 (+)
Lotus corniculatus	100 (+ - 1)	90 (r - 2)	72 (r - 1)
Agrostis tenuis	18 (+ - 2)	5 (r)	45 (1 - 2)
Carex arenaria	18 (+)	58 (r - 2)	66 (r - 2)
Rumex acetosella	18 (+ - 2)	.	66 (+ - 2)
Elytrigia repens	6 (2)	14 (+ - 2)	27 (r - 2)
Holcus lanatus	6 (r)	.	58 (r - 1)
Ammophila arenaria	.	100 (+ - 2)	100 (1 - 2)
Rumex crispus	.	19 (r - +)	39 (r - 1)
Plantago lanceolata	.	74 (r - 1)	58 (+ - 1)
Stellaria media	.	10 (r)	27 (+ - 1)
Galium verum	.	.	34 (+ - 2)

Addenda:

Carex distans	7	(6, 1)	Trifolium pratense	8b	(5, 1)
Leontodon nudicaulis	7	(18, r - +)	Cirsium arvense	8b	(5, +)
Silene otites	8a	(5, r)	Achillea millefolium	8b	(5, 1)
Rumex acetosa	8a	(5, r)	Galium mollugo	8b	(5, r)
Sedum acre	8a	(5, r)	Hypochaeris radicata	8b	(5, r)
Juncus gerardii	8a	(14, +)	Taraxacum sp.	8b	(5, +)
Potentilla anserina	8a	(5, r)	Linaria vulgaris	8b	(5, 2)
Spergularia media	8a	(5, r)	Senecio jacobaea	8b	(5, +)
Vicia cracca	8b	(5, +)	Hippophae rhamnoides	8b	(10,1)
Trifolium dubium	8b	(5, r)			

Table 4. Area (ha) of the communities in 1971 and 1976 of both the grazed and ungrazed part of the study area; percentages are given parentheses, and in addition the unchanged part (percentage) of the 1971 area of each community.

		Grazed area					Ungrazed area				
	Community	1971		1976		unchanged	1971		1976		unchanged
		ha	%	ha	%	area (%)	ha	%	ha	%	area (%)
1a	Puccinellia with Spartina	0.28	(1.2)	0.28	(1.2)	62	0.39	(4.2)	0.09	(0.9)	10
1b	Puccinellia with Aster	0.27	(1.2)	0.16	(0.7)	13	0.09	(1.0)	0.25	(2.7)	17
1c	Puccinellia with Limonium	0.32	(1.4)	0.23	(1.0)	45	-		-		-
1d	Puccinellia with Plantago	0.74	(3.3)	1.03	(4.5)	71	-		0.01	(0.1)	-
1e	Puccinellia with Halimione	-		-			-		0.17	(1.8)	-
2	Juncus gerardii with Glaux	0.89	(3.9)	0.99	(4.3)	76	0.22	(2.3)	0.19	(2.0)	72
3a	Artemisia with Puccinellia	1.49	(6.3)	0.64	(2.8)	42	2.09	(22.6)	1.95	(21.1)	74
3b	Artemisia with J. maritimus	0.03	(0.1)	0.23	(1.0)	17	0.28	(3.1)	0.70	(7.5)	33
4a	J. maritimus with Puccinellia	2.38	(10.4)	2.06	(9.0)	53	1.39	(15.1)	0.54	(5.9)	24
4b	J. maritimus with Potentilla	1.79	(7.8)	2.44	(10.7)	71	0.70	(7.6)	0.85	(9.2)	77
4c	J. maritimus with Elytrigia	0.21	(0.9)	0.14	(0.6)	1	0.15	(1.7)	0.01	(0.1)	0
5a	Elytrigia with Artemisia	0.39	(1.7)	0.96	(4.2)	17	0.60	(6.5)	1.17	(12.6)	29
5b	Elytrigia with Halimione	1.21	(5.3)	0.10	(0.4)	6	0.98	(10.6)	1.13	(12.3)	51
6a	Festuca with Puccinellia	1.53	(6.7)	1.15	(5.0)	44	0.12	(1.2)	0.11	(1.1)	49
6b	Festuca with Glaux	1.76	(7.7)	2.10	(9.2)	50	0.20	(2.1)	0.07	(0.8)	32
6c	Festuca with Agrostis	0.28	(1.2)	0.37	(1.6)	24	-		0.01	(0.1)	-
6d	Festuca with J. gerardii	0.65	(2.9)	1.03	(4.5)	25	-		0.05	(0.5)	-
6e	Festuca with Artemisia	-		0.23	(1.0)	-	-		-		-
6f	Festuca with C. distans	1.83	(8.0)	1.61	(7.0)	36	0.76	(8.2)	0.55	(6.0)	51
6g	Festuca with Elytrigia	1.44	(6.3)	0.10	(0.5)	1	0.29	(3.1)	0.56	(6.1)	43
7	Armeria with P. coronopus	-		3.31	(14.5)	-	-		0.07	(0.8)	-
8a	Ammophila with Elytrigia	3.84	(16.8)	2.12	(9.3)	37	0.44	(4.8)	0.31	(3.4)	44
8b	Ammophila with Galium	1.44	(6.3)	1.09	(4.8)	49	0.23	(2.5)	0.15	(1.6)	51
	bare soil	0.05	(0.2)	0.08	(0.4)	71	-		-		-
	water	0.11	(0.5)	0.10	(0.5)	75	0.20	(1.2)	0.15	(1.6)	74
	total	22.90	(100)	22.90	(100)		9.24	(100)	9.24	(100)	

of alpha-diversity. Only the *Puccinellia maritima* comm. show a decrease of alpha-diversity which may be due to the destruction of the turf. Structural changes not only favour the species already present but also facilitate the establishment of new species, predominantly annuals, such as *Salicornia europaea, Suaeda maritima, Sagina maritima, Cochlearia danica, Trifolium arvense* and *Bromus mollis* (Table 5).

Despite a similarly large area for several communities between 1971 and 1976 the unchanged area of the communities is often rather small (Table 4). Each coenon mapped in 1971 may have changed into several other coena in 1976. This is quantified in the transition matrix of Fig. 3. Each coenon mapped in 1976 on the other hand can originate from several other coena from 1971, an aspect quantified, too, in a transition matrix (Fig. 4). Comm. with *Festuca rubra* (coenon 6g) and with *Armeria maritima* (coenon 7) arise from comm. with *Ammophila arenaria* (coena 8a and 8b) (Table 3). A comm. with *Festuca rubra* (coenon 6a) originates from a comm. with *Artemisia maritima* (coenon 3b) (Table 2). Comm. with a large cover of *Juncus gerardii* (coenon 6d) and a large cover of *Limonium vulgare* (coenon 1d) can arise due to the reduction in cover of *Festuca rubra* (coena 6f and 6a, respectively). From comm. with a large cover of *Elytrigia* spp. (coena 5b and 6g) comm. with a large cover of *Festuca rubra* (coenon 6e), with a large cover of *Armeria maritima* (coenon 7) and with a large cover of *Juncus maritimus* (coenon 4c) arise. On the other hand, development of both a comm. with a large cover of *Artemisia maritima* (coenon 3b) and one with a large cover of *Elytrigia* spp. (coenon 5a) from comm. with *Juncus maritimus* (coena 4a and 4b) demonstrates the complexity of the transitions. A scheme of registrated lines of succession between the coena from 1971–1976 is given in the linkage diagram of Fig. 5. On the grazed mid- and upper salt-marsh a clear trend can be discerned. The communities dominated by

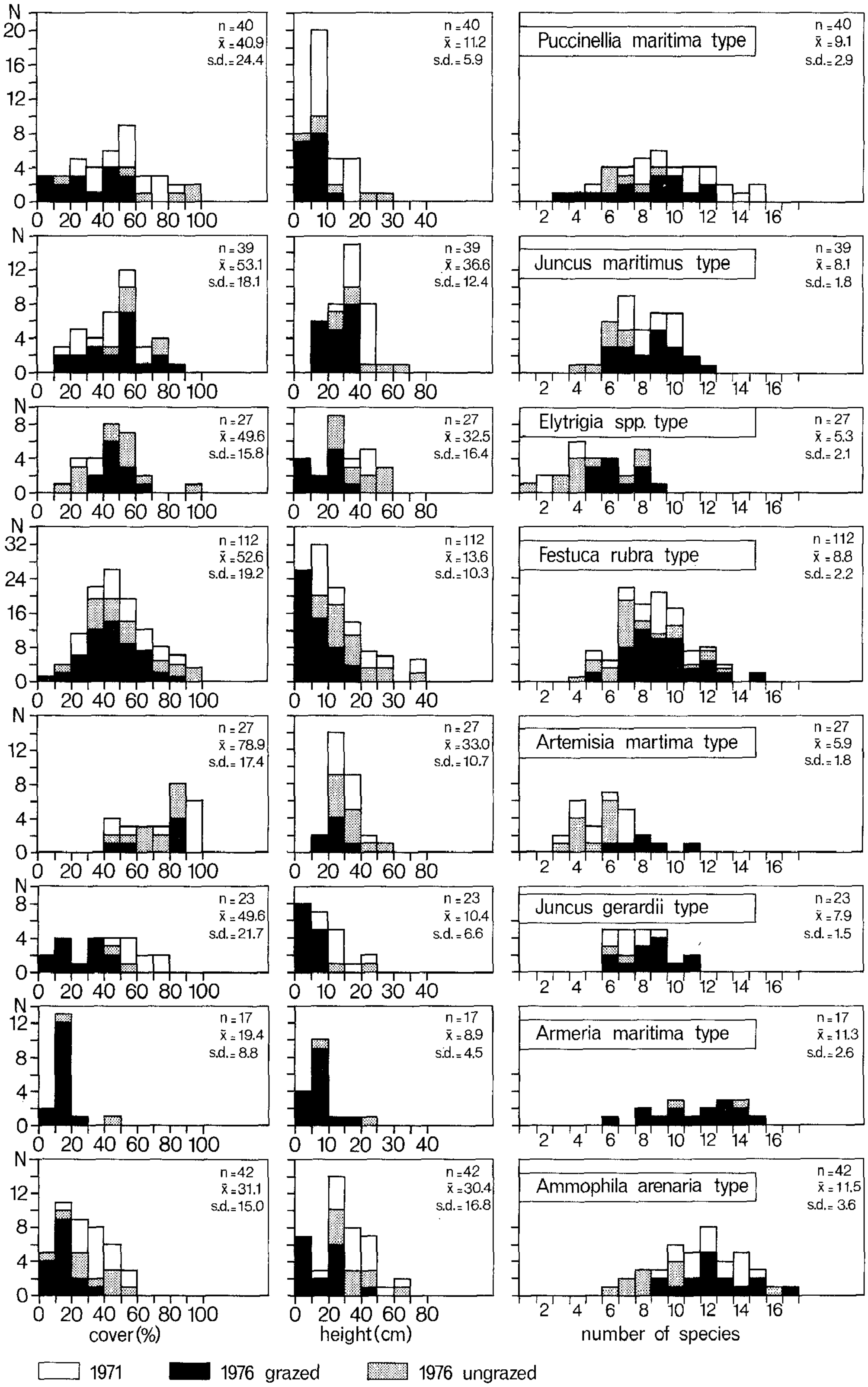


Fig. 2. Structural characteristics (height, cover and number of species) (1971, 1976 grazed and 1976 ungrazed). For explanation of communities see Fig. 1. n = relevés, $\bar{x}$ = mean, s.d. = standard deviation.

Communities 1976 \ Communities 1971	1a	1b	1c	1d	1e	2	3a	3b	4a	4b	4c	5a	5b	6a	6b	6c	6d	6e	6f	6g	7	8a	8b	bare soil	water
1a	62	9	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	.
1b	9	13	18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1c	8	9	45	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1d	12	39	3	71	.	.	.	.	.	.	.	.	.	14	3	6	.	.	.	.	.	.	.	.	.
1e	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2	.	.	.	.	.	76	.	.	.	.	.	.	.	.	.	6	19	4	.	.	.	.	.	.	.
3a	.	.	.	.	.	.	42	8	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
3b	.	.	.	.	.	.	.	17	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4a	.	.	.	.	.	.	.	33	53	16	7	42	5	.	.	.	.	.	.	.	.	.	.	.	.
4b	.	.	.	.	.	.	.	.	18	71	62	22	16	.	.	.	.	.	.	.	.	.	.	.	.
4c	.	.	.	.	.	.	.	.	1	1	1	.	7	.	.	.	.	.	.	.	.	.	.	.	.
5a	.	.	.	.	.	.	.	.	12	3	8	17	37	.	.	.	.	.	.	.	.	.	.	.	.
5b	.	.	.	.	.	.	.	.	1	.	.	1	8	.	.	.	.	.	.	.	.	.	.	.	.
6a	.	.	.	2	.	.	27	.	.	.	.	.	.	44	3	.	.	.	.	.	.	.	.	.	.
6b	.	.	.	17	.	3	19	.	.	.	.	.	.	35	50	4	10	.	.	.	.	.	.	.	.
6c	.	.	.	.	.	1	.	.	.	.	.	.	.	.	11	24	6	.	1	.	.	.	.	.	.
6d	.	.	.	.	.	9	.	.	.	.	.	.	.	.	2	16	25	.	25	.	.	.	.	.	.
6e	.	.	.	.	.	.	2	.	.	.	.	.	7	.	6	.	.	.	.	1	.	.	.	.	.
6f	.	.	.	.	.	1	3	.	.	.	.	.	.	.	16	11	18	.	36	11	.	.	.	.	.
6g	.	.	.	.	.	.	.	.	.	.	.	.	6	.	1	.	.	.	3	5	.	1	1	.	.
7	.	.	.	.	.	.	.	.	.	.	.	.	7	.	.	.	.	.	20	62	.	41	13	.	.
8a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9	.	37	33	.	.
8b	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9	49	.	.
bare soil	3	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	71	.
water	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	75
D	.	.	.	.	.	.	2	.	2	3	.	.	.	1	2	.	.	.	.	6	.	9	2	.	.
F	7	25	22	5	.	10	3	42	7	5	21	18	6	5	5	34	23	.	11	5	.	3	2	19	25

Fig. 3. Percentage of change of the 1971 coena into the 1976 coena for the grazed salt-marsh. For F- and D-changes compare tex

Communities 1976 \ Communities 1971	1a	1b	1c	1d	1e	2	3a	3b	4a	4b	4c	5a	5b	6a	6b	6c	6d	6e	6f	6g	7	8a	8b	bare soil	water	D	F
1a	61	8	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	3	13
1b	16	22	34	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14	13
1c	10	10	63	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	7
1d	3	10	.	51	.	.	.	.	.	.	.	.	.	21	6	2	.	.	.	.	.	.	.	.	.	2	4
1e	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2	.	.	.	.	.	69	.	.	.	.	.	.	.	.	.	2	13	.	7	.	.	.	.	.	.	6	4
3a	.	.	.	.	.	.	96	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	2
3b	.	.	.	.	.	.	2	2	73	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	23
4a	.	.	.	.	.	.	.	1	62	14	1	8	3	.	.	.	.	.	.	.	.	.	.	.	.	.	12
4b	.	.	.	.	.	.	.	.	17	52	5	4	8	.	.	.	.	.	.	.	.	.	.	.	.	.	14
4c	.	.	.	.	.	.	.	.	19	11	2	.	63	.	.	.	.	.	.	.	.	.	.	.	.	.	6
5a	.	.	.	.	.	.	.	.	30	6	2	7	47	.	.	.	.	.	.	.	.	.	.	.	.	.	6
5b	.	.	.	.	.	.	.	.	13	.	.	3	75	.	.	.	.	.	.	.	.	.	.	.	.	.	9
6a	.	.	.	1	.	.	34	.	.	.	.	.	.	59	4	.	.	.	.	.	.	.	.	.	.	.	1
6b	.	.	.	6	.	1	13	.	.	.	.	.	.	26	42	.	3	.	.	.	.	.	.	.	.	.	8
6c	.	.	.	.	.	1	.	.	.	.	.	.	.	.	53	18	10	.	3	.	.	.	.	.	.	5	9
6d	.	.	.	.	.	8	.	.	.	.	.	.	.	.	4	4	16	.	45	.	.	.	.	.	.	21	2
6e	.	.	.	.	.	.	.	.	.	.	.	.	35	.	11	.	.	.	.	7	.	46	.	.	.	.	2
6f	.	.	.	.	.	1	2	.	.	.	.	.	.	.	18	2	7	.	41	10	.	.	.	.	.	12	6
6g	.	.	.	.	.	.	.	.	.	.	.	.	29	.	10	.	.	.	10	7	.	24	12	.	.	.	7
7	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	11	27	.	48	6	.	.	.	6
8a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	67	23	.	.	.	5
8b	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30	65	.	.	.	5
bare soil	9	21	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	46	.	.	24
water	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	80	.	20

Fig. 4. Percentage of change of the 1976 coena originating from the 1971 coena for the grazed salt-marsh. For F- and D-changes compare text.

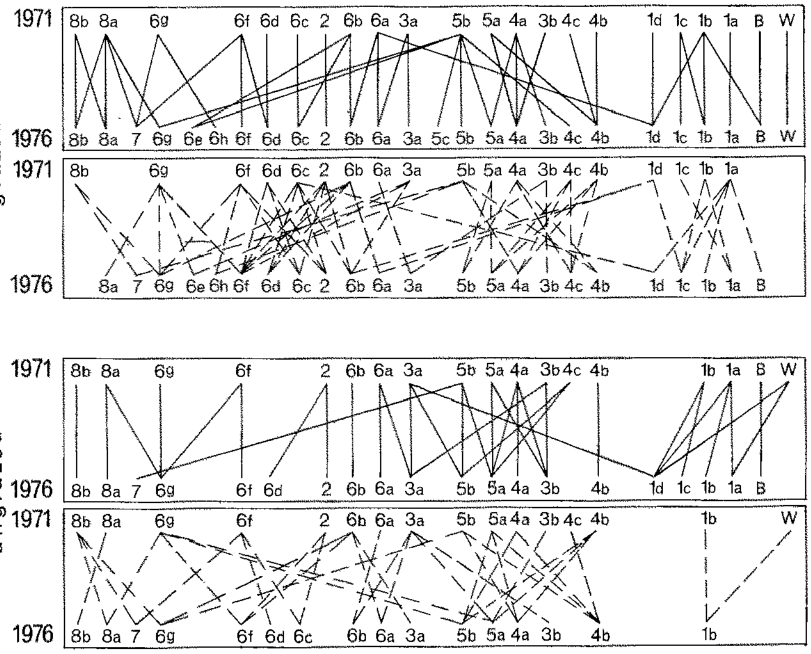


Fig. 5. Succession scheme. Drawn line: major succession lines (>20% in Figs. 3 and 4). Broken line: minor succession lines (<20% in Figs. 3 and 4). B: bare soil, W: water.

Artemisia maritima (coenon 3a) and *Elytrigia* spp. (coenon 5b) always change into communities richer in species (Fig. 2) (viz. the coena 6a, 6b, 6e, 6g and the coena 4a, 4c, 5a, 6e and 6g, respectively).

The effect of five years grazing on single species is summarized in Table 5.

At nearly half of all points of the dot grid (48%) a change in communities was found between 1971 and 1976 (Fig. 6). The grid cells with large areas of *Elytrigia* spp. and *Juncus maritimus* communities sometimes show both a very high (nearly 100%) percentage of change (Figs. 1 & 6). In grid cells with

Table 5. Effects of five years of grazing upon single species on the Oosterkwelder Schiermonnikoog.

positive		indifferent	local disparities[1]	negative
area and cover increase,				area and cover decrease
Agrostis stolonifera	Plantago coronopus	Glaux maritima	Artemisia maritima	Ammophila arenaria (incl. Ammocalamagrostis baltica)
Armeria maritima	Puccinellia maritima	Juncus maritimus	Atriplex hastata	
Bromus mollis	Rumex acetosella	Plantago maritima	Festuca rubra	Aster tripolium
Bupleurum tenuissimum	Sagina maritima		Limonium vulgare	
Carex distans	Sagina procumbens		Salicornia europaea	
Cerastium holosteoides	Spergularia marina		Suaeda maritima	
Cerastium semidecandrum	Stellaria graminea			
Cochlearia danica	Stellaria media			
Juncus gerardii	Trifolium arvense			
Lotus corniculatus	Triglochin maritima			
cover increase				cover decrease
Galium verum	Silene otitis			Potentilla anserina
Holcus lanatus	Spergularia media			Spartina anglica
Poa pratensis	Trifolium repens			Elytrigia pungens (& E. x obtusiuscula)

1) local disparities: cover decrease in existing communities, area and thus cover increase in communities where the species did not exist before grazing.

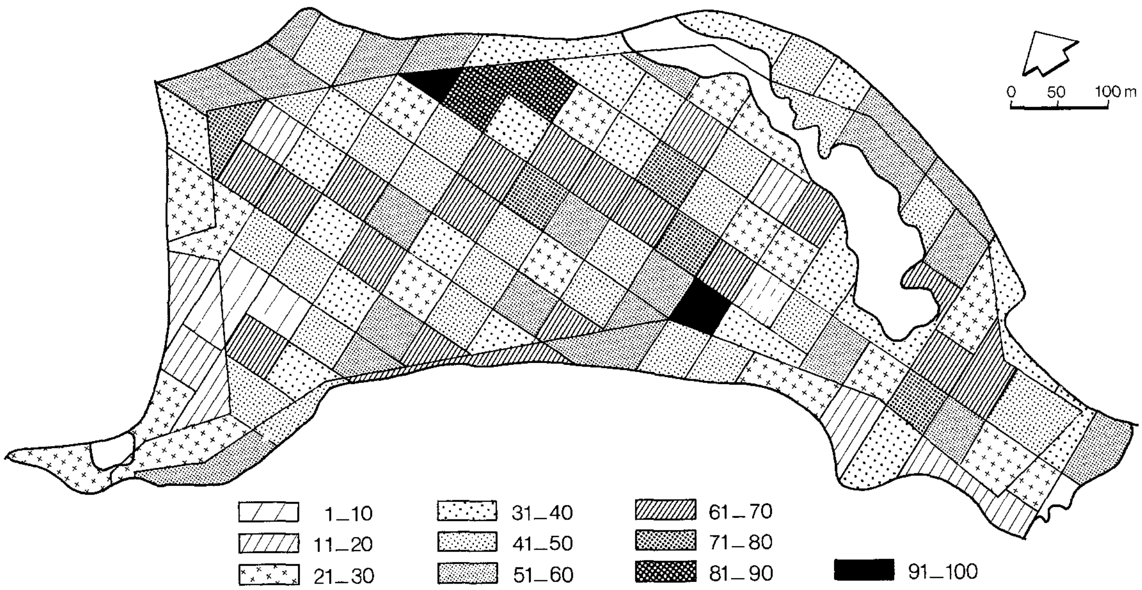


Fig. 6. Percentage vegetation change (1971–1976) per grid cell of ¼ ha.
□ Area not involved in the calculations (see text);
— fence.

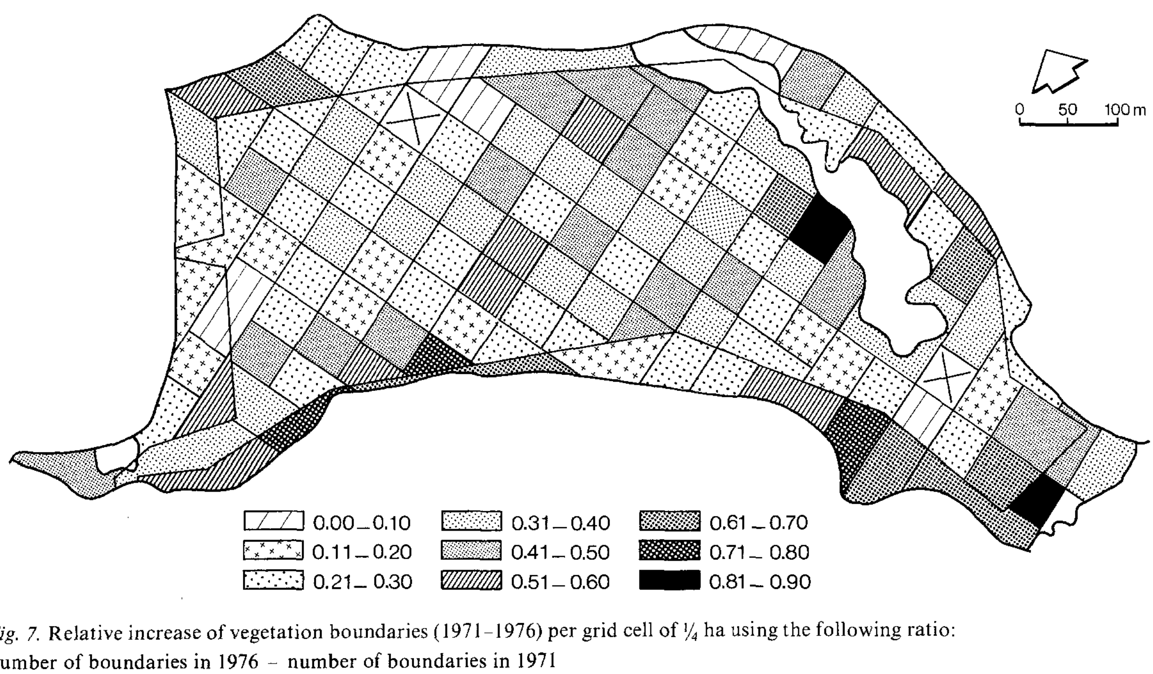


Fig. 7. Relative increase of vegetation boundaries (1971–1976) per grid cell of ¼ ha using the following ratio:

$$\frac{\text{number of boundaries in 1976} - \text{number of boundaries in 1971}}{\text{number of boundaries in 1976} + \text{number of boundaries in 1971}}$$

☒ decrease of number of vegetation boundaries; — fence;
□ area not involved in the calculations.

large areas of *Festuca rubra* and *Ammophila arenaria* comm. there are rather large changes in community composition (Fig. 6), an increase of the beta-diversity, and an increase of the number of vegetation boundaries (Fig. 7). The grid cells covering the gradient from salt-marsh depression to the low dunes, in the *Armeria maritima* comm. have strongly different communities in the two years. Grid cells with large areas of *Artemisia maritima* and *Juncus gerardii* comm. show little change.

The number of vegetation boundaries often increases, and in addition some boundaries appear to become 'sharper' (more distinct) due to grazing. This can be seen on the aerial photographs (Fig. 8a, b, c).

Changes on the ungrazed salt-marsh

On the ungrazed area the communities with a large cover of *Elytrigia* spp. (coena 5a, 5b and 6g) show an increase (Fig. 1 & Table 4), together with an *Artemisia maritima* comm. (coenon 3b), a comm. with a large cover of *Suaeda maritima* (coenon 1b) and the *Halimione portulacoides* comm. (coenon 1e). On the other hand, comm. with *Ammophila arenaria* (coena 8a and 8b), *Juncus maritimus* comm. (coena 4a and 4c), comm. with a large cover of *Festuca rubra* (coena 6b and 6f) and the *Spartina anglica* comm. (coenon 1a) show a decrease. The transition matrix of coena mapped in 1971 changing into other coena in 1976 is given in Fig. 9. The transition matrix of coena mapped in 1976 originating from other coena in 1971 is given in Fig. 10. The *Elytrigia* spp. comm. originate from a number of communities viz.: *Juncus maritimus* comm. (coena 4a and 4c), *Ammophila arenaria* comm. (coena 8a and 8b), an *Artemisia maritima* comm. (coenon 3a) and a *Festuca rubra* comm. (coenon 6f) (Table 2). *Artemisia maritima* comm. originate from a *Juncus maritimus* comm. (coenon 4a), an *Elytrigia* spp. comm. (coenon 5a) and a *Festuca rubra* comm. (coenon 6a). The *Halimione portulacoides* comm. (coenon 1e) can arise from the *Spartina anglica* comm. (coenon 1a) and from the comm. with a large cover of *Suaeda maritima* (coenon 1b). Coenon 1b can originate from coenon 1a, moreover, due to the increase of *Suaeda maritima* cover.

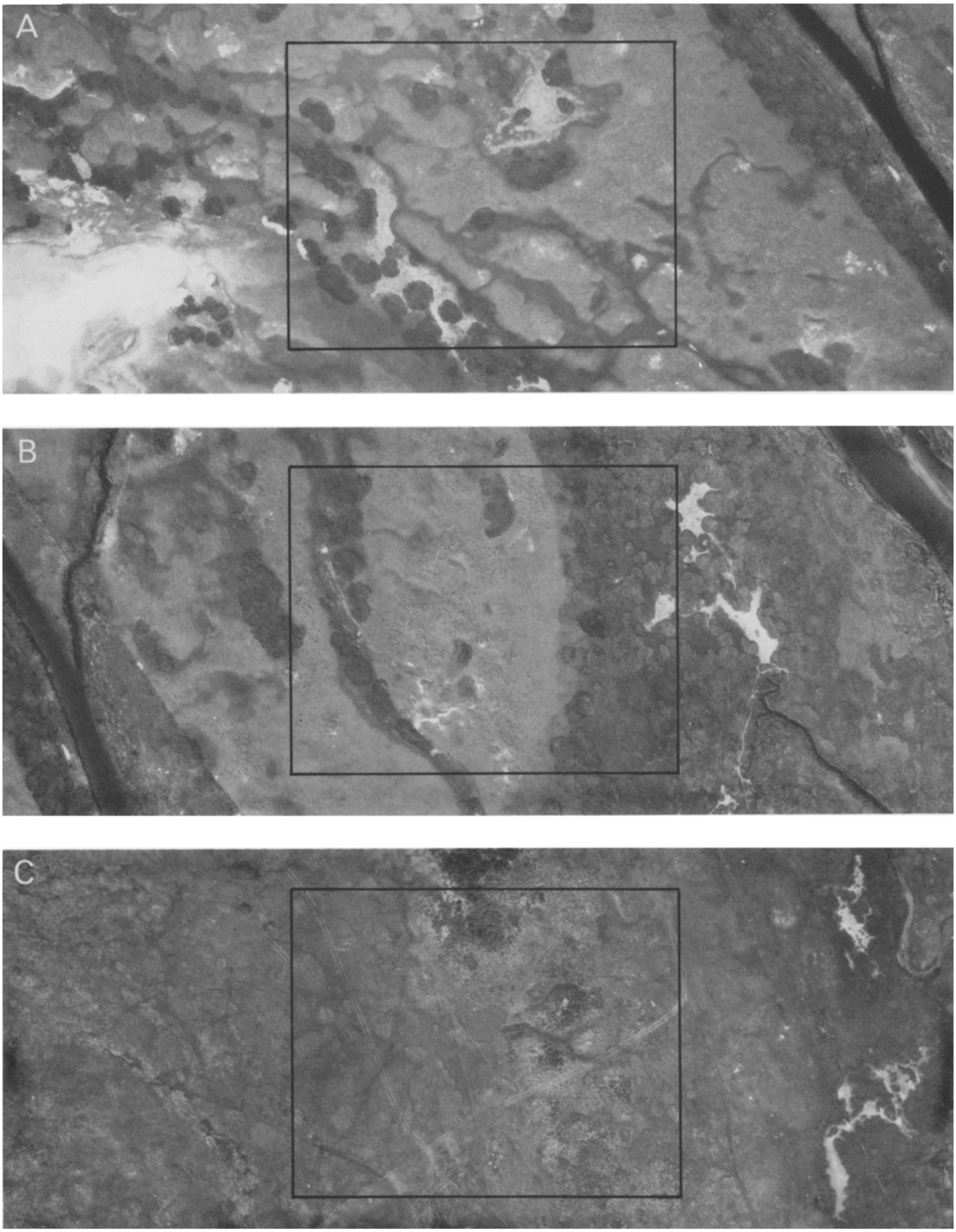
Like for the grazed area the scheme of lines of succession between the coena from 1971 up to and included 1976 is given in Fig. 5.

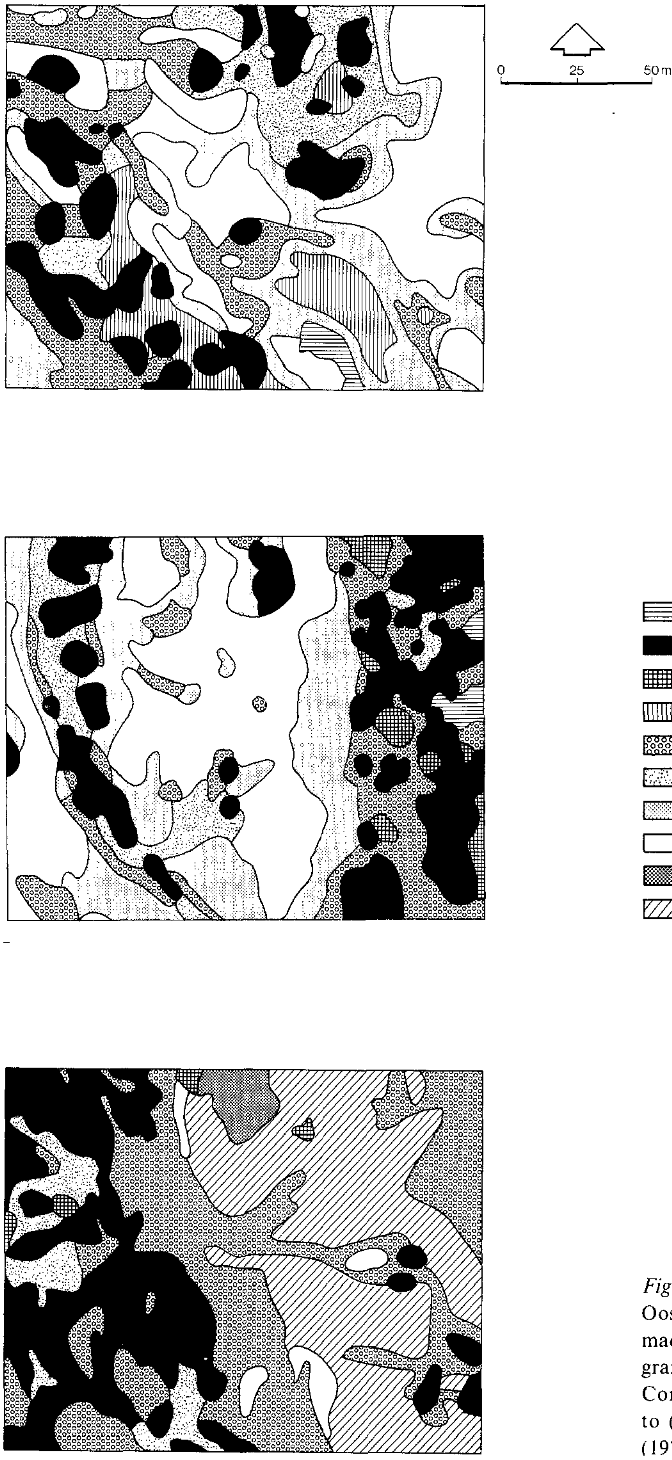
Vegetation structure changes slightly between 1971 and 1976 (Fig. 2). In general there is a small increase of mean herb cover, mean litter cover and a small decrease of alpha-diversity. The annuals occurring on the grazed area are absent from the ungrazed area. The cover of *Armeria maritima, Agrostis stolonifera, Juncus gerardii, Puccinellia maritima* and *Limonium vulgare* on the ungrazed area may be decreased because they are hampered by the dense canopy. All these species increase in cover on the grazed area.

At 39% of all points of the dot grid (Fig. 6) a change in communities was found between 1971 and 1976 resulting in some increase in beta-diversity and an increase in the number of vegetation boundaries per grid cell (Fig. 7). The greater increase in the number of vegetation boundaries per grid cell of the ungrazed compared to the grazed area seems at variance with the evidence from aerial photographs where more distinct boundaries are visible in the grazed area. This is especially caused by the local increase in clones of *Elytrigia* spp. which will probably combine after several years to form one large area dominating other communities. Introduction of grazing in such a situation gives the result illustrated in the sequence of Fig. 8a, b, c in which rather large areas covered with more or less homogeneous communities are broken up into smaller ones.

Discussion

The communities identified in the present study do not all fit into the existing syntaxonomical classification of salt-marsh communities. Although a lot of recognisable coena (Beeftink, 1965, 1977a; Westhoff & den Held, 1969) can be observed at the study area, there are many transitional coena. The communities with a large cover of *Juncus maritimus* and of *Elytrigia* spp. create some classification problems. According to Westhoff & den Held (1969) *Juncus maritimus* shows an optimum in the transitional habitat between *Agropyro-Rumicion crispi* and *Armerion maritimae*. The species is not a real halophyte, but seems tolerant to a broad range of soil salinity and moisture conditions (Ranwell, 1972). According to


A
B
C



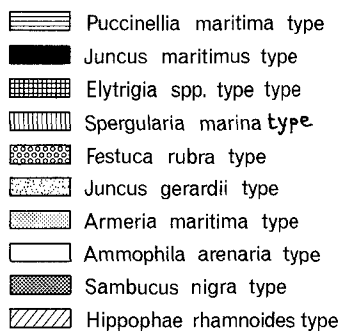


Fig. 8. A, B, C. Aerial photographs (June 1976) of parts of the Oosterkwelder of Schiermonnikoog (left) with independently made vegetation maps of (A) continuous grazing, (B) 1972 grazing reintroduced and (C) since 1958 ungrazed (right). Communities are characterized by dominant species according to (A) Bakker & Masselink (unpubl.), (B) Norder & Ruyter (1977) and (C) van Dijk (1974).

Communities 1976 \ Communities 1971	1a	1b	1c	1d	1e	2	3a	3b	4a	4b	4c	5a	5b	6a	6b	6c	6d	6e	6f	6g	7	8a	8b	bare soil	water
1a	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1b	47	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1d	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1e	13	20	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2	.	.	.	.	.	72	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3a	.	.	.	.	.	.	74	53	.	.	.	.	.	34	10	.	.	.	.	.	.	.	.	.	.
3b	.	.	.	.	.	.	4	33	21	.	.	23	.	.	.	.	.	.	.	.	.	.	.	.	.
4a	.	.	.	.	.	.	.	.	24	3	.	12	4	.	.	.	.	.	.	.	.	.	.	.	.
4b	.	.	.	.	.	.	.	.	6	77	8	17	2	.	.	.	.	.	.	.	.	.	.	.	.
4c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5a	.	.	.	.	.	.	2	4	28	4	66	29	27	.	.	.	.	.	.	7	.	.	.	.	.
5b	.	.	.	.	.	.	14	3	8	3	23	13	51	.	9	.	.	.	.	10	.	.	.	.	.
6a	.	.	.	.	.	.	1	.	.	.	.	.	.	49	3	.	.	.	.	.	.	.	.	.	.
6b	.	.	.	.	.	.	.	.	.	.	.	.	.	6	32	.	.	.	.	.	.	.	.	.	.
6c	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
6d	.	.	.	.	.	11	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
6e	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
6f	.	.	.	.	.	4	.	.	.	.	.	.	.	.	10	.	.	.	51	8	.	.	.	.	.
6g	.	.	.	.	.	.	.	.	.	.	.	.	7	.	3	.	.	.	25	43	.	27	17	.	.
7	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	1	.	.	.	2	.	.
8a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15	.	44	16	.	.
8b	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	51	.	.
bare soil	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
water	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	74
D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11	8	.	.
F	30	57	.	.	.	12	3	7	12	11	3	6	5	11	27	.	.	.	22	17	.	15	6	.	26

Fig. 9. Percentage of change of the 1971 coena into the 1976 coena for the ungrazed salt-marsh. For F- and D-changes compare text.

Communities 1976 \ Communities 1971	1a	1b	1c	1d	1e	2	3a	3b	4a	4b	4c	5a	5b	6a	6b	6c	6d	6e	6f	6g	7	8a	8b	bare soil	water	D	F
1a	44	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	41	.	15
1b	75	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	.	11
1c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1d	.	67	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33
1e	30	11	.	.	.	.	27	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	23	.	9
2	.	.	.	.	.	83	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	17
3a	.	.	.	.	.	.	80	8	.	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	10
3b	.	.	.	.	.	.	12	13	43	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12
4a	.	.	.	.	.	.	.	.	61	4	.	13	6	.	.	.	.	.	.	.	.	.	.	.	.	.	14
4b	.	.	.	.	.	.	.	.	10	63	2	12	2	.	.	.	.	.	.	.	.	.	.	.	.	.	11
4c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5a	.	.	.	.	.	.	3	1	33	2	9	15	23	.	.	.	.	.	.	2	.	.	.	.	.	.	13
5b	.	.	.	.	.	.	25	.	10	2	3	7	44	.	2	.	.	.	.	3	.	.	.	.	.	.	4
6a	.	.	.	.	.	.	12	.	.	.	.	.	.	55	5	.	.	.	.	.	.	.	.	.	.	.	29
6b	.	.	.	.	.	.	3	.	.	.	.	.	.	10	86	.	.	.	.	.	.	.	.	.	.	.	.
6c	.	.	.	.	.	50	.	.	.	.	.	.	.	.	.	.	.	.	25	.	.	.	.	.	.	.	25
6d	.	.	.	.	.	50	.	.	.	.	.	.	.	.	.	.	.	.	17	.	.	.	.	.	.	33	.
6e	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
6f	.	.	.	.	.	1	.	.	.	.	.	.	.	.	4	.	.	.	70	4	.	.	.	.	.	10	11
6g	.	.	.	.	.	.	.	.	.	.	.	.	12	.	.	.	.	.	33	22	.	21	7	.	.	.	4
7	.	.	.	.	.	.	.	.	.	.	.	.	66	.	.	.	.	.	7	.	.	.	7	.	.	.	21
8a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14	.	62	12	.	.	.	12
8b	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	80	.	.	.	15
bare soil	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
water	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	54	.	46

Fig. 10. Percentage of change of the 1976 coena originating from the 1971 coena for the ungrazed salt-marsh. For F- and D-changes compare text.

Adam (1977) *Juncus maritimus* is not limited to one syntaxon. In the study area *Juncus maritimus* communities are found in particular in transitions from the lower salt-marsh to low dunes and of salt-marsh depressions to creek bank levees. These are gradient situations: wet – dry, 'fresh'-salt transitions, typical for the *Agropyro-Rumicion crispi*. The *Agropyro Rumicion crispi* covers a wide range of communities united by a tendency to occur in what might loosely be termed 'transitional' habitats (Westhoff & den Held, 1969). Adam (1977) mentions that assignment of the upper-marsh *Juncus maritimus* communities to the *Agropyro-Rumicion crispi* implies a belief in the ecological importance of transition per se and that these communities are relatively easily distinguished from those of the mid-marsh. It is, however, very difficult to draw lines between communities assigned to the mid-marsh *Armerion maritimae* and the upper-marsh *Agropyro-Rumicion crispi* (Fresco, 1971).

The communities with a large cover of *Elytrigia* spp. have relationships with the *Atriplici-Agropyretum pungentis, Agropyro-Rumicion crispi, Armerion maritimae* and *Saginion maritimae*. These *Elytrigia* spp. communities are not easily syntaxonomically classified because of the fragment remnants of the communities which *Elytrigia* spp. invades after deposition of drift material (Beeftink, 1965). It might therefore be more correct to distinguish an *Elytrigia* facies of several communities instead of an *Atriplici-Agropyretum pungentis*. A study of *Elytrigia*-dominated communities following the approach of Adam (1977) for *Juncus maritimus* comm., (bearing in mind that both *Elytrigia pungens* and *E. x obtusiuscula* occur) might clarify the problem. However, since there is no satisfactory syntaxonomical classification of *Elytrigia* spp. comm., the name *Atriplici-Agropyretum pungentis* is used.

Changes in the vegetation which involve an increasing number of species and an increasing complexity of structure are considered to be progressive succession e.g. the sere *Salicornietum europaeae* – *Puccinellietum maritimae* – *Juncetum gerardii* – *Agropyro-Rumicion crispi*. The sere in the opposite direction is called retrogressive succession (Beeftink, 1965). The causes of retrogressive succession can be both natural (e.g. erosion) and man-made (e.g. grazing). When the disturbance stops a recovery succession such as that on the ungrazed parts of the study area after grazing stopped in 1958, could begin. The changes on the ungrazed area from bare ground to coenon 1a, from coenon 1a to coenon 1b, from coenon 1a to coenon 1e, from coenon 1b to coenon 1e, from coenon 1b to coenon 1d, and from coenon 2 to coenon 6d (Fig. 5) can all be called progressive succession. The production on the ungrazed area of the almost pure *Elytrigia* spp. comm. (coena 5a, 5b and 6f) from the *Juncus maritimus* comm. (coena 4a, 4b and 4c), from communities with a large cover of *Artemisia maritima* (coena 3a and 3b) and from the *Ammophila arenaria* comm. (coena 8a and 8b) can hardly be called progressive succession, because it should be attributed to deposition of drift material (Beeftink, 1965). On the other hand, *Elytrigia* spp. comm. can persist for a long time without deposition of drift material (Beeftink, 1965). Drift material was not deposited at all the sites where the *Elytrigia* spp. comm. developed or extended on the study area indicating that *Elytrigia* spp. are very 'agressive' invading various communities by underground stolons.

Considering the observed linkages (Fig. 5) four lines of 'cyclic' succession could be postulated in the ungrazed area: (i) coenon 8b into coenon 8a into coenon 6g into coenon 8b, (ii) coenon 3a into coenon 5b into coenon 5a into coenon 3b into coenon 3a, (iii) coenon 4a into coenon 5a into coenon 4b into coenon 4a, (iv) coenon 4a into coenon 4b into coenon 5a into coenon 4a. The rise and fall of populations of the dominant species *Elytrigia* spp., *Artemisia maritima, Juncus maritimus* is probably very important. *Juncus maritimus* cover may become thinner due to a developmental phase (Hulscher, 1962) in which growth occurs at the clone's fringe while the center dies off; later on this centre can be 'filled in' again from the periphery. Large fluctuations of e.g. *Halimione portulacoides* are known, possibly due to the effect of severe winters (Beeftink, 1977a).

Changes due to reintroduction of grazing should be called retrogressive succession. This holds for changes of coena 1b and 1c into coenon 1a, of coena 6a and 6b into coenon 1d at the lower salt-marsh (Fig. 5). Changes in the opposite direction, however, can also be observed. According to the above definition these changes should be called progressive succession, despite grazing. The area covered by coenon 1d increases (Table 4) while it is assumed (Beeftink, 1965; Westhoff & Den Held, 1969) that the *Plantagini-Limonietum* is characteristic of the ungrazed saltmarsh changing into *Puccinellietum maritimae* under grazing. It is possible that this increase is a temporary effect, being a transitional phase in a retrogressive succession of the *Artemisietum maritimae* to *Puccinellietum maritimae.* On the grazed salt-marsh both progressive and retrogressive succession can be found. Grazing animals tend to return to formerly closely-grazed swards to graze protein rich young tillers and avoid rugged areas, thus reinforcing structural differences of the vegetation (Hafez, 1969; Harper, 1977). The sharpening of the vegetation boundaries (Figs. 8a, b, c) accords with this idea. Dry and wet summers with related differences in forage production may lead to cyclic succession. Differences in grazing intensity exist on the study area, between communities, within one community at any moment, and also between seasons (Allersma, 1977). Further detailed investigations should relate differences in grazing intensity to changes in the vegetation.

The observed linkages (Fig. 5) on the grazed area suggest six lines of cyclic succession possibly due to temporal differences in grazing intensity: (i) coenon 1a into coenon 1b into coenon 1d into coenon 1c into coenon 1a, (ii) coenon 1d into coenon 6b into coenon 6a into coenon 1d, (iii) coenon 1d into coenon 6a into coenon 6b into coenon 1d, (iv) coenon 2 into coenon 6c into coenon 6f into coenon 6d into coenon 2, (v) coenon 4a into coenon 5a into coenon 4b into coenon 4a, (vi) coenon 4a into coenon 4b into coenon 5a into coenon 4a. The latter two possibly cyclic successions, involving *Juncus maritimus,* can also be observed on the ungrazed part of the study area. A low grazing intensity (Allersma, 1977) could be the explanation for this coincidence.

Changes of the coena 5b, 6f, 6g, 8a and 8b into the comm. of *Armeria maritima* and *Cochlearia danica* (coenon 7) somewhat resembling the *Saginion maritimae* could be related to 'concertina'-like succession (Tüxen & Westhoff, 1963; Beeftink 1977a). The *Saginion maritimae* ecologically fits between the halophilic *Armerion maritimae* and the halophobic *Galio-Koelerion* and occurs on places with strong changes in soil salinities and soil moisture caused by a combination of gales in spring and warm and dry periods in summer. Under these conditions the *Armerion maritimae,* the *Agropyro-Rumicion crispi* and the *Galio-Koelerion* dry out and die. This produces open areas enhancing the development of the *Saginion maritimae* (Beeftink, 1977a). Tüxen & Westhoff (1963) refer to a subassociation of *Elytrigia pungens* of the *Sagino-Cochlearietum danicae* coming into close contact with the *Atriplici-Agropyretum pungentis* on old drift deposits. This seems in accordance with the fact that coenon 5b can change into coenon 7. The same authors describe a subassociation *Sagino-Cochlearietum juncetosum gerardii* which may result from the *Juncetum gerardii* in a real line of succession. It therefore seems likely that coenon 6f changes into coenon 7. Grazing apparently encourages the formation of the *Saginion maritimae,* judging from the large area occupied by coenon 7 after five years of grazing. Removing species like *Elytrigia* spp., *Festuca rubra* and *Ammophila arenaria* probably enhances the process of drying out during the summer period. To what extent the thin crust of amalgamated soil particles, typical for this vegetation (Beeftink, 1977a), can result from a grazing regime with periodical trampling of the turf is not yet clear. *Armeria maritima* and *Plantago maritima* were sometimes found growing on 3 cm high 'stilt-roots', indicating that the top soil had been compacted after reintroduction of grazing. The possibility that a thin crust could form under such conditions seems small.

The cessation of grazing often leads to a dominance of one species viz. *Halimione portulacoides, Artemisia maritima, Festuca rubra, Elytrigia* spp. A dominance of *Festuca rubra* (Schmeisky, 1974, also citing more authors), *Elytrigia repens* (Schmeisky, 1974), *Puccinellia maritima* (Ranwell in Beeftink, 1977a), *Phragmites australis* (Jensen, 1978; Westhoff & Sykora, 1979) after grazing has stopped is reported elsewhere. The accumulation of litter following the cessation of grazing will decrease the number of species (Grime, 1978). Reintroduction of grazing opens up the canopy and bares the soil providing gaps for the establishment of new species (Grubb, 1977). Changes can be large and sudden in *Elytrigia* spp. communities or small and gradual in *Festuca rubra*/*Armeria maritima* comm. (Bakker, 1978).

Removing of the dominant species can perhaps be named retrogressive succession. The succession which follows leading to new equilibria between different grazing intensities, different substrates and the vegetation can not be named retrogressive succession, despite grazing. The above mentioned successions can be understood as consequences of rise and fall of single dominant species rather than a community development that is reasonably directional and, therefore, predictable (Drury & Nisbet, 1973).

Many species have established (Table 5) due to the canopy getting more open. Halophytic species (both annuals and perennials) establish higher (A.O.D.) on the salt-marsh. The same holds for communities. On the gradient from the lower salt-marsh to the creekbank levee the zoning of bare soil – coenon 1a – coenon 1b – coenon 1c – coenon 1d – coenon 6a – coenon 6b – coenon 3a – coenon 5b can be observed. This zoning coincides with a gradient of decreasing salinity (Schwabe in Ellenberg, 1978). On the grazed area most changes are towards coena previously occurring lower on the gradient whereas on the ungrazed area the reverse is true. Westhoff & Sykora (1979) reported the disappearance of all species of the *Asteretea tripolii* within ten years after grazing was abandoned whereas in the grazed and mown quadrat 33 years after the start of the experiment this class was still represented by *Juncus gerardii* and *Triglochin maritima*. The salt content of the soil in the abandoned area decreased more than in the grazed and mown area. All these suggest an increasing salinity on the grazed salt-marsh. Schmeisky (1974) indeed finds a higher salinity on a grazed salt-marsh in comparison with an ungrazed one. Halophytes rarely occur above their main zone of distribution because they are unable to survive competition with glycophytes (Waisel, 1972).

It is generally accepted that halophytes require high light intensities (Ellenberg, 1978), so abandoning grazing may lead to overgrowth of the assimilatory organs in a dense canopy. Moreover, in laboratory experiments a high light intensity leads to growth reduction of glycophytes at increased salt concentrations of the root medium (Brouwer, 1963). *Puccinellia maritima* above its main zone of distribution is restricted to local hollows (hoofmarks?) or areas opened up by turf-cutting (Gray & Scott, 1977). Certainly Beeftink's (1977a) suggestion that the position of different communities and species with respect to A.O.D., soil salinities and soil moisture can be influenced by grazing, seems to be confirmed in the present study.

Beeftink (1977b) recommends low stocking rates (0.33 cattle.ha^{-1}) for management purposes. Grazing intensity at the Oosterkwelder is rather high (1.3–1.7 cattle-ha^{-1}). A direct comparison, however, is difficult because of the application of fertilizers at part of the salt-marsh adjacent to the study area and accessible to the same animals. Grazing intensity in fact is too high especially during warm summer periods when soil salinity increases and suppresses forage production (Beeftink, 1977b). Another criterion of Beeftink (1977b) for management purposes, to graze large areas as one unit, is fulfilled, because the area of the entire grazed salt-marsh is ca. 110 ha. The practical management problem of the salt-marsh vegetation becoming rugged when it is not grazed (especially due to *Elytrigia* spp. and to a lesser extent *Juncus maritimus*) can very well be solved by the reintroduction of grazing. After five years species richness (alpha-diversity) increased especially in the *Elytrigia* spp. comm. and in the *Juncus maritimus* comm. In the *Festuca rubra* communities and in the *Ammophila arenaria* comm. the number of comm. (beta-diversity) increased and the vegetation pattern became more intricate. The *Artemisia maritima* comm. and especially the *Juncus gerardii* comm. show a rather small increase in diversity. Alpha-diversity decreased only in the *Puccinellia maritimae* comm. due to trampling of the silty turf. Moreover, vegetation structure may change in such a way that it influences the value of the area as a habitat for birds. In the study area grazing improved the foraging possibilities for Barnacle Geese *(Branta leucopsis)* (Ebbinge *et al.*, 1975), and may also have had a positive effect in creating a habitat for breeding birds of short swards (van Dijk, 1974).

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