To graze or not to graze: that is the question

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Abstract

Changing land use in both natural and artificial salt marshes shifted the focus from coastal protection and agricultural exploitation towards nature conservation interest. Transformation of large areas into nature reserves or national parks included abandoning of livestock grazing by some authorities in charge of management. Succession in natural salt marshes that have never been grazed by livestock, shows a climax of the shrub *Atriplex portulacoides* at the lower marsh and the tall grass *Elymus athericus* at the higher marsh of Schiermonnikoog. As this salt marsh has an age of about 40 years, the long-term climax of natural succession is not known. Exclosure experiments at the always cattle-grazed marsh of Schiermonnikoog, reveals an increase of *Atriplex portulacoides* at the lower and of *Elymus athericus* at the higher marsh. The species richness in permanent plots (4 m^2) decreases in abandoned areas on the marshes at Schiermonnikoog, Terschelling and Skallingen. The species richness is always higher in grazed plots ranging from 0.01-2500 m2 in artificial marshes in the Netherlands.
Long-term (over 20 years) experiments with exclosures and different stocking rates of cattle and sheep in the Netherlands and Germany, show that the *Elymus athericus* community can get dominant in both natural and artificial marshes. Subsequently, the number of plants communities decreases. Exceptions seem to be related to low rates of sedimentation or influence of fresh water. Experiments lasting less than 10 years show no dominance of the *Elymus athericus* community. Changes in canopy structure towards a taller vegetation after abandoning or decreasing stocking rate, has negative effects on winter and spring staging geese, and positive effects on some breeding birds. As with natural succession, further changes may take place at the longer term. Continuation of these experiments and monitoring are of vital importance to draw further conclusions. As results of abandoning or reduction of stocking rate may affect various organisms in different ways, the task for salt-marsh management is to define the management goal. After that the means to reach the target can be decided upon, and the question 'to graze or not to graze' can be answered.

Nomenclature of plant species follows Van Der Meijden 1990

Introduction

Salt marshes could establish in the Wadden Sea area since 600 BC as a result of slowing down of the sea-level rise after the last Glacial Period (Behre, 1996). They resulted from sedimentation of silt during tidal inundation. As the sediment included nutrients, salt marshes harbour fertile soil with subsequent high plant production capacity. Therefore, it is no surprise that salt marshes have been agriculturally exploited from their very origin as grazing ground for livestock. Landuse by grazing in the entire Wadden Sea area has been practised for about 2600 years now. Initially it took place on natural salt marshes, but since several centuries also on artificial salt marshes, that mainly developed along the mainland coast. More details on salt-marsh development and its landuse are reviewed by Esselink (2000).

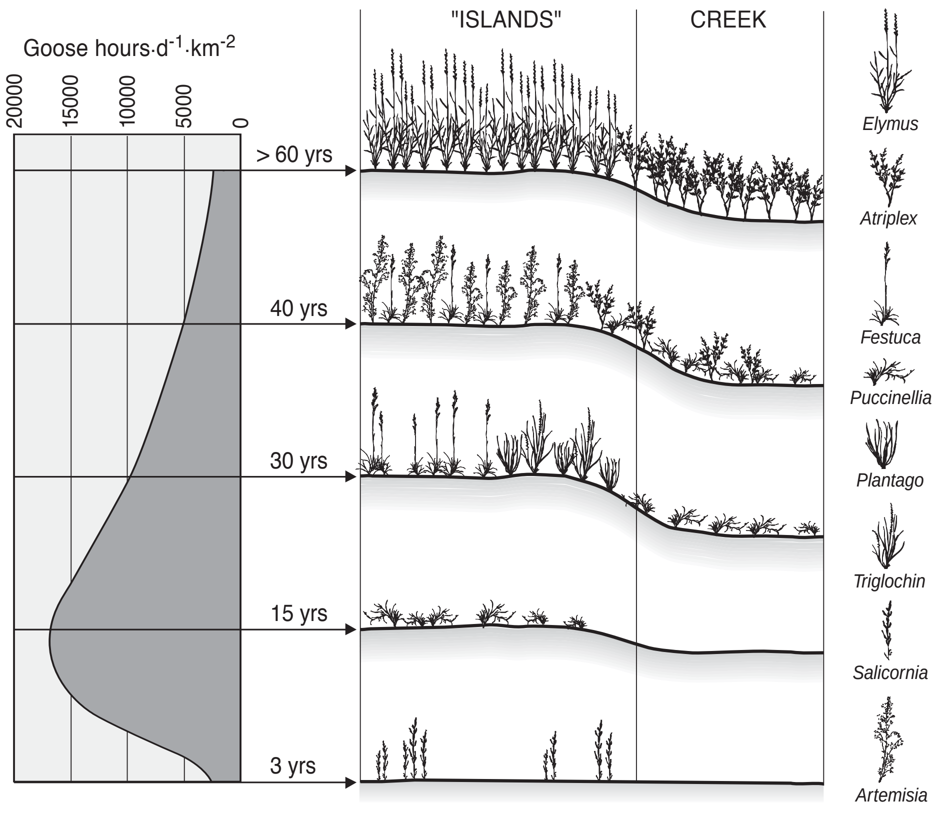
Currently about 50% of the salt-marsh area in the international Wadden Sea is grazed by livestock (De Jong *et al.*, 1999). Large areas have been taken out of grazing over the past twenty years. These changes in landuse have two reasons. Locally, farmers are loosing interest in these nowadays marginal areas compared to the high intensity farming in inland areas. Secondly, several authorities in charge of nature conservation stop all human interference, including livestock grazing. This especially holds for heavily grazed artificial marshes in Germany, where the management aim is to turn these marshes into more natural salt marshes (Stock, 1993; Kiehl & Stock, 1994).

To understand the effects of cessation of grazing, we will first discuss the natural succession on salt marshes and compare these to livestock-grazed marshes. The back barrier salt marsh of the Dutch island of Schiermonnikoog shows documented natural succession. The eastern part continuously extends further eastward. Salt-marsh development takes place in the shelter of dunes fringing the North Sea beach. Hence, a chronosequence, representing succession (De Leeuw *et al.*, 1993; Olff *et al.*, 1997) has established featuring very young marsh at the east

Figure 1. Development of the eastern part of Schiermonnikoog. Different age classes of the vegetation as derived from maps and aerial photographs are indicated.

and older marshes more to the west, ranging from zero to about 150-200 years (Figure 1). Increasing age of the marsh coincides with thicker layer of sediment resulting from tidal inundations. The thickness of the sediment layer correlates positively with the nitrogen pool (Olff *et al*., 1997; Van Wijnen & Bakker, 1997). The increasing nutrient availability results in more plant biomass and a taller canopy (Van De Koppel *et al*., 1996). In this chronosequence species replacement can be recorded. The lower salt marsh starts with *Salicornia* spp., *Puccinellia maritima* followed by *Spergularia maritima*, *Plantago maritima*, *Limonium vulgare*, and *Atriplex portulacoides* at the oldest stage. The higher marsh features *Puccinellia maritima*, *Festuca rubra* followed by *Artemisia maritima*, and eventually *Elymus athericus* (Olff *et al*., 1997) (Figure 2).

Figure 2. Changes in vegetation during salt-marsh succession at Schiermonnikoog. Lower marsh transforms into an Atriplex portulacoides marsh. The higher marsh turns from a Puccinellia maritima sward into Festuca rubra, after which Artemisia maritima and eventually Elymus athericus invade. Brent goose grazing pressure is highest towards the younger salt-marsh stages, after which succession evicts the geese (after Drent & Van Der Wal 1999).



The oldest part (150-200 years) of the salt marsh of Schiermonnikoog has always been cattle grazed and harbours communities with *Salicornia* spp., *Plantago maritima*, *Limonium vulgare*, *Puccinellia maritima* at the lower marsh and with *Festuca rubra*, *Juncus maritimus*, and locally *Elymus athericus* at the higher marsh. Despite the high age, thick layer of sediment and large nutrient pool (Van Wijnen & Bakker, 1997), cattle have prevented the tall plant species *Atriplex portulacoides* and *Elymus athericus* from becoming dominant. Instead, they have set back the successional clock to plant communities harbouring species naturally occurring at younger salt marshes, be it at different abundances (Olff *et al*., 1997). We expect under such conditions, where the successional clock has been reset that the cessation of grazing will quickly result in a vegetation composition that matches the nutrient pool; i.e. a vegetation that would have occurred without livestock grazing. We will try to place the effects of cessation of livestock grazing into the framework of the undisturbed succession at the natural salt marsh of Schiermonnikoog. Several case studies on the effects of the cessation of grazing have been carried out on natural island and artificial mainland salt marshes in Denmark, Germany and the Netherlands. The scale of recording ranges from permanent plots of 4 m^2, surveys up to 2500 m^2 and vegetation mapping of larger study sites.

The aim of the present paper is (i) to compare natural succession and secondary succession after the cessation of grazing, (ii) to bring together individual studies at different spatial scale on the effects of cessation of livestock grazing, (iii) to conclude to which extent generalisation for the international Wadden Sea is possible. Finally, we will discuss grazing as a tool for salt-marsh management in relation to possible targets.

Methods

Study sites for permanent plots

All study sites with permanent plots are classified as barrier-connected salt marshes (De Jong *et al*., 1999).

The first study site is located at the island of Schiermonnikoog, The Netherlands (Table 1). Stocking rates decreased from 1.5 cattle.ha^{-1} in the 1970s to 0.5 cattle ha^{-1} from 1995 onwards. Two exclosures (50 x 12.5 m) were erected in 1973, one at the transition of a low dune to the higher salt marsh, the other at the somewhat lower marsh (Bakker, 1989). We established 15 paired permanent plots (inside and outside the exclosures). The vegetation composition in the plots was recorded annually.

The second study site is located at the island of Terschelling, The Netherlands (Table 1). The site was grazed for over a century. The Terschelling marsh 'De Groede' is grazed with 175 cattle and about 15 horses amounting to 0.5 livestock ha^{-1}(authorities in charge of management, pers. comm.). Two exclosures (30 x 30 m) were erected in 1971 (Bakker, 1983). One at the transition of a low dune to the higher marsh, the other at the high marsh. Both exclosures were adjacent to larger dunes systems, hence received fresh seepage water. The third experimental site was at a transect of higher to lower marsh. Here the position of the fence was changed in such a way that four situations were established: control ungrazed, experimentally grazed, control

Table 1. Overview of the study sites: substrate, position, area, level with respect to Mean High Tide (MHT), grazing management (1 sheep unit equals 2.8 sheep).

Site	position	cm +MHT		area (ha)	stocking rate *(animals ha^{-1})*
permanent plots					
Schiermonnikoog NL	53°30'N 6°10'E	high excl.	41-181	120 1970s	1.5 cattle
natural/sand		ow excl.	17-45	400 1990s	0.5 cattle
Terschelling NL	53°26'N 5°28'E	high excl.	139-268	400	0.5 cattle and
natural/sand		transect	28-99		some horses
Skallingen DK	55°30'N 8°20'E	high excl.	56-179	600	0.5 cattle
natural/sand		low excl.	39-44		0.5 sheep
vegetation mapping					
Schiermonnikoog NL	53°30'N 6°10'E	high excl.	41-181	120 1970s	1.5 cattle
natural/sand		low excl.	17-45	400 1990s	0.5 cattle
Leybucht DE	53°30'N 7°10'E	high marsh	0-30	50	2.0 cattle
artificial/clay		low marsh	60-80		
Süderhafen DE	54°30'N 8°50'E		30-50	50	none
artificial/clay					
Friedrichskoog DE	54°03'N 8°55'E	high marsh	40-80	50	3.4 sheep units
artificial/clay		low marsh	0-40		
Sönke-Nissen-Koog DE	54°37'N 8°45'E		20-40	50	3.4 sheep units
artificial/clay					
scale effects					
Friesland NL					
ungrazed	53°22'N 5°55'E		40-60	40	none
intensively grazed	53°20'N 5°50'E		40-60	10	cattle sheep horses
artificial/clay					
Groningen NL					
ungrazed	53°25'N 6°21'E		20-30	5	none since 1974
intensively grazed	53°25'N 6°32'E		20-30	10	cattle/sheep
artificial/clay					

grazed and experimentally ungrazed. The latter two situations were used in the present study. We established 58 permanent plots in total at Terschelling. The vegetation in the plots in the transect was recorded every three or two years from 1973 onwards, in the plots near the low dune and at the high marsh from 1976 onwards.

The third study site is located at the peninsula of Skallingen, Denmark (Table 1). The site was grazed for over 60 years excluding cattle (0.5 cattle ha^{-1}) by a single wire, but giving free access to sheep (0.5 sheep ha^{-1}). Sheep grazing stopped in 1999. Four exclosures (60 x 40 m) were erected in 1973 (Jensen, 1985). Three exclosures were at the transition of low dunes to the higher marsh. These exclosures were adjacent to larger dunes systems, hence received fresh seepage water. The fourth exclosure was erected at the transition of higher to lower marsh. We established 52 permanent plots. The plots were recorded every three or two years from 1975 onwards. From 1990 onwards more and more exclosures at Skallingen got damaged and at present only 8 plots are left excluded.

Permanent plots of 2 x 2 m were established inside and outside the exclosures. This enabled to compare control grazed and experimentally ungrazed plots in a pairwise way. The relevés were made in late summer, initially according to the cover abundance scale of Braun-Blanquet (see Westhoff & Van Der Maarel, 1973), from 1976 onwards according to the decimal scale (Londo, 1976). The Braun-Blanquet data were transformed into cover percentages fitting into the decimal scale according to r=1%, +=2%, 1=4%, 2m=4%, 2a=10%, 2b=20%, 3=40%, 4=60%, 5=90%. The authors JPB and YDV performed 37% of all relevés. The remainder was carried out by various groups of students in the presence of one of them.

Species-specific responses to the two treatments over time were analysed using the procedure described by Huisman *et al.* (1993). Using the programme VEGRON (Fresco *et al*., 2001), the best fitting significant model, from a predefined set of five hierarchical models, was selected for each species and treatment. Hence, the simplest model was chosen that significantly explained the variance whereby more complex models did not have >25% better fit. The analysis was restricted to five species, the low and early successional species *Puccinellia maritima* and *Festuca rubra*, and the tall and late successional species *Artemisia maritima* , *Atriplex portulacoides* and *Elymus athericus* . No transformation took place. The models were tested per study site, to assess the generality of the patterns found. For each relevé, the number of species present was counted and average species richness was calculated per experimental group and salt marsh zone (high or low). Differences in species number between grazing treatments were tested for statistical significance using a paired T-test (Zar, 1996).

Study site for spatial scale effects on species richness

The two study sites are located at the artificial mainland marsh of Friesland and Groningen, The Netherlands (Table 1). The sites harbour grazed and ungrazed (at least since 30 years) parts. During the summer of 2000, the presence of occurring vascular plant species was recorded in series of plots with increasing size ranging from 0.01 - 2500 m^2. The position of each sampling series was determined a priori on a vegetation map. The location was chosen randomly within the high salt marsh (De Jong *et al*., 1998) of a given grazing regime. At the study sample location, the position of each individual plot was decided randomly. All series of plots were replicated 8 times per treatment. Due to limited availability of long-term ungrazed sites, the 4 replica's per study site were all occurring within a radius of one kilometre from each other.

Study sites for vegetation mapping

The first study site is located at the barrier island of Schiermonnikoog, The Netherlands (Table 1). Some of the aforementioned permanent plots are positioned in these two exclosures. It includes two areas of 50 x 25 m half experimentally ungrazed and half control grazed. One area included the transition from a low dune towards the higher marsh with *Juncus maritimus*. The other area was at the mid marsh with *Festuca rubra* and *Puccinellia maritima*. It was intersected with bare soil covered with some *Salicornia* spp. and *Suaeda maritima*. Mapping was carried out in 1973, the year of establishment of the exclosures in late autumn and in 1978, 1985, 1988, 1990, 1995, 2000.

The legend units of the first mapping in 1973 were derived from other mapping work at the salt marsh of Schiermonnikoog. From 843 relevés detailed units were composed (see Bakker (1989) for detailed synoptic tables). These were lumped into units characterised by one or two species that were often dominant in cover. Thus were assigned the communities of *Puccinellia maritima*, *Festuca rubra*, *Juncus maritimus*, Juncus gerardi, *Elymus athericus*, *Ammophila arenaria*, *Atriplex portulacoides*, *Artemisia maritima*, *Armeria maritima*, *Plantago maritima* /*Limonium vulgare* (Bakker, 1989). Cover percentages of the dominant species are given in Table 2. If two species were co-dominant a mixed unit was established. This was often necessary to indicate complexes of *Elymus athericus* with other units.

The second study site is at the artificial mainland salt marsh in the Ley Bucht, Germany (Table 1). The site was grazed since its formation after 1950. The site was established as an experiment to study the effect of different stocking rates on the entomofauna (Andresen *et al*., 1990). The control area with 2 cattle ha^{-1} was compared to areas with stocking rates of

Table 2. Criteria to assign plant communities at salt marshes according to Bakker (1989) and SALT97 (De Jong *et al*. 1998). Percentages indicate cover percentages.

	Bakker (1989)	SALT97
Pioneer zone		
Spartina anglica	35%	*Spartina*>*Salicornia* + *Suaeda*
Salicornia spp.	10%	*Salicornia* and/or *Suaeda* > *Spartina*
Low marsh		
Atriplex portulacoides	90%	>25%, or *Atriplex* >15%, *Limonium* <15%
Puccinellia maritima	5-20%	other low marsh
Mid/high marsh		
Artemisia maritima	30%	>15%, or *Artemisia* > *Festuca*
Atriplex portulacoides	-	>15%
Limonium vulgare/*Plantago maritima*	10%/10%	*Limonium* >15%
Juncus gerardi	30%	*Juncus gerardi* > *Festuca*
Juncus maritimus	15%	>10%
Elymus athericus	30%	>25%
Festuca rubra	30%	other mid/high marsh
Armeria maritima	5%	-
Ammophila arenaria	5%	dune

1, 0.5 cattle.ha^{-1} and cessation of grazing. Each area was 700 x 100 m perpendicular to the zonation from the seawall towards the intertidal flats (Dahl & Heckenroth, 1978). This zonation included *Elymus repens/E. athericus* and *Festuca rubra* communities close to the seawall, the *Agrostis stolonifera* at the transition, *Puccinellia maritima* community at the lower marsh, and *Spartina anglica* and *Salicornia* spp. communities near the intertidal flats. Unfortunately the study site was not mapped before or at the start of the experiment in 1980. From 41 relevés units were composed for the first mapping we carried out in 1988 (Andresen *et al*., 1990). The units were similar to those that had emerged at Schiermonnikoog. We subsequently mapped the study site in 1995, 1997 and 2000, adopting the same legend units as used for the study site at Schiermonnikoog. In 1997 it was difficult to have enough cattle from the farmers, so the control area was grazed by a too low stocking rate. For that reason the area was not mapped from that years onwards except for the abandoned area. Reinforcement of the seawall in the framework of coastal protection caused problems for grazing, and since 1998 the entire southern part of the Ley Bucht was abandoned. As the fences were not removed, the since 1980 ungrazed area can still be found and mapped.

The third study site is in Süderhafen, Germany (Table 1). It developed as a natural marsh with creeks in the shelter of the former salt-marsh island of Nordstrand after 1925. The site was mapped by Raabe in 1968. Due to poor accessibility it was only accidentally grazed before 1968. The site was not grazed since 1971, and was mapped again in 1995 by Heinze (1997). Both the vegetation maps of 1968 and 1995 included detailed legend units. We lumped these in such a way that units emerged similar to those for the Schiermonnikoog and Ley Bucht sites, namely, communities dominated by *Puccinellia maritima* , *Festuca rubra* etc. (see Table 2).

The fourth study site is located at the artificial mainland salt marsh of Friedrichskoog, Germany (Table 1). It developed after 1854 and was long-term grazed. The site was established in 1988 to study the effects of different stocking rates on the soil and vegetation (Kiehl *et al*., 1996; Kiehl, 1997). The stocking rate was expressed in sheep units, i.e. adult sheep including her lambs (1 sheep unit equals 2.8 sheep). The area was heavily grazed by 3.4 sheep units ha^{-1}, which means about 10 sheep ha^{-1} at the end of the summer period. The control area with 3.4 sheep units ha^{-1} was compared with 1.5 and 1.0 sheep units ha^{-1} and cessation of grazing. Each area was 500 x 50 m perpendicular to the coast. At the start of the experiment this salt marsh mainly harboured the *Festuca rubra* community, at the lower marsh the *Puccinellia maritima* community, and at the intertidal flats *Spartina anglica* and *Salicornia* spp. communities were found (Kiehl, 1997). All salt marshes in the Nationalpark Schleswig-Holsteinisches Wattenmeer were mapped at the scale 1:5,000 in 1988 and in 1996. We mapped the Friedrichs-koog site for the present purpose in more detail in 1999 adopting the legend units that were derived from the classification according to SALT97 (De Jong *et al*., 1998). The units were for the present purpose lumped to plant communities dominated by *Puccinellia maritima*, *Festuca rubra*, *Elymus athericus* etc. Criteria for the plant communities according to SALT97, and the comparison with the plant communities adopted for the mapping at Schiermonnikoog are given in Table 2.

The fifth study site is located at the artificial mainland salt marsh of Sönke Nissen-Koog, Germany (Table 1). It developed after 1924 and was long-term grazed. The experimental treatments were established at the same time and had the same lay-out as the Friedrichskoog site. At the start of the experiment this salt marsh mainly harboured the *Puccinellia maritima* community with locally some *Festuca rubra* and *Elymus athericus* communities and with *Spartina anglica* and *Salicornia* spp. communities near the intertidal flats (Kiehl, 1997). The same procedure for vegetation mapping was adopted as in the Friedrichskoog site.

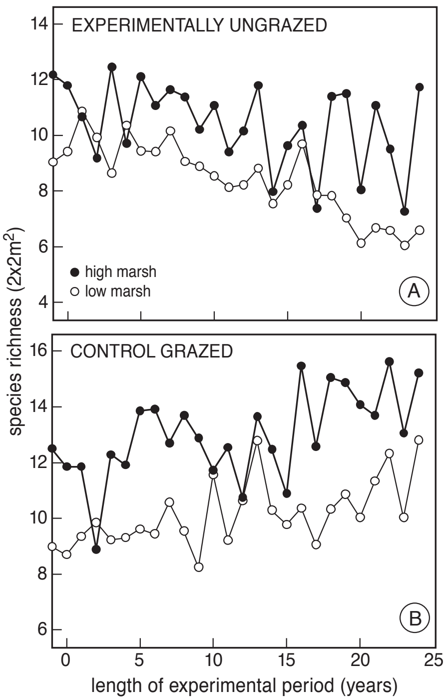
Results

Permanent plots

The species richness at 4 m^2 of the experimentally ungrazed plots became significantly lower than the richness in the paired control plots, during the 25 years study period (T test results after 15 years of study all significant at $p < 0.05$ with sample sizes varying from 12 to 58, Figure 3).

The cover percentages of five species dominant in any stage of succession, namely, *Elymus athericus*, *Artemisia maritima*, Atrtiplex portulacoides, *Festuca rubra* and *Puccinellia maritima* did not change in the control plots at the different sites in the Wadden Sea area. In the experimentally ungrazed plots *Elymus athericus* increased and *Festuca rubra* and *Puccinellia maritima* decreased significantly from the start of the experiment

Figure 3. Number of plant species at (2x2)m^2 in paired grazed and experimentally ungrazed plots at natural sandy back-barrier marshes at Schiermonnikoog, Terschelling and Skallingen.

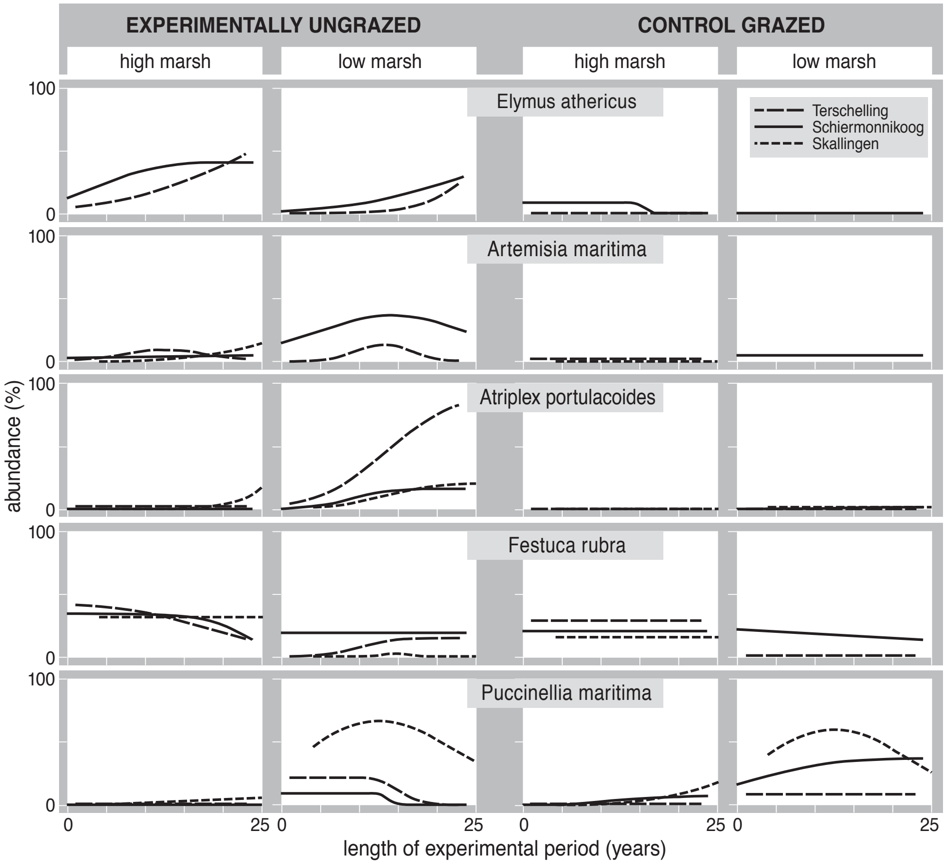


onwards at the high salt marsh, whereas *Elymus athericus* and *Atriplex portulacoides* increased significantly at the lower marsh but only later during the study period. *Artemisia maritima* initially increased, but decreased again (Figure 4).

Increasing area of relevés

The species richness of relevés increased ranging from 0.01 - 2500 m^2, according to the well-known species-area effect (e.g. Magurran, 1988). This was true for both the grazed and long-term ungrazed part of the study area (Figure 5). Although the differences between species richness at the grazed and ungrazed plots

Figure 4. Long-term changes in cover of five important species in grazed and experimentally ungrazed permanent plots at the salt marshes of Schiermonnikoog, Terschelling and Skallingen. Sample sizes for Skallingen are 87 and 19, for Terschelling 192 and 20 and for Schiermonnikoog 125 and 182 , for the high and low marsh, respectively.



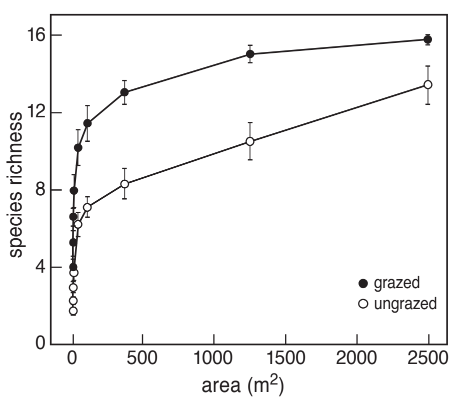


Figure 5. Number of plant species at areas ranging from 0.01-2500 m^2 in grazed and long-term (at least 30 years) ungrazed sites at artificial marshes along the coast of Groningen and Friesland.

slightly decreased with increasing plot size, the number of species per unit area of grazed marsh was always higher than at the ungrazed marsh. The species included are typical salt-marsh species.

Vegetation mapping

The *Elymus athericus* community established at the cost of the *Juncus maritimus* community within five years after the cessation of grazing at the higher back-barrier salt marsh at Schiermonnikoog. The deposition of driftline initiated temporarily spots with the annual *Atriplex prostrata*, but within two years these were taken over again by the *Elymus athericus* community. This community also spread at the transition to the low dune, but only gradually and after 27 years still parts of the *Festuca rubra* community are present. It seems that *Elymus athericus* is also spreading in the grazed area, but this is mainly due to the fact that the ratio of the cover of *Juncus maritimus* and *Elymus athericus* fluctuates from year to year (Figure 6A). At the lower marsh the *Artemisia maritima* community dominated within five years at the relatively higher parts. It took 12 years before the first clone of *Elymus athericus* had established and after 22 years of cessation of grazing the *Elymus athericus* community expanded (Figure 6B). The initially bare soil at the lowest places became covered by the *Plantago maritima* /*Limonium vulgare* community after about 10 years. The *Atriplex portulacoides* community took over after 22 years. The latter has been locally replaced by the *Elymus athericus* community 27 years after the cessation of grazing (Figure 6B).

Eight years after the cessation of grazing, the *Elymus athericus* community covered large areas at the higher part and one spot at the lower part of the artificial mainland marsh of the Ley Bucht. It hardly occurred at the different grazing regimes (Figure 7). The *Elymus athericus* community quickly spread over both the higher and the lower salt marsh and covered nearly the entire gradient 20 years after the cessation of grazing, at the expense of the *Festuca rubra* and *Agrostis stolonifera* communities and the *Puccinellia maritima* community, respectively (Figure 7). Also the 0.5 cattle.ha^{-1} grazing regime revealed a spread of the *Elymus athericus* community 15 years after the start of the experiment both at the higher and lower salt marsh, but to a lesser degree than the abandoned area (Figure 7).

The repeated mapping of Süderhafen showed that 27 years of no grazing resulted in an expansion of the *Elymus athericus* community at the cost of the *Festuca rubra* community, and of the *Atriplex portulacoides* community at the expense of the *Puccinellia maritima* community. Particularly in the northern part of the marsh, the vegetation mosaic became more diverse (Figure 8).

The vegetation at the artificial salt marsh of Friedrichskoog revealed a relatively small coverage of the *Elymus athericus* community after the cessation of grazing, 11 years after the start of the experiment. The community covered even smaller areas at the low stocking rates (Figure 9).

The artificial salt marsh of Sönke-Nissen-Koog showed a large coverage of the *Elymus athericus* community after the cessation of grazing. The community covered smaller areas at the low stocking rates, 11 years after the start of the experiment (Figure 10).

Figure 6. Top panel: Changes at the higher salt marsh of Schiermonnikoog after the establishment of an exclosure in 1973. The *Elymus athericus* community established within five years and covered most of the exclosure with the exception of the *Ammophila arenaria* community and locally the *Festuca rubra* community. Bottom panel: Changes at the lower salt marsh of Schiermonnikoog after the establishment of an exclosure in 1973. Initially the *Artemisia maritima* community took over, but after 15 years the *Elymus athericus* community established and got dominant after 25 years. At the lowest parts the *Atriplex portulacoides* community reached dominance.

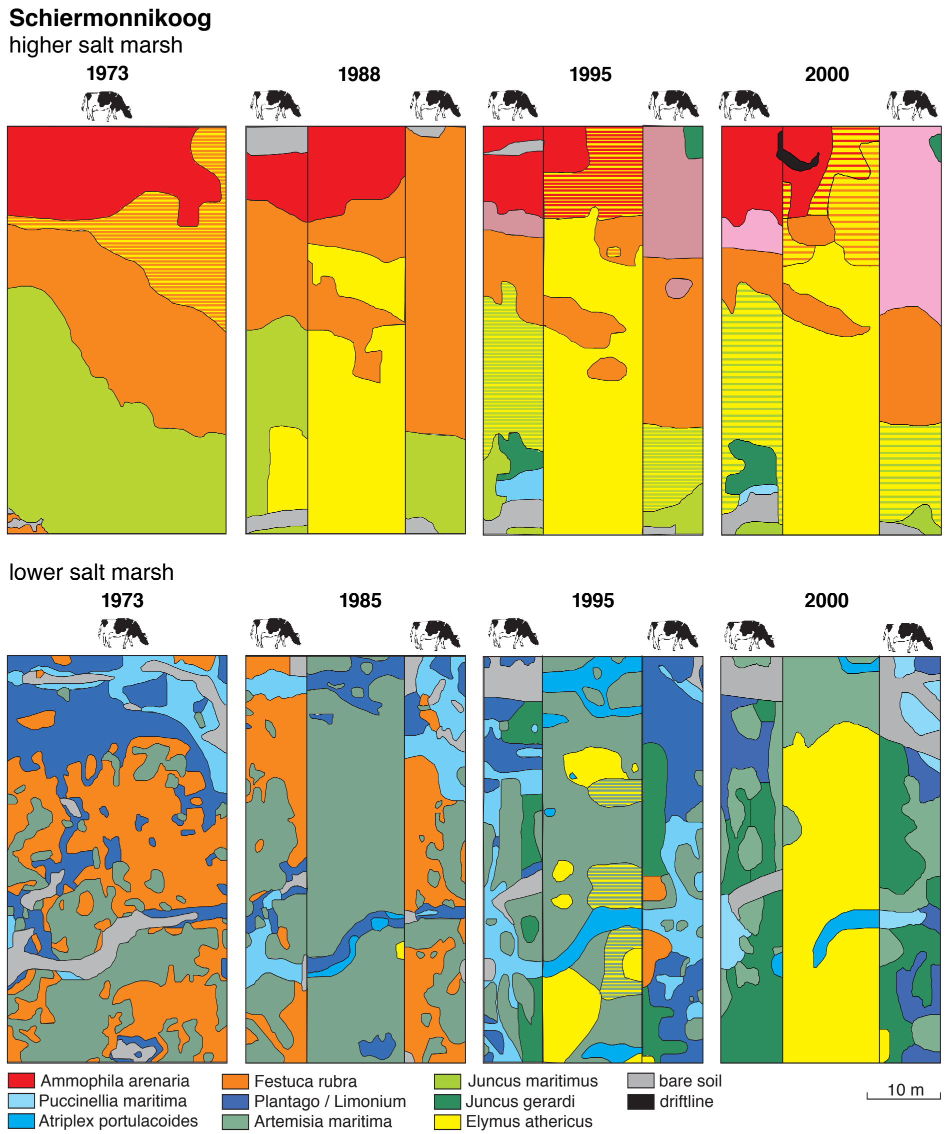
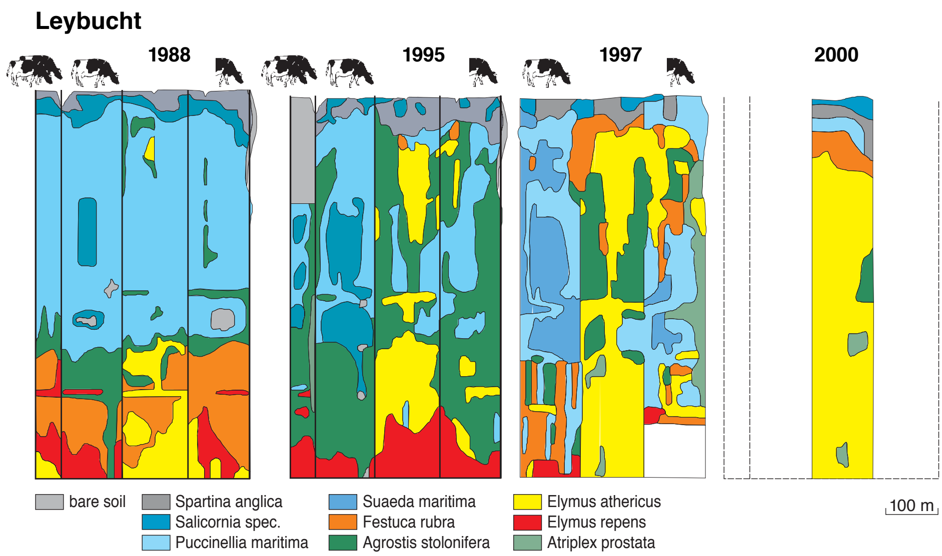


Figure 7. Changes in the artificial salt marsh of the Ley Bucht after the establishment of different stocking rates in 1980. The *Elymus athericus* community had established within 10 years at the higher marsh and also at the lower marsh after 15 years in the abandoned area, where it got dominant after 20 years. From 15 years onwards the *Elymus athericus* community also spread in the lowest stockig rate section.



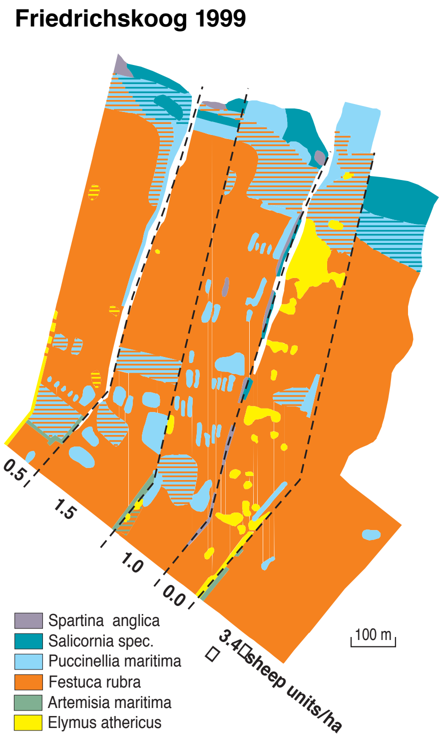
Discussion

Natural succession and the cessation of grazing

The example of the back-barrier salt marsh of Schiermonnikoog shows dominance of *Atriplex portulacoides* and *Elymus athericus* at the lower and higher marsh, respectively. Since cattle grazing was restricted to the oldest parts of the marsh, the new salt marsh that established from that period onwards (compare Fig. 1) reveals natural succession in the absence of livestock grazing. The maximum age of marsh that has never been grazed by cattle on Schiermonnikoog is 40 years. Therefore, it is not known whether *Atriplex portulacoides* and *Elymus athericus* are the climax species of natural succession. The ungrazed salt marsh of the Hon at the island of Ameland, The Netherlands, is also getting covered by the *Elymus athericus* community at the higher parts (Westhoff & Van Oosten, 1991; Janssen, 2001). The Boschplaat salt marsh at Terschelling established from 1932 onwards in the shelter of an artificial sand dike and has never been grazed by livestock. Permanent plot data collected from 1953 onwards revealed that *Elymus athericus* reached dominance from 1979 onwards (or earlier, the plots were not recorded between 1967 and 1979) at the higher marsh (Roozen & Westhoff, 1985; Leendertse *et al*., 1997). Westhoff & Van Oosten (1991) expect that the *Elymus athericus* community will eventually establish at the higher parts and the *Atriplex portulacoides* community at the lower parts of the Boschplaat.

Figure 8. Long-term vegetation development at the ungrazed natural marsh of Süderhafen. The *Festuca rubra* community largely transformed into an *Elymus athericus* community, the *Puccinellia maritima* community into an *Atriplex portulacoides* community.

Figure 9. Vegetation in the Friedrichskoog artifical salt marsh in 1999. The experiment with different stocking rates of sheep started in 1988. The *Elymus athericus* community covers small parts of the *Festuca rubra* sward in the abandoned section.



Early successional stages at the natural marsh of Schiermonnikoog, with relatively low plant biomass and canopy, harbour winter and spring staging *Barnacle Branta* leucopsis and Brent *Branta bernicla* geese and resident hares *Lepus europaeus*. These stages include the favourite forage species *Triglochin maritima*, *Plantago maritima* , *Puccinellia maritima* for the geese and *Festuca rubra* for the hares (Prop & Deerenberg, 1991; Van Der Wal *et al.*, 2000A). Both groups of small herbivores are evicted by ongoing succession (Van De Koppel *et al.*, 1996; Drent & Van Der Wal, 1999). Cattle facilitate for the small herbivores at the grazed

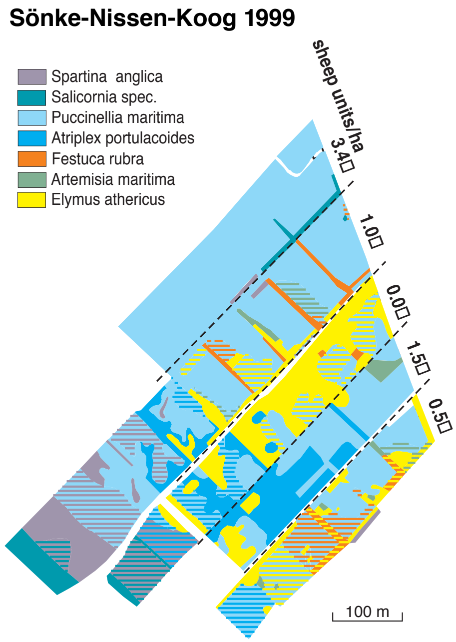


Figure 10. Vegetation in the Sönke-Nissen-Koog artificial salt marsh in 1999. The experiment with different stocking rates of sheep started in 1988. The *Elymus athericus* community covers large parts of the *Puccinellia maritima* sward in the abandoned section.

salt marsh (Olff *et al.*, 1997). The latter cannot maintain the early successional stages. On their turn the resident hares facilitate for geese by foraging on the tall *Artemisia maritima* and *Atriplex portulacoides* during winter periods. Hares can retard natural succession with several decades as is revealed from exclosure experiments at the very young salt marsh (Van Der Wal *et al.*, 2000B). This is in agreement with observations at the islands of Rottumerplaat, The Netherlands, and Mellum, Germany, where hares are absent. Already at a relatively young marsh, this island features a zonation of *Atriplex portulacoides* and *Elymus athericus* communities only at the lower and higher marsh, respectively (D.P.J.Kuijper, pers. comm.).

Livestock grazing can reset the successional clock (Olff *et al.*, 1997). After the cessation of grazing at the natural high salt marsh *Elymus athericus* rapidly spreads. Eventually the lower marsh gets covered by *Atriplex portulacoides* after about 20 years. Unfortunately no ungrazed successional series are known from artificial salt marshes. After the cessation of grazing in the Ley Bucht, the *Elymus athericus* community spread over the entire gradient from the seawall towards the intertidal flats where the *Spartina anglica* and *Salicornia* spp. communities occurred. From the aforementioned we conclude that the outcome of succession after cessation of grazing at natural back-barrier salt marshes is similar to that of natural succession. Moreover, the effects of cessation of livestock grazing at an artificial marsh seems to mimic that of a natural marsh. However, it should be taken into account that at the highest marshes and in brackish marshes *Elymus repens* will get dominant (Esselink, 2000).

Effects of cessation of grazing at different scales

Elymus athericus rapidly spreads vegetatively from existing (often heavily grazed) tillers at the high salt marsh within a few years both at the natural marsh of Schiermonnikoog (Figure 6A) and the artificial marsh of the Ley Bucht (Figure 7). It may take up to 10 years but the species seems to start from generative establishment and initially builds individual clones at the mid or lower marsh (Figure 6B, Andresen *et al.*, 1990). These clones, once established, grow together to a dense sward within a few years.

The amount of time it takes for *Elymus athericus* or *Atriplex portulacoides* to get dominant (Figure 4), and the decrease in cover of *Artemisia maritima* after an initial increase, stresses the importance of long-term studies to assess the effects of the cessation of grazing. Short-term studies would result in only a part of the answer.

The number of species increased with increasing area in the study sites along the mainland coast of Groningen and Friesland. This was also recorded at Friedrichskoog and Sönke-Nissen-Koog, namely, from 4-5 species at 1 m^2 to 14-15 species at 800 m^2 five years after the start of the experiment. At these sites, no differences were found for different stocking rates and the cessation of grazing (Kiehl, 1997). It would be interesting to see the results after some decades and to compare these with the Dutch sites. Here species richness showed consistently higher numbers at grazed than at 30 years ungrazed areas ranging from 0.01 - 2500 m^2. From these long-term results we conclude that 4 m^2 plots seem representative to study the effects of long-term cessation of grazing on species density.

Changes in cover percentages of individual species (Figure 4) are at the basis of changes at the community level, such as the increase of communities of *Atriplex portulacoides* and *Elymus athericus* and decrease of *Puccinellia maritima* and *Festuca rubra*. The aforementioned implies that the cessation of grazing eventually results in a decrease of species richness and is likely to result in a decrease of the number of plant communities.

The comparison of over 1400 relevés in long-term (>20 years) grazed and ungrazed back-barrier salt marshes in the Wadden Sea area revealed that most species showed a higher incidence at grazed than at ungrazed sites. Of the 30 most relevant salt marsh species, only *Artemisia maritima* , *Atriplex prostrata*, A. portulacoides and *Elymus athericus* have a higher chance to be found at ungrazed than at grazed sites (Bos *et al*., 2002).

Generalisation for the Wadden Sea

Both natural succession and cessation of grazing eventually seem to result in the communities of *Atriplex portulacoides* and *Elymus athericus* at the lower and higher marsh, respectively. This appears to be true for back-barrier marshes as well as artificial salt marshes in the entire Wadden Sea. Hence the zonation may feature only these two plant communities. So far a few exceptions can be recorded, where *Elymus athericus* is not dominant in the absence of livestock grazing. The will be discuused at the end of the present paragraph.

The study sites of natural marshes at Terschelling and Skallingen include large dune systems with fresh seepage water. The cessation of grazing has resulted in a strong representation of *Phragmites australis* in 8 plots at Skallingen and 3 plots at Terschelling (Bos *et al*., 2002). This species also largely spread after the reduction of stocking rates in the brackish estuarine marsh of the Dollard, The Netherlands (Esselink *et al*., 1999).

Locally the *Festuca rubra* community was not replaced after 27 years of cessation of grazing by the *Elymus athericus* community at the natural salt marsh of Schiermonnikoog. These spots are at the transition of higher marsh to a low dune and hence have a thin layer of sediment due to low inundation frequency. Similar phenomena were recorded at an other part of this salt marsh that was abandoned in 1958 from cattle grazing and grazed anew from 1972 onwards. Permanent plots in exclosures revealed that different plant communities were replaced by the *Elymus athericus* community after different periods of cessation of grazing: *Juncus maritimus* community after 30 years, *Plantago maritima* /*Limonium vulgare* community 30 years, *Artemisia maritima* community 30 years, *Juncus gerardi* community 35 years. Only the *Festuca rubra* / *Armeria maritima* community was not replaced after 35 years of cessation of grazing (Van Wijnen *et al*., 1997). Maybe the combination of a thin layer of sediment (low nutrient pool) and evapotranspiration during summer periods and subsequent temporary high soil salinity prevent replacement of the community with *Sagina maritima*.

At the higher end of the zonation *Elymus athericus* may be constrained by abiotic conditions such as salinity in the case of the sites of the community of *Sagina maritima* or competition for light in the case of the taller *Phragmites australis* at sites with fresh seepage water. The possible abiotic constraint is interesting, as transplantation experiments by Snow & Vince (1984) demonstrated only biotic constraints at the higher part of an elevational gradient. At the lower end of the zonation it may be constrained by the higher inundation frequency that favours *Atriplex portulacoides* . However, at the long term the *Elymus athericus* community starts to take over the *Atriplex portulacoides* community at Schiermonnikoog (Figure 6B). Experimental removal of *Atriplex portulacoides* gave way to adjacent *Elymus athericus* at the artificial marsh of Tümlauer Bucht, Germany (Bockelmann & Neuhaus, 1999). In both cases *Elymus athericus* may have spread vegetatively. The scarce occurrence of *Elymus athericus* at Skallingen might be due to biogeographical reasons. Only longer periods of undisturbed succession or cessation of grazing will reveal whether *Atriplex portulacoides* and *Elymus athericus* represent the climax.

The cessation of grazing results in a denser and taller canopy as shown in the marshes of Sönke-Nissen-Koog (Kiehl *et al*., 1996) and the nearby Hamburger Hallig, Germany (Stock & Kiehl, 2000). This had positive effects on the rate of sedimentation in the Friedrichskoog and Sönke-Nissen-Koog (Kiehl, 1997) and the Dollard (Esselink *et al*., 1998). Also the Ley Bucht site revealed higher rates of sedimentation in the ungrazed as compared to the heavily grazed area in the *Puccinellia maritima* zone in the first period of the experiment (Andresen *et al*., 1990). After 17 years this process resulted in a 10-15 cm higher soil level at the ungrazed areas in comparison to the heavily grazed treatment (Van Wijnen, 1999). A positive feed back seems to have occurred between the rate of sedimentation and the establishment of the *Elymus athericus* community in the Ley Bucht. Maybe similar processes take place in the *Puccinellia maritima* marshes of Sönke-Nissen-Koog.

In contrast, an exclosure established in 1978 at Hamburger Hallig in the *Puccinellia maritima* community revealed only some individual clones of *Elymus athericus* after 17 years. No differences in soil level were found inside and outside the exclosure (Heinze, 1997; Kiehl *et al*., 2000). The distance between the intertidal flats and the exclosure is about 800 m.

Sedimentation in the 1990s mainly took place in the first 200 m from the intertidal flats (15 mm yr^{-1}) and strongly decreased further away (<2 mm yr^{-1}) (Schröder *et al.*, 2002). This is in agreement with measurements in the Dollard (Esselink *et al.*, 1998). The rates of sedimentation at the peninsula of Skallingen also strongly decrease with increasing distance from the intertidal flats (C. Christiansen, pers. comm.). This may explain the absence of dominance of *Elymus athericus* after ecluding livestock.

Targets and methods of salt-marsh management

The cessation of live stock grazing revealed a lower number of plant species at the small scale and a possible lower number of plant communities as compared to grazed sites. The tall species *Artemisia maritima* , *Atriplex prostrata*, *A. portulacoides* and *Elymus athericus* are favoured by the cessation of grazing, and the communities of *Atriplex portulacoides* and *Elymus athericus* at the low and high marsh, respectively. This holds for long-term cessation of grazing. Before a single community takes over, a mosaic of different plant communities establishes, with a high spatial variation. Moreover, a few years after the cessation of grazing many plant species that were heavily grazed so far, spread and start flowering. Therefore, short-term cessation of grazing is beneficial for many groups of entomofauna (Irmler & Heydemann, 1986). However, eight years after the cessation of grazing in the Ley Bucht the characteristic zonation of halobiontic entomofauna disappeared and was replaced by inland communities typical for tall forb plant communities (Andresen *et al.*, 1990).

So far we discussed the occurrence of plant communities and individual plant species at grazed versus ungrazed salt marshes. When the stocking rate is such that the animals eat and trample the entire seasonal plant production, a homogeneous short sward is the result. The height of the canopy at ungrazed marsh depends on the canopy height of individual plant communities, but short canopy is likely to be lacking. When stocking density is below the level of full utilisation, part of the seasonal production is not eaten. The result is not an homogeneous lower canopy, but a pattern of places where the animals regularly return to forage on high quality tillers, and places that are avoided due to poor forage quality. The area of heavily grazed patches relative to that of the ungrazed ones is a measure of the ratio between utilisation and production. Hence, intermediate stocking rates can only be defined relatively to these parameters (Bakker, 1998). Intermediate stocking rates reveal large scale grazing gradients resulting in short canopy near the seawall and taller canopy near the intertidal flats in the Leybucht (Andresen *et al.*, 1990), at Sönke-Nissen-Koog (Kiehl *et al.*, 1996) and the Dollard (Esselink *et al.*, 1998). Intermediate stocking densities also maintain a mosaic of different plant communities at the scale of study sites, with heavily grazed areas alternating with patches that are hardly grazed and have a taller canopy (Figures. 7, 9, 10). Moreover, at the smaller scale, micro-patterns were only found at intermediate stocking rates and revealed the highest spatial variation at 1 sheep unit.ha^{-1} (Berg *et al.*, 1997). We conclude that the highest variation at small and larger scale, i.e. at the levels of diversity of plant communities, structural classes and species richness can be achieved by intermediate stocking densities.

At the natural salt marsh of Schiermonnikoog cattle facilitate for geese (Olff *et al.*, 1997). Similar data are available for the aforementioned experimentally grazed sites at Sönke-Nissen-Koog, Friedrichskoog and the Leybucht, where the ungrazed parts of the marsh consistently had lower grazing pressure by geese in April and May 1999 (Bos, 2002). Another large-scale grazing experiment is carried out at the Hamburger Hallig. From 1991 onwards 256 ha is still heavily grazed by 3.9 sheep units ha^{-1}, 278 ha is extensively grazed by 0.6 sheep unit ha^{-1} (0.3 sheep unit ha^{-1} since 1995), and 516 ha is ungrazed. Especially tall species such as *Aster tripolium*, *Artemisia maritima* and *Atriplex portulacoides* have spread at the expense of *Puccinellia maritima* in the extensively grazed and abandoned areas. Subsequent numbers of Barnacle and Brent geese decreased in autumn. As a result of above-ground die-off and winter storms the canopy is lower again in spring, and only little reduction in goose numbers was recorded. As a result of increasing goose numbers along the entire Wadden Sea, the numbers have increased in the entire area of Hamburger Hallig (Stock & Hofeditz, 2000).

Can increasing goose numbers affect the vegetation themselves without livestock grazing? In the Dollard the area has become wetter due to cessation of drainage, and the numbers of Barnacle geese have strongly increased. This combination might be responsible for the transformation of large areas (60 ha out of 460 ha in the study area) of the *Puccinellia maritima* community in secondary pioneer communities of *Salicornia* spp. and *Suaeda maritima* . The geese only can have this effect in the presence of cattle, as exclosure experiments have shown (Esselink, 2000).

Reduction of stocking density and cessation of grazing also affects the breeding birds at the Hamburger Hallig. A decrease was recorded for *Sterna paradisaea* and *Recurvirostra avosetta*, but an increase was found for *Tadorna tadorna*, *Larus argentatus* and *Tringa totanus* (Eskildsen *et al.*, 2000). Long-term studies have to reveal future trends. Thyen (1997) suggests that grazing may negatively affect the breeding success of *Tringa totanus*, but was not able to demonstrate differences in densities of breeding pairs after 8 years of no grazing. On the contrary, Norris *et al.* (1997) found high densities of *Tringa totanus* in grazed and ungrazed marshes on the Wash in Great Britain, with a positive relation between redshank density and cover of *Elymus athericus*. *Tringa totanus* is decreasing in salt marshes in Great Britain. This is attributed to increasing stocking rates with resulting lower cover of *Elymus athericus* that gives shelter to the breeding birds (Norris *et al.*, 1998). The decreasing numbers of Tringa totanus in the Dollard may be attributed to increasing numbers of Branta bernicla that remove *Elymus repens* (Esselink, 2000). Hielen and Bach (1999) found no clear effect on waders after 6 years of no grazing, but Stock *et al.* (1992) observed a clear increase in typical birds for the Halligen after a heavy reduction in grazing pressure.

Along the mainland coast of Friesland and Groningen, The Netherlands, a trend towards older salt-marsh vegetation has been recorded. The area of artificial salt marshes remained constant from the early 1960s onwards. However, the relative contribution of mid salt marshes increased at the cost of pioneer salt marshes that significantly declined since the mid 1960s (Esselink, 2000). The cessation of grazing and subsequent positive feed back between dense, tall canopy and sedimentation might fasten this process of ageing of salt-marsh vegetation. However, these effects should be assessed with respect to the position of individual marshes in relation to their position along the coast, to the tidal watershed, their level with respect to MHT, the distance to the intertidal flats, and drainage activities.

Conclusions

We have elucidated the fact that cessation of grazing affects plant communities and plant species. Moreover, some effects on structure of the canopy, entomofauna, breeding birds and winter/spring staging birds are discussed. It is clear that effects can only be judged positive or negative once targets for management have been set. Grazing or the cessation of grazing is a means to reach previously defined ecological targets, and long term monitoring is a prerequisite to judge to which extent targets are fulfilled. Hence the question for nature conservation in salt marshes is not: 'to graze or not to graze', but 'what are the targets and which role can grazing management play to reach these targets?' To answer these questions we need to establish and maintain long-term experiments including grazing with different livestock and stocking densities such as Friedrichskoog, Sönke-Nissen-Koog and Hamburger Hallig. Sites that have never been grazed by livestock should be maintained such as the eastern parts of Schiermonnikoog, Terschelling, Ameland. These are also interesting for comparison with islands where hares are absent such as Rottumerplaat and Mellum. In all these sites multidisciplinary research is needed on the interplay between sedimentation, plants, mammals, entomofauna and birds.

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