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Twenty years of salt marsh succession on a Dutch coastal barrier island

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Abstract. After a formerly grazed salt marsh was released from cattle grazing, changes in plant species composition were monitored for 20 yr, using vegetation maps and permanent plots. Three areas, differing in age and nutrient status were compared. The number of plant species and plant communities decreased. *Elymus athericus* (*Elytrigia pungens*) became dominant in most plant communities after 5 - 20 yr on the oldest and most productive salt marsh. In younger areas it took more time for *E. athericus* to become dominant. At least 7 cm of clay seemed to be a prerequisite for this plant species to increase in dominance. The results from monitoring over decades are discussed in view of the knowledge on succession over centuries as derived from a chronosequence.

Keywords: Cattle grazing; Nitrogen pool; Permanent plot; Response curve; Vegetation map.

Nomenclature: van der Meijden et al. (1990).

Introduction

Many studies dealing with succession have presented spatial arrangements of sites representing supposed successional stages, for example colonisation of glacial moraines (Crocker & Major 1955), sand-dune development (Gerlach et al. 1994) and salt marsh development (Olff et al. in press). The concept of chronosequence has become indispensable in the experimental approach of succession (Tilman 1988). Several authors have addressed the question whether succession in salt marsh vegetation can be studied on the basis of the zonation pattern. It appeared that salt marshes with high accretion rates, which in northwestern Europe are mainly found along the mainland coast, show a zonation which indeed represents a successional sere (de Leeuw et al. 1993). However, the zonation pattern in salt marshes with low accretion rates, mainly found on coastal barrier islands, rather reflects the variation in geomorphology of the soil (Roozen & Westhoff 1985; de Leeuw et al. 1993). Some of these islands are moving eastward and show the establishment of salt marsh stages from east to west. The chronosequence in such marshes is characterized by an increasing thickness of the clay layer towards the older zones (van Wijnen & Bakker 1997; Olff et al. in press).

The thickness of the clay layer is positively correlated with the total nitrogen pool (Olff et al. 1997). Hence older marshes have more nitrogen in the soil and a higher above-ground standing crop (Bakker et al. 1993; van de Koppel et al. 1996). The salt marsh on Schiermonnikoog seems to parallel the beach plain succession in which N was shown to be limiting the plant production. *Elymus athericus* is one of the main dominant plant species at the older stages of the salt marsh where it covers a large part of the zonation (Bakker 1989; Olff et al. in press; van Wijnen & Bakker 1997).

Elymus athericus is one of the main dominant plant species of the older stages of the salt marsh where it covers a large part of the zonation (Bakker 1989; van Wijnen & Bakker, this issue). The dominance of *Elymus athericus* is not found on cattle-grazed salt marshes. Grazed salt marshes support several plant communities along the gradient from high to low marsh elevation (Dijkema 1983), each containing more plant species than a community dominated by *Elymus athericus* (Bakker 1989).

The coastal barrier island of Schiermonnikoog features a chronosequence representing salt marsh sites varying from a few years to 200 yr old (Olff et al. in press). Most of the oldest part of this salt marsh was grazed by cattle up to 1958 (den Hartog 1952; Bakker 1989). Locally, grazing was stopped when exclosures were established (Bakker 1989). The effects of cessation of grazing have been monitored for more than 20 years, which enables the study of long-term succession. These results will be compared with patterns derived from chronosequences.

For our study, we formulated two hypotheses: (1) succession after the cessation of grazing will result in a dominance of a few species and hence a decrease in the number of plant communities and the number of plant species, (2) at the older salt marsh with a thicker layer of clay and a larger nitrogen pool, more rapid succession will take place than at younger salt marsh sites.

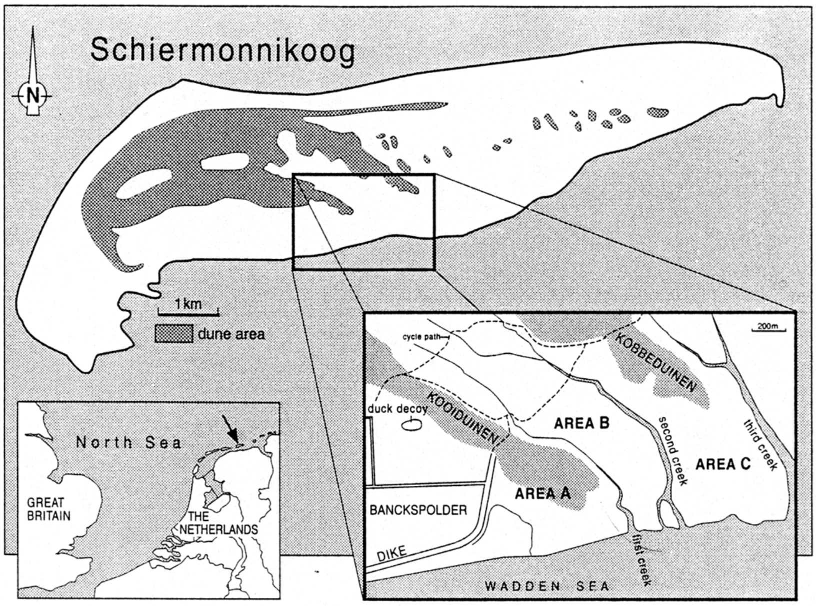

Fig. 1. Map of the study area on Schiermonnikoog. A, B and C indicate areas with different grazing regimes (see text). (After Bakker 1989.)

Methods

Site description

Vegetation changes were monitored in the most western and therefore oldest part of the salt marsh of Schiermonnikoog, The Netherlands (Fig. 1). The age of the marsh in area A was estimated from historical records to be 200 yr. Cattle have grazed the marsh since ca. 1850. Two exclosures (10m × 50m) were established in 1973 in this area to monitor changes after grazing stopped. One was established at high elevation, from a dune downwards, the other one was established at low elevation.

Area B was estimated to be 120 yr old. Grazing by cattle stopped in 1958 but was reintroduced in 1972. In this year, exclosures were established, each in a different plant community. Six plant communities were recognized at that time, characterized by (1) *Plantago maritima*, (2) *Juncus maritimus*, (3) *Elymus athericus*, (4) *Juncus gerardi*, (5) *Festuca rubra* and (6) *Artemisia maritima*.

Area C was estimated to be 100 yr old. Grazing by cattle stopped in 1958 and was reintroduced in 1987.

This all means that the exclosed parts of area A have not been grazed for 22 yr, the exclosed parts of area B have not been grazed for 37 yr and area C was not grazed for 29 yr in 1987, but is now being grazed again by cattle. Cattle were present in these areas from the end of May until October. From 1972-1987, the stocking rate was ca.1.6 animals/ha. After 1987, the stocking rate decreased to 1.0 animals/ha.

Permanent plots

In area A, 14 permanent plots were established inside the exclosures and 12 permanent plots outside them. The vegetation was recorded in these permanent plots (2m × 2m) in August, using cover estimations according to Westhoff & van der Maarel (1978). These recordings were made in 1973, directly after the cessation of grazing, and were repeated in 1995. In addition, the thickness of the clay layer on top of the sandy substrate was measured with a soil corer in the permanent plots

In each exclosure in area B, one permanent plot was established. From 1971-1995, vegetation recordings were carried out in the permanent plots (2m × 2m) each year in August (see Bakker 1989, p. 194). Clay thickness was measured in each permanent plot. The permanent plots in the areas A and B were levelled relative to Dutch Ordnance Level (N.A.P.) and related to Mean High Tide (MHT) level. MHT averaged 100 cm +N.A.P.

No permanent plots were established in area C. Clay thickness in this area was measured along a transect of 50 m, which ran from a dune to the low salt marsh. In several plant communities along this transect, the thickness of the clay layer and the elevation of the marsh surface relative to MHT-level was measured with a soil corer.

Vegetation mapping

The exclosures in area A were mapped in 1973, 1978, 1985, 1990 and 1995 according to Londo (1974), using black and white aerial photographs scale 1:10000. Mapping of vegetation complexes was avoided (Bakker 1989, p. 217). Area B was mapped in 1971, 1976, 1981 and 1986, and area C was mapped in 1974 and again in 1986. The plant communities were classified on the basis of ca. 1000 vegetation analyses (see Bakker 1989, p. 186). The same classification of plant communities was adopted for all vegetation maps.

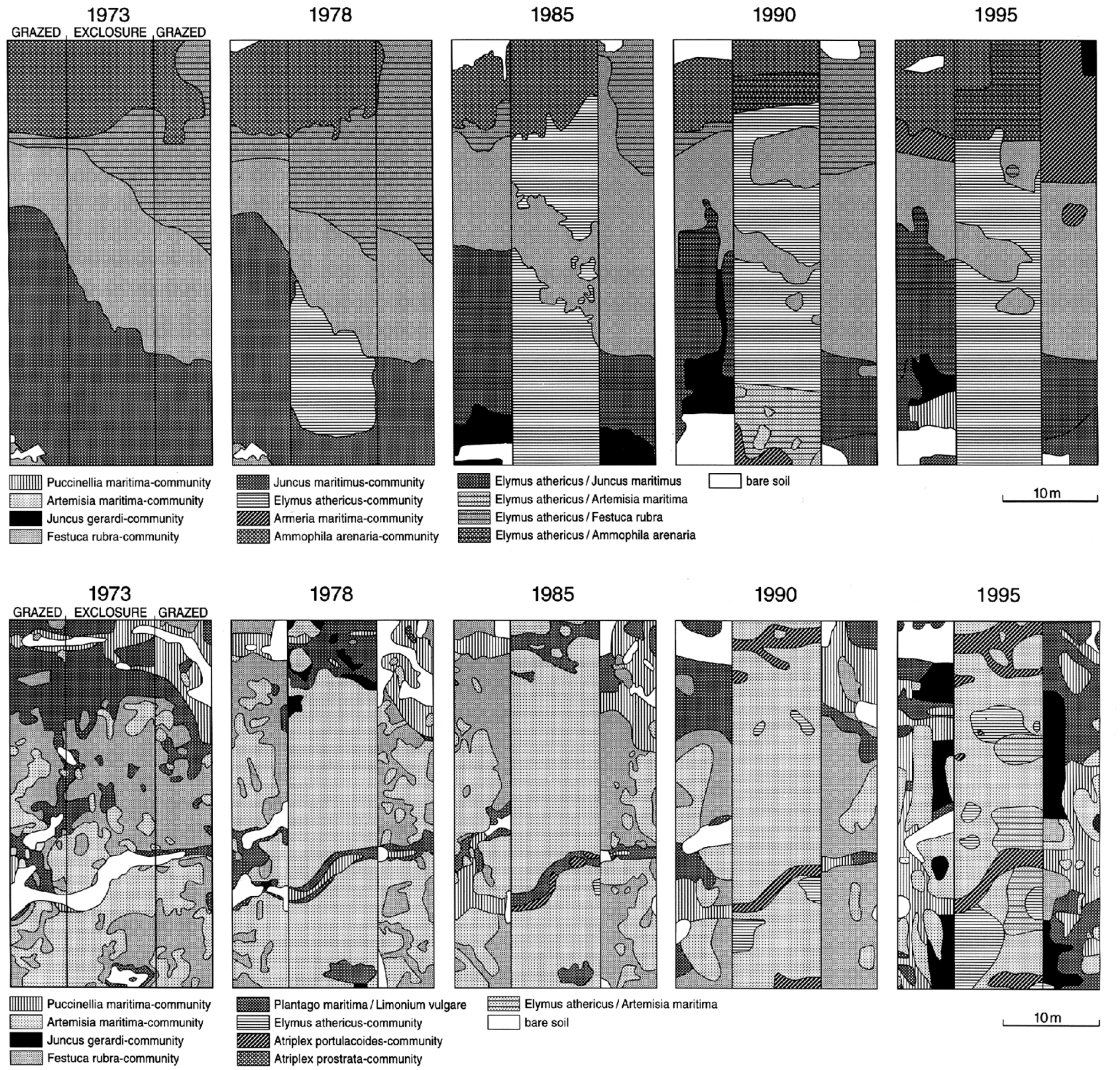

Fig. 2. Maps of the exclosure on the high salt marsh in area A (top) and maps of the exclosure on the low salt marsh in area A (bottom).

Analysis

The permanent plot data sampled in area B from 1971 until 1994 were analyzed using response analysis (Huisman et al. 1993). Percentage species cover was fitted against time, using non-linear regression. The simplest possible out of five models with increasing complexity was selected. The five models are given in App. 1.

The nitrogen pool in the sediment of area A, B and C was calculated, using the equation: Np = 19 $*C$ + 125 (van Wijnen & Bakker 1997), where Np = Nitrogen pool in the sediment (g N m^{-2} yr^{-1}, 0 - 50 cm depth) and C = thickness of the clay layer (cm).

Results

Area A, salt marsh 200 yr old, ungrazed for 22 yr

The maps of the high salt marsh in Fig. 2 (top) show an increase of *Elymus athericus* resulting in a large area covered by the *Elymus athericus* community inside the exclosure after 22 yr. In the grazed area *Elymus athericus* increased as well, but this occurred only under the protection of *Juncus maritimus* stands. In the low salt marsh (Fig. 2 bottom), the *Artemisia maritima* community became the main dominant community together

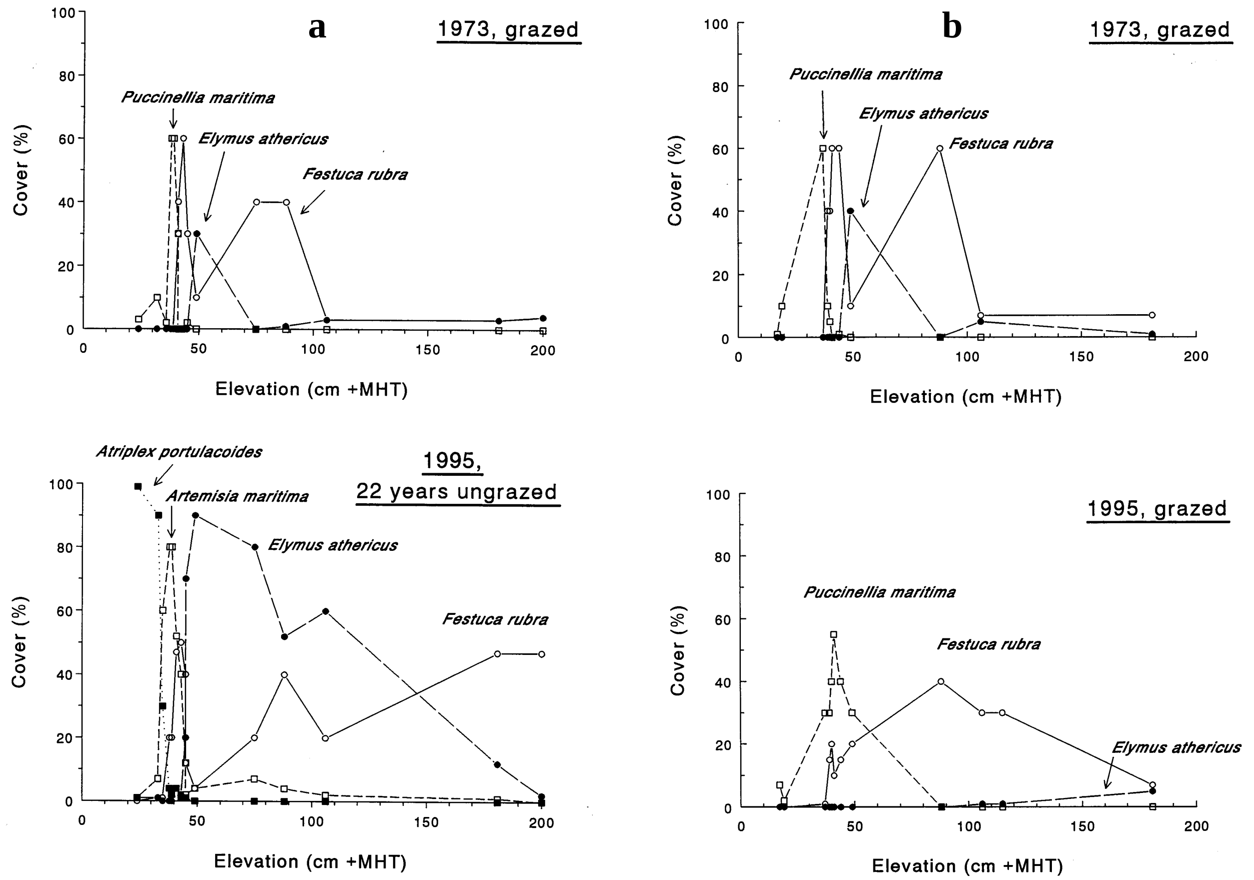

Fig. 3a. Plant cover in relation to elevation for the most abundant plant species in the salt marsh of area A, which was grazed in 1973 but had been ungrazed for 22 yr in 1995. **b.** Plant cover in relation to elevation for the most abundant plant species in a salt marsh of area A which was continuously grazed from 1973-1995.

with the *Atriplex portulacoides* community in the lower parts. The *Elymus athericus* community has started to invade the *Artemisia maritima* community after 15 yr. A decrease in patchiness of the plant communities was found in the ungrazed area.

When relating the cover per plant species in the permanent plots in 1973 and 1995 to the elevation of the marsh surface (Fig. 3a), it became clear that *Puccinellia maritima* decreased when the marsh was not grazed for a period of 22 yr, whereas *Atriplex portulacoides*, *E. athericus*, *Artemisia maritima* and *Festuca rubra* increased. *Atriplex portulacoides* showed an optimum below 25 cm +MHT, *A. maritima* at 40 cm +MHT, *E. athericus* at 50 cm +MHT, with high abundance towards 150 cm +MHT, and *Festuca rubra* increased in cover above 150 cm +MHT. The decrease of *P. maritima* seemed to be filled up by *A. maritima*. The continuously grazed area did not change much in species distribution (Fig. 3b). *P. maritima* replaced *F. rubra* at 40 cm +MHT.

Area B, salt marsh, 120 yr old, ungrazed for 37 yr

The area inside the broken line (fence) in Fig. 4 had been grazed after 1971. An increase in area cover of the communities characterized by *Festuca rubra*, *Juncus gerardi*, *Armeria maritima* and *Juncus maritimus* was found. The communities characterized by *Elymus athericus*, *Ammophila arenaria* and *Artemisia maritima* decreased in area. Outside the fence, near the creeks and the mud flat, the area had been ungrazed since 1958. Especially the *Elymus athericus* community showed a large increase in area.

The community characterized by *Plantago maritima* and *Festuca rubra* at 65 cm +MHT (Fig. 5) remained relatively unchanged. *Plantago maritima* showed a small optimum, 32 years after cessation of grazing. The community characterized by *Juncus maritimus* at 59 cm +MHT, changed towards a community with *Festuca rubra* when the marsh had not been grazed for 27 yr. *Elymus athericus* became dominant 5 yr later with more than 80 % cover. In an originally *Elymus athericus*

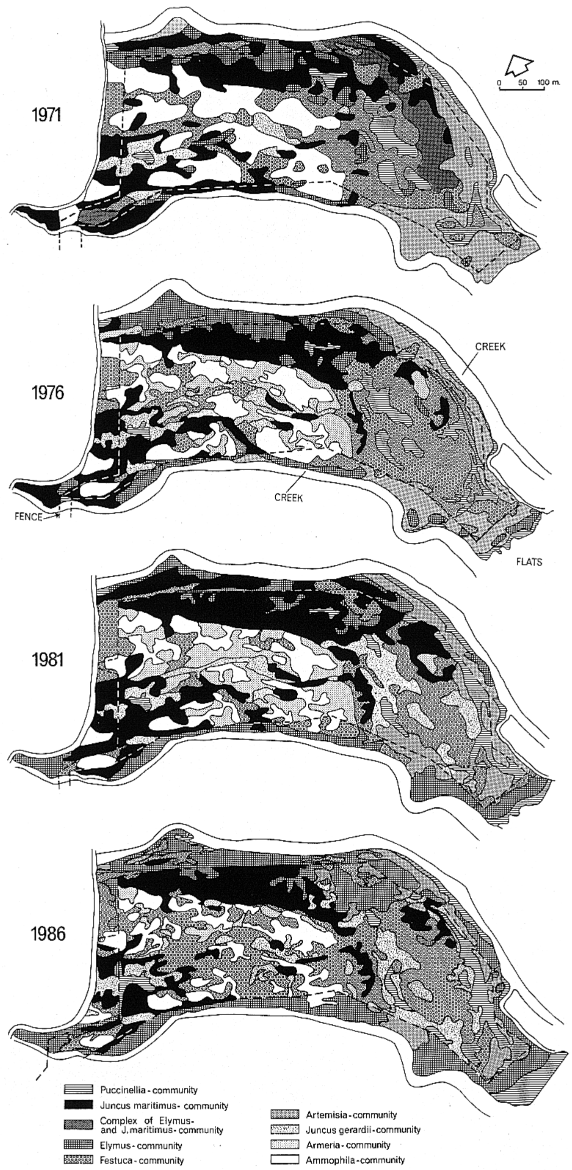

Fig. 4. Maps of area B in four different years. The broken line represents a fence. Inside the fence, the area has continuously been grazed since 1972. Outside the fence, the area has been ungrazed since 1958.

community at 54 cm +MHT, *E. athericus* remained dominant with more than 80% cover. In a *Juncus gerardi* community at 53 cm +MHT, *F. rubra* increased in cover after 15 years of non-grazing. Both *J. gerardi* and *F. rubra* remained present with more than 30%. Ca. 30 yr after grazing ceased, *Artemisia maritima* and *Elymus athericus* were invading and *Juncus gerardi* disappeared. At an elevation of 51 cm +MHT, the community characterized by *Festuca rubra* changed into a community with *A. maritima*. *E. athericus* became dominant 30 yr after cessation of grazing. Finally at 47 cm +MHT, the *A. maritima* community changed temporarily towards a community characterized by *F. rubra* and after 30 yr, *E. athericus* became the most dominant plant species. For details on the regression curves, see App. 1.

Area C, salt marsh, 100 yr old, abandoned for 29 yr

The major changes in area C occurred in the *Artemisia maritima*, *Juncus maritimus* and *Elymus athericus* communities (Fig. 6). A decrease in area cover was found for the *Artemisia maritima* and *Juncus maritimus* communities, whereas the *Elymus athericus* community increased after 29 yr of non-grazing. The *Elymus athericus* community covered more than 50 % of area C after this period. Other communities like those characterized by *Festuca rubra* and *Juncus gerardi*, remained relatively unchanged.

Table 1. Time after cessation of grazing (TC) in years, needed for *Elymus athericus* to become dominant with a cover percentage of > 50 % in several plant communities. Elevation classes in cm+MHT, the thickness of the clay layer in cm and the nitrogen pool size, in gN/m^2, 0-50cm.

Plant community	Elevation	A			B			C		
		TC	clay	N	TC	clay	N	TC	clay	N
Ammophila arenaria	100 - 200	>22	0	125	>36	0	125	>36	0	125
Armeria maritima	60- 100	20	7	258	>36	4	201	>36	0	125
Festuca rubra	50- 70	22	10	315	30	8	277	>36	4	201
Juncus maritimus	50- 60	10	14	391	30	10	315	30	8	277
Elymus athericus	50 -60	10	14	391	30	10	315	30	8	277
Juncus gerardi	40- 50	>22	15	410	>36	12	353	>36	10	315
Artemisia maritima	40-50	>22	17	448	30	12	353	>36	12	353
Puccinellia maritima	30-40	>22	17	448	>36	12	353	>36	12	353
Salicornia europaea	20-30	>22	17	448	>36	12	353	>36	12	353

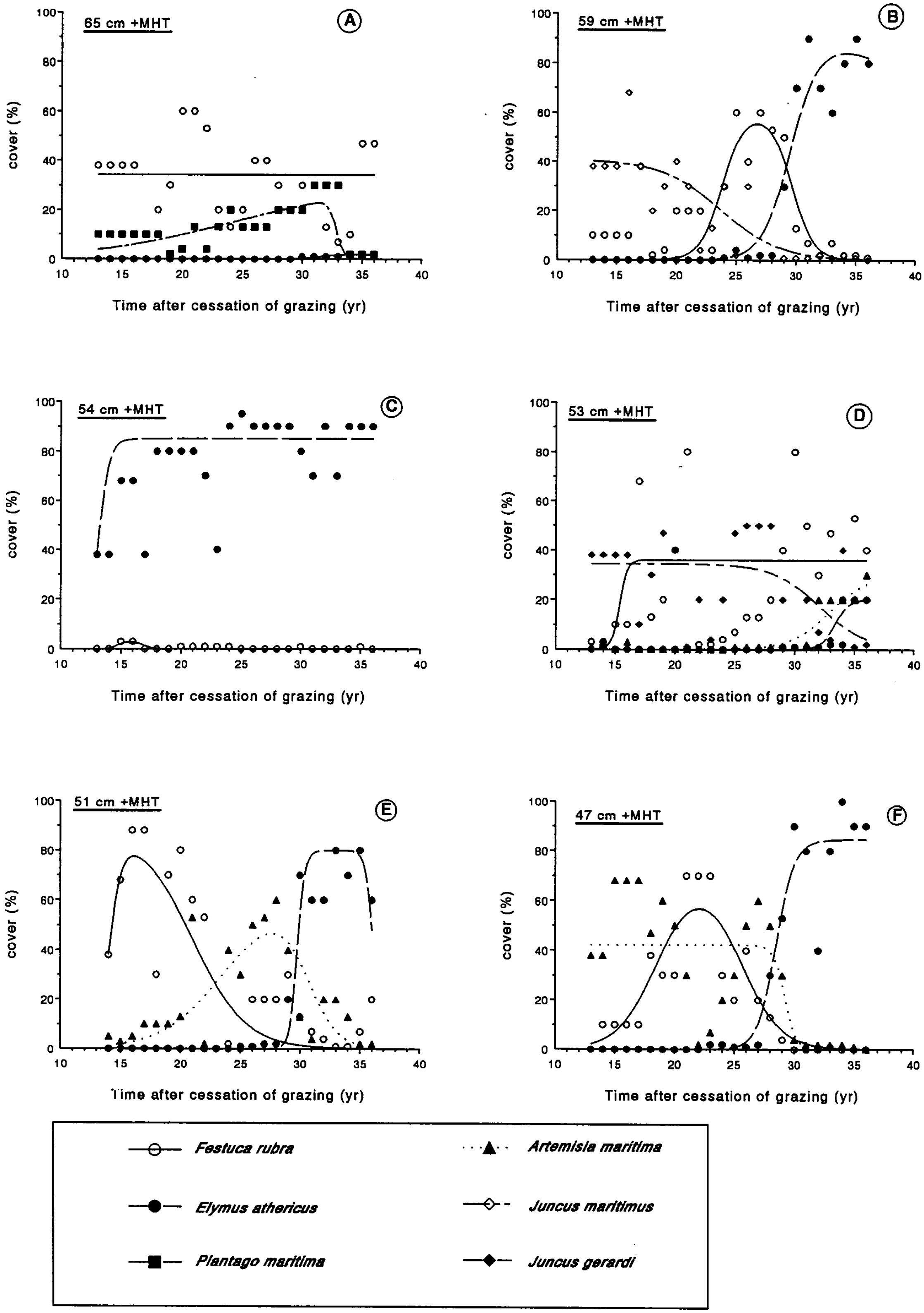

Fig. 5. Changes in plant species cover from 13 - 36 years after cessation of grazing for six sites in area B. These sites differed in elevation and plant community at the time the exclosures were established. Site A was a *Festuca rubra*/*Plantago maritima* community; B was a *Juncus maritimus* community; C was an *Elymus athericus* community; D was a *Juncus gerardi* community; E was a *Festuca rubra*/*Artemisia maritima* community and F was an *Artemisia maritima* community.

Extension of Elymus athericus

In the communities between 50 and 100 cm +MHT, the mid and upper salt marsh, *Elymus athericus* became dominant in area A earlier than in B and C (Table 1). This difference was not found for the low salt marsh plant communities below 50cm +MHT, nor for the *Ammophila arenaria* community at the foot of the low dunes. At least 7 cm of clay (which is equivalent to 258 g N/m^2; see Table 1) is necessary for *Elymus athericus* to become dominant in the high salt marsh plant communities. A thicker clay layer resulted in an earlier dominance of this species.

In the grazed salt marsh, the number of plant species did not change between 1973 and 1995 (Table 2). For the salt marsh that was released from grazing, a clear decrease in the number of species was found. This holds only true for the salt marsh between 37 and 88 cm +MHT. At a similar elevation, *Elymus athericus* has previously been found to become dominant (Fig. 3a).

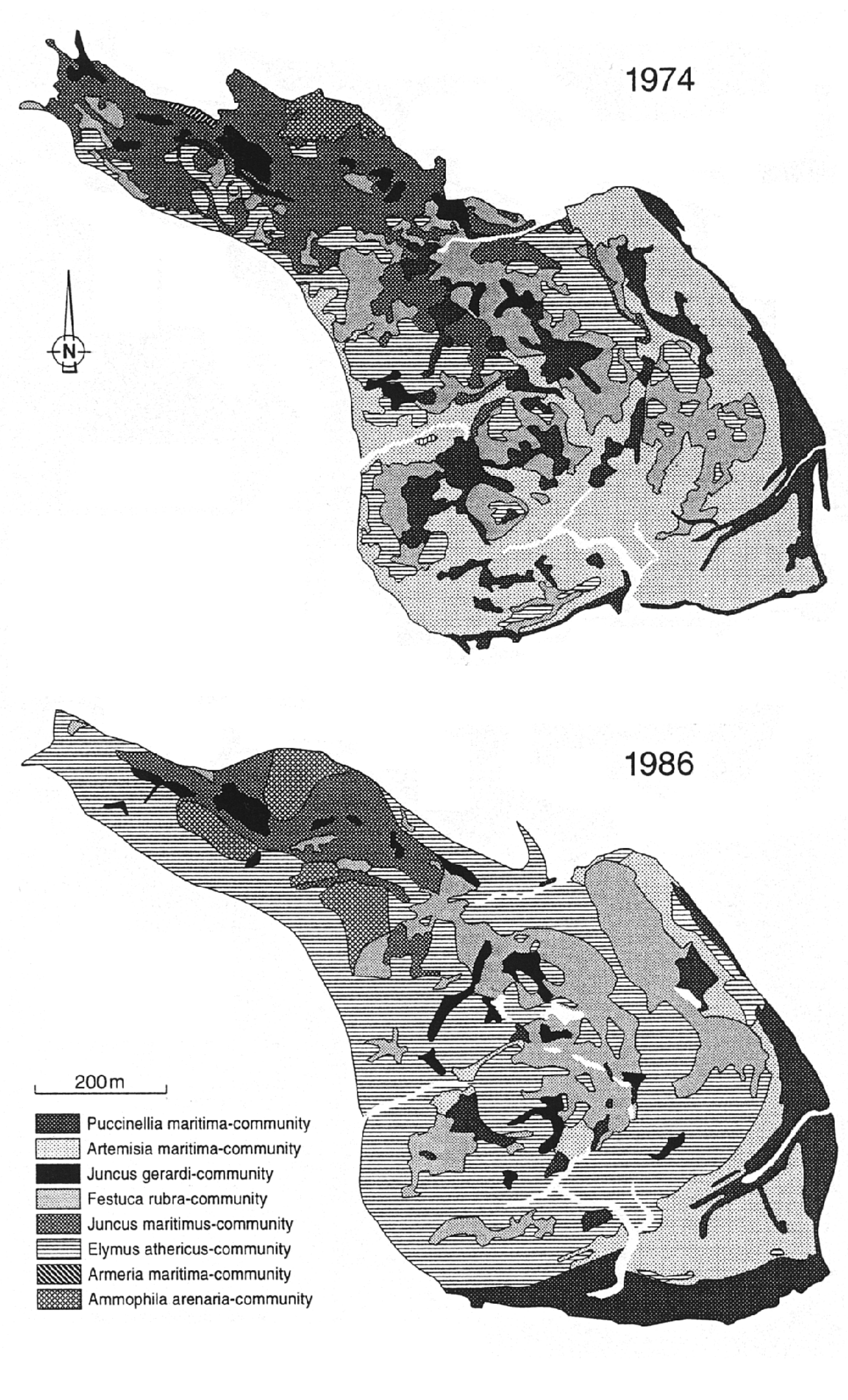

Fig. 6. Map of area C in 1974 (top) and in 1986 (bottom).

Discussion

Permanent plots in this study gave detailed information about changes in species composition at a particular site for a long period. However, a limited number of permanent plots was monitored, which raises the question how representative these sites are. Therefore, vegetation mapping allowed us to generalize a certain successional pattern for a larger area (Londo 1974).

We hypothesized that succession after cessation of grazing will result in a dominance of a few species and hence a decrease in the number of plant communities and plant species. *Elymus athericus* became dominant in most plant communities after ca. 30 yr of non-grazing. This resulted in a reduction of the number of plant communities from six communities at the end of the grazing regime to three communities after 30 yr of non-grazing. In addition, the number of plant species declined when grazing was stopped. In a potentially productive environment such as area A, plant species density will be low when there is no disturbance, such as the removal of above-ground biomass caused by cattle grazing (Grime 1979). Probably, the dominance of tall growing species such as *Atriplex portulacoides*, *Artemisia maritima* and *Elymus athericus* which are supposed to be superior competitors for light (Tilman 1985; Scherfose 1993) are responsible for this effect.

The second hypothesis was that at the older salt marsh sites with a thicker clay layer and hence a larger nitrogen pool, more rapid succession will take place than at younger salt marsh sites (cf. Table 1). *Elymus athericus* became dominant earlier on the older site (area A) than on the younger sites, dependent on the elevation of the marsh surface. This species did not become dominant in the permanent quadrats below 50 cm +MHT, although from the maps it became clear that *Elymus athericus* already had started to spread in these low salt marsh communities. This discrepancy is due to the fact that the permanent plots only represent small-scale changes and hence do not always represent larger scaled changes (Londo 1974).

Table 2. Number of plant species in a continuously grazed salt marsh of area A and a salt marsh which had been ungrazed between 1973 and 1995, in relation to the elevation of the marsh surface (cm +MHT).

	Grazed		Ungrazed	
Elevation	1973	1995	1973	1995
24	-	-	3	6
32	-	-	5	9
37	12	11	14	6
39	11	12	10	7
41	11	10	11	7
44	10	15	11	5
49	11	16	10	5
69	-	-	9	7
88	9	9	14	8
106	14	10	13	13
181	15	18	16	16

Primary succession, described for a 100-yr old salt marsh on Schiermonnikoog (Olff et al. in press) and a 60-yr old salt marsh on Terschelling (Roozen & Westhoff 1985), showed a similar shift in species composition as presented here. *Atriplex portulacoides* became dominant on the lowest salt marsh and *Elymus athericus* became dominant on the higher salt marsh after 60-100 yr of succession. Species such as *Artemisia maritima* and *Festuca rubra* had an optimum in intermediate stages. In the chronosequence on Schiermonnikoog, the primary succession proceeded from a bare sand flat to a salt marsh with high nutrient pools. The rate of succession depended on the accumulation rate of the nutrients (van de Koppel et al. 1996). Succession in our case did not start in a low productive environment, but at the productivity level of a 100-200 yr old salt marsh. This could be an explanation for the fact that the rate of succession after cessation of grazing was found to be higher in our case. Dependent on the elevation of the marsh, *Atriplex portulacoides* and *Elymus athericus* will become dominant when the marsh is completely abandoned from cattle grazing. So far, there are no indications that other species will replace *Elymus athericus* and *Atriplex portulacoides* when salt marshes become older.

Management

Finally, we will discuss some perspectives for management of salt marshes. Some controversies exist whether salt marshes should be grazed by domestic cattle in order to achieve a high diversity in plant species and plant communities. The designation of man-made salt marshes as nature reserves and national parks has led to a change of management aims from reclamation of land and intensively agricultural exploitation, especially of man-made marshes, towards restoration of ÔnaturalÕ marshland. The latter option includes the cessation of livestock grazing (Kiehl & Stock 1994). Salt marsh management may consist of laissez-faire, grazing or haymaking. The effects of haymaking are more or less similar to those of grazing at high stocking rate. The constraint is that the plant species richness is lower than at grazing because of the dense turf at continued haymaking (Bakker 1989). In sandy barrier-island marshes, with a clay layer thicker than 7cm Ð as shown in the present study Ð cessation of grazing by livestock will eventually result in a dominance of *Elymus athericus* in the higher and middle marsh zone. The thicker the layer of clay and hence the higher nutrient availability, the lower down the salt marsh *Elymus* may spread. At the feet of larger dunes *Phragmites australis* will become dominant as a result of fresh water seepage. In the lower part of the salt marsh *Atriplex portulacoides* will become dominant, while in the pioneer zone *Salicornia procumbens* will be the dominant species. This will be the climax vegetation at the never grazed Boschplaat at Terschelling, The Netherlands, as predicted by Westhoff & van Oosten (1991). Only at young barrier islands with a clay layer thinner than 7 cm will *Elymus athericus* not reach dominance. In such relatively low productive conditions, plant species such as *Limonium vulgare*, *Plantago maritima* and *Artemisia maritima*, attractive for the characteristic halobiontic entomofauna, can maintain themselves (Dijkema 1990). These plant species do thrive on older salt marshes after livestock has been excluded for some years, but eventually disappear as shown in the present study. Succession towards older salt marshes also includes the disappearance of small herbivores like geese and hares (van de Koppel et al. 1996). Special attention should be paid to salt marshes that never have been grazed by livestock as they are very rare (Dijkema 1990). These areas give a unique opportunity to study natural succession of geomorphological conditions, plants, animals and their interactions. Grazing on these salt marshes is, therefore, not recommended.

Within 10yr, *Elymus athericus* started to spread in a no-longer-grazed salt marsh (Andresen et al. 1990), and *Elymus repens* reached dominance in a brackish marsh (Esselink et al. in press). As in other brackish marshes and in estuaries of the Wadden Sea, abandonment of grazing will ultimately lead to a climax vegetation of *Phragmites australis* in the entire marsh and the disappearance of the halophytic vegetation (Aerts et al. 1996). Not only the vegetation will change after cessation of grazing by livestock, but also the entomofauna (Andresen et al. 1990) and the avifauna, including both breeding and migrating birds (Bakker et al. in press). The short-term studies on the effects of excluding livestock on man-made salt marshes carried out until now, may be misleading in relation to long-term effects (Irmler & Heydemann 1985; Meyer et al. 1995; Kiehl et al. 1996).

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App. 1. Model parameters and characteristics per species for six sites in area B (salt marsh, Schiermonnikoog). Per site are given: elevation in cm +MHT, the type pf model used (I - V), four parameters (a -d), the maximum value (M) and the proportion of variance explained by the model (R^2). E = elevation;

Model I: M*(1/(1+exp(*a*)))
Model II: M*(1/(1+exp(*bx* + *a*)))
Model III: M*(1/(1+exp(*bx* + *a*)))*(1/(1+exp(*c*)))
Model IV: M*(1/(1+exp(*bx* + *a*)))*(1/(1+exp(*Đbx* +*d*)))
Model V: M*(1/(1+exp(*bx* + *a*)))*(1/(1+exp(*dx* + *c*)))

E	Plant species	Model	a	b	c	d	M	R^2
65	*Elymus athericus*	II	19.8	Đ 24.8	-	-	1.98	0.97
	Festuca rubra	I	Đ65.0	-	-	-	34.2	-
	Plantago maritima	V	Đ60.2	69.8	1.9	Đ3.9	22.8	0.80
59	*Elymus athericus*	V	Đ9.2	6.8	14.2	Đ19.8	83.7	0.98
	Festuca rubra	IV	Đ18.2	25.1	11.8	-	55.2	0.83
	Juncus maritimus	III	Đ4.3	9.2	Đ0.4	-	40.1	0.83
54	*Elymus athericus*	II	0.2	Đ49.8	-	-	40.1	0.83
	Festuca rubra	V	Đ10.2	59.8	5.2	Đ70.2	2.8	0.82
53	*Artemisia maritima*	II	12.2	Đ14.1	-	-	26.1	0.95
	Elymus athericus	II	35.2	Đ39.8	-	-	19.8	0.92
	Festuca rubra	V	0.2	0	7.2	Đ70.2	36.0	0.39
	Juncus gerardi	III	Đ9.8	11.8	Đ0.8	-	34.5	0.50
51	*Artemisia maritima*	V	Đ13.8	18.2	3.8	Đ8.8	46.8	0.76
	Elymus athericus	IV	Đ70.2	69.8	50.1	-	80.0	0.99
	Festuca rubra	V	Đ3.2	10.0	0.2	Đ40.2	77.4	0.85
47	*Artemisia maritima*	III	Đ35.2	49.8	Đ0.5	-	42.2	0.75
	Elymus athericus	III	20.2	Đ30.0	Đ1.7	-	85.0	0.99
	Festuca rubra	IV	Đ7.8	14.2	3.4	-	56.7	0.93