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Large-scale effects of a small herbivore on salt-marsh vegetation succession – A comparative study on three Wadden Sea islands

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Abstract. Grazing by livestock is used as a management tool to prevent the dominance of a single tall-growing species during succession on European salt marshes. The effects of natural small herbivores are often neglected by managers. Long-term exclosure experiments on the island of Schiermonnikoog show that hares retard vegetation succession at the early stages of salt-marsh development. In the present study we test whether we can scale-up these exclosure studies to a whole salt-marsh system. We compared 30 years of undisturbed vegetation succession at the Wadden Sea islands of Schiermonnikoog, Rottumerplaat (both The Netherlands) and Mellum (Germany). Salt-marsh development started at all sites in the early 1970s. Hares have been present only on Schiermonnikoog. At each site an area was selected covering a gradient from high to low salt marsh. Surface elevation and clay thickness were measured and a vegetation map was made on the three islands. The areas showed similar clay thickness at low surface elevation, indicating similar sedimentation rates and hence nitrogen inputs. Rottumerplaat and Mellum showed a higher dominance of the late successional species *Atriplex portulacoides* in the low marsh and *Elymus athericus* in the high marsh compared to Schiermonnikoog. Typical mid-successional, important food plant species for hares and geese had a higher abundance at Schiermonnikoog. Patterns of vegetation development in the absence of hares followed the observed patterns in the small-scale exclosure experiments at Schiermonnikoog. Without hare grazing, vegetation succession proceeds more rapidly and leads to the dominance of tall-growing species in earlier stages of succession. The present study shows that next to large herbivores, small herbivores potentially have large-scale effects on salt-marsh vegetation succession during the early successional stages.

Keywords: Exclosure; Goose; Hare; Mellum; Rottumerplaat; Schiermonnikoog; Waterfowl.

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

Introduction

Undisturbed vegetation succession on coastal salt marshes of the Wadden Sea leads to the dominance of the shrub *Atriplex portulacoides* in the lower marsh and the tall-growing grass *Elymus athericus* in the higher marsh (Leendertse et al. 1997; Roozen & Westhoff 1985). Grazing by large herbivores, including livestock, has a great impact on salt-marsh succession. Numerous experiments show that they are able to prevent the vegetation being dominated by tall-growing species (Bakker et al. 2003; Bos et al. 2002; Kiehl et al. 1996; Andresen et al. 1990). Grazing by livestock can set back the successional clock to plant communities harbouring species from the young successional stages. Therefore, grazing by livestock is successfully used as a management tool to increase species richness on salt marshes (Bakker et al. 1993).

The effects of naturally occurring small herbivores on salt-marsh succession are often neglected by managers. However, studies on American salt marshes show that truly small herbivores (snails and crabs) can top-down regulate plant productivity and play an important role in structuring salt-marsh communities (Silliman & Zieman 2001; Bortolus & Iribarne 1999). Also grazing by other small herbivores, such as geese (Zacheis et al. 2001; Srivastava & Jefferies 1996) and muskrats (Connors et al. 2000) strongly affect salt-marsh communities.

Studies in European marshes mainly focus on the effects of geese and hares on salt-marsh vegetation. Joenje (1985) and Rowcliffe et al. (1998) showed that grazing by waterfowl and migratory Brent geese (*Branta bernicla*) created a *Salicornia*-dominated stand and retarded succession towards a stand dominated by *Puccinellia maritima*. This indicates that geese do affect succession in its initial stage, but both studies showed no effect on the establishment of typical late successional species, such as *Atriplex portulacoides* and *Elymus athericus*. Van der Wal et al. (2000b) showed that both Brent geese (*Branta bernicla*) and Barnacle geese (*Branta leucopsis*) did not retard succession and that both goose species decreased once late successional species invaded the marsh (van der Wal et al. 2000a). Grazing by the far less abundant Brown hare (*Lepus europaeus*) negatively affected these late successional species. Exclosure studies on Schiermonnikoog showed that *Atriplex portulacoides* and *Elymus athericus* increased in abundance once the vegetation is protected from hare grazing (van der Wal 2000b; Kuijper et al. in prep). Grazing by hares retarded succession by more than 25 years (van der Wal et al. 2000b).

The effects of hares were most pronounced in young salt marshes. This implies that when hares are not present from the initiation of salt-marsh development, succession should proceed rapidly. Hence, late successional species should dominate at an earlier stage of development compared to salt marshes that developed in the presence of hares. In the present study we tested this by comparing the hare-grazed vegetation at Schiermonnikoog with that at two Wadden Sea islands where the vegetation has developed in the absence of hares for 30 years. We tested whether islands without hares showed a higher dominance of typical late successional species and a lower abundance of early successional species at a similar stage of development. This comparison should show whether we could scale-up the results of the exclosure studies at Schiermonnikoog. Salt-marsh succession on an island without hares should show the same increase in species as observed in the small-scale experimental plots (which are 8 m × 10 m) excluded from hare grazing at Schiermonnikoog.

Methods

Comparison between islands

We compared salt marshes, covering the whole range from high to low marsh, on two islands which developed in the absence of hares with an island that developed in the presence of hares. We compared these marshes in several ways. The input of clay by means of the continuous flooding of the sea, has been regarded as the major factor driving salt-marsh succession (Olff et al. 1997). Therefore, we compared the thickness of the clay layer, at similar surface elevation, between the sites as a measure of the sediment input. The occurrence of vegetation types over the gradient from high to low marsh were compared by making vegetation maps of selected areas. As we are interested in the speed of succession in these salt marshes, we compared the presence and abundance of several salt-marsh species that are typical of early and late successional stages. We looked at *Festuca rubra*, *Plantago maritima* and *Puccinellia maritima* as plant species that show a peak in abundance at early to mid-successional stages (Olff et al. 1997).

Plantago and *Puccinellia* dominate the lower salt marsh and are important food plant species for geese (Prop & Deerenberg 1991; Prins & Ydenberg 1985). *Festuca rubra* dominates the higher salt marsh and is the most important food plant for hares (van der Wal et al. 1998). As typical late successional species we selected *Atriplex portulacoides* and *Elymus athericus*. *A. portulacoides* is a species which dominates the lower salt marsh while *E. athericus* dominates the higher salt marsh of late successional stages of salt-marsh succession (Leendertse et al. 1997; Roozen & Westhoff 1985).

To be able to compare the salt-marsh vegetation development on different islands, these islands had to meet several requirements. Firstly, vegetation succession should have started at all sites at the same time. In this way we are able to compare sites in a similar developmental stage. Based on aerial photographs we determined the year when first salt-marsh vegetation established at each site. Secondly, no livestock grazing should have occurred, as this can largely affect vegetation development (Bos et al 2002). Thirdly, hares should have been present since the beginning of salt-marsh development on the hare-grazed island and hares should have been absent since the beginning of salt marsh development on the hare-free islands. The following islands were selected that met the requirements (Fig. 1).

Rottumerplaat

In 1950 Rottumerplaat consisted mainly of unvegetated bare sand (Bouwsema 1983). In 1956/1957 an artificial sand dike was created on this island that was partly destroyed and subsequently repaired during several years. On the lee side of this sand dike a salt marsh has developed since 1961/1962 (de Meulmeester & Janssen 1997). In 1970 the artificial sand dike was re-created, it was increased by depositing more sand and it moved 60 meters landwards. Since the early 1970s there has been a steady development of the salt-marsh that is protected by the sand dike and it increased in area rapidly (Horsthuis et al. 1996; Huizing et al. 1996). Rabbits have been introduced on the island and still occur, but Brown hares have never been introduced (Mitchel-Jones 1999; van Laar 1983). Annual monitoring of all bird species (1982-2000) show maximum counts of Brent geese between 500 and 1800 in spring (unpubl. results). Barnacle geese are rarely observed. The salt marsh has never been grazed by livestock (de Meulmeester & Janssen 1997).

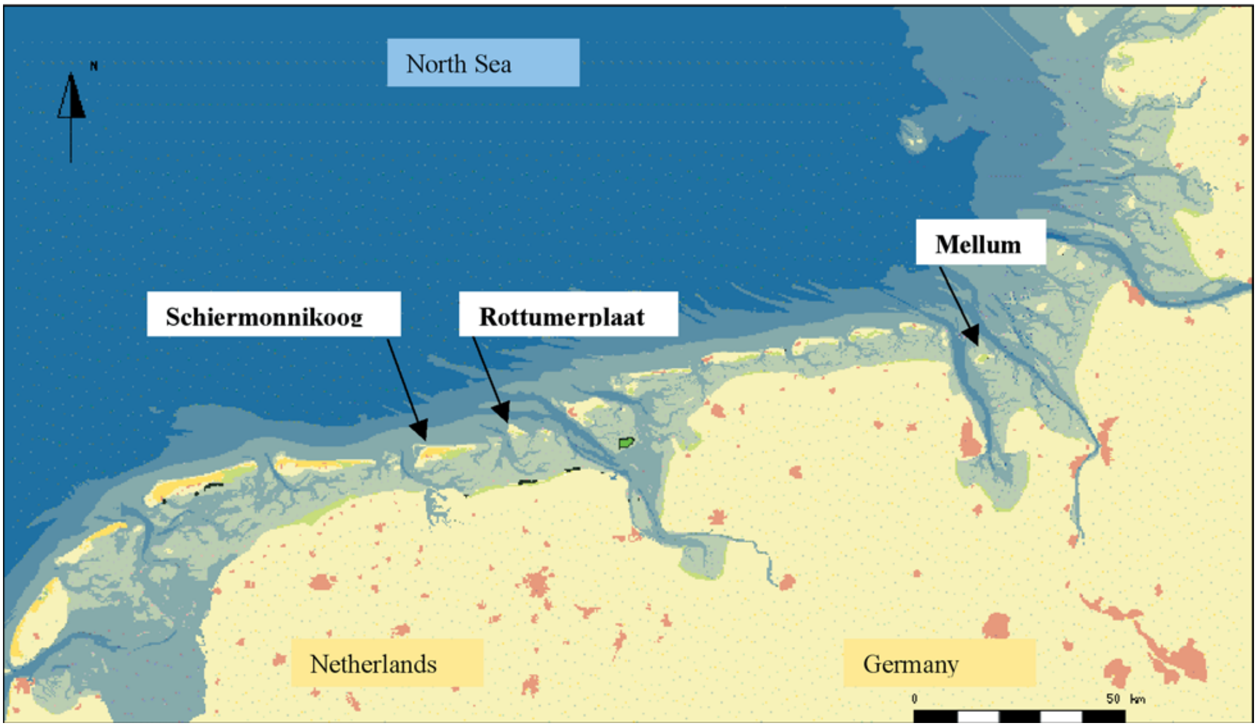

Fig. 1. Map of the Wadden Sea area showing the location of the study sites Schiermonnikoog, Rottumerplaat and Mellum.

Mellum

The salt marsh on this island developed completely naturally without human intervention. Between 1960 and 1970 a dune developed that enclosed the present study area (Kuhbier 1987). On the lee site of this dune a salt marsh developed. The present study area was unvegetated in the early 1970s (Hartung 1987), but vegetation started to establish at this site during the subsequent years (Kuhbier pers. comm.). Hares and rabbits are not present on this island (Mitchel-Jones 1999; van Laar 1983). Annual monitoring of all bird species (1974-2000) show maximum spring counts of 2000 to 7000 Brent geese. Barnacle geese are rarely observed. The marsh has also never been grazed by livestock.
These sites were compared with:

Schiermonnikoog

Due to the dominant westward sea currents there is a net transport of sediment along the shore of Schiermonnikoog from west to east. This results in an eastward expansion of the island creating a series of salt marshes at different developmental stages. A well-developed chronosequence is found from east to west across the island (Olff et al. 1997). We selected a site that has been vegetated since 1974 based on aerial photographs of the island (Olff et al. 1997). Hares and rabbits were present since the beginning of salt-marsh development. Hares counted between 1997 and 2002 ranged between 379 and 596 individuals in a 550 ha counting area overlapping the study site (pers. obs.). From 1997 to 1999, the maximum spring numbers of Barnacle geese ranged between 5000 and 9000. Corresponding numbers of Brent geese were between 3000 and 4000 individuals (Stahl et al. 2002). Livestock grazing has never occurred at the study site.

Measurements

As many people carried out the measurements, the main author joined the fieldwork at the three islands, to control for observer effects in the measurements. At each site an area was selected, 100 m in width and between 900 and 1000 m in length (Fig. 2). One boundary started at the foot of a dune and another was positioned at the intertidal flats, thus each area covered the entire gradient from high to low salt marsh. Every 20 m, the thickness of the clay layer and surface elevation were measured on three parallel transects (lines A, B, C in Fig. 2) separated by 50 m and running from the high to low salt marsh along this area. One transect ran

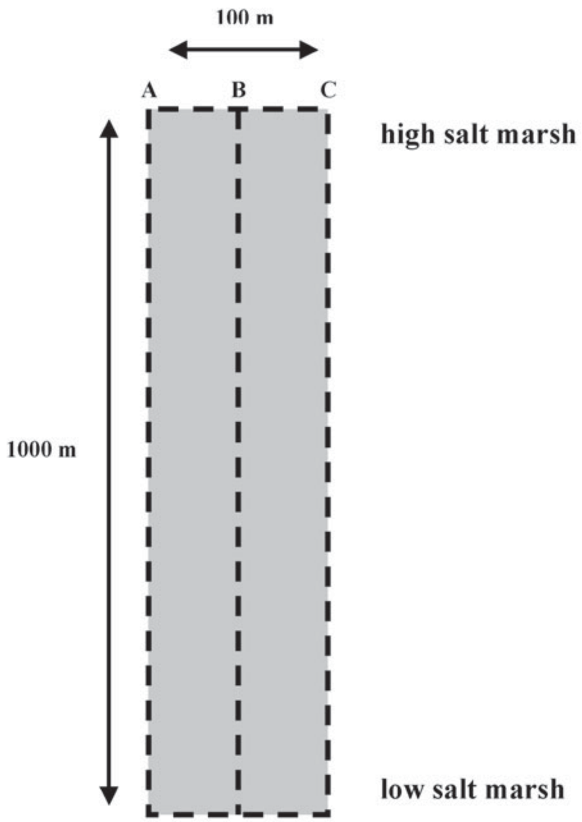

Fig. 2. Diagram of a transect that was established on each island. A transect started at the foot of a dune in the high salt marsh and ended in the low salt marsh at the border of the mudflats. On the lines A, B, and C the thickness of the clay layer and surface elevation were measured every 20 m.

through the centre of the area, and the other two were located at the periphery. Thickness of the clay layer was measured by means of a soil corer, surface elevation by the use of a theodolite relative to a point with known height above Dutch Ordnance level (+NAP), or 'Normal null' at Mellum (+NN). As the islands are positioned at different locations in the Wadden Sea, the tidal amplitude differs (van Wijnen & Bakker 1997). Surface elevation was therefore expressed relative to Mean High Tide (+MHT) at each site (Schiermonnikoog: 1 m +NAP; Rottumerplaat: 1.1 m +NAP; Mellum 1.53 m +NN). In the field, homogeneous patches of vegetation were recognized and their boundaries were drawn on a map. These patches of homogeneous vegetation were described by making ten analyses of randomly selected quadrats of 2 m × 2 m. All plant species were recorded and cover was estimated visually using the decimal scale of Londo (1976). These relevés were assigned to vegetation types according to criteria used in SALT97 by de Jong et al. (1998). Later on these vegetation maps were digitized, and surface areas for each vegetation type were determined. The mean cover of the plant species under study (*Elymus athericus, Atriplex portulacoides, Festuca rubra, Plantago maritima* and *Puccinellia maritima*) was calculated per vegetation type and plotted against the average surface elevation of all points measured within each vegetation type.

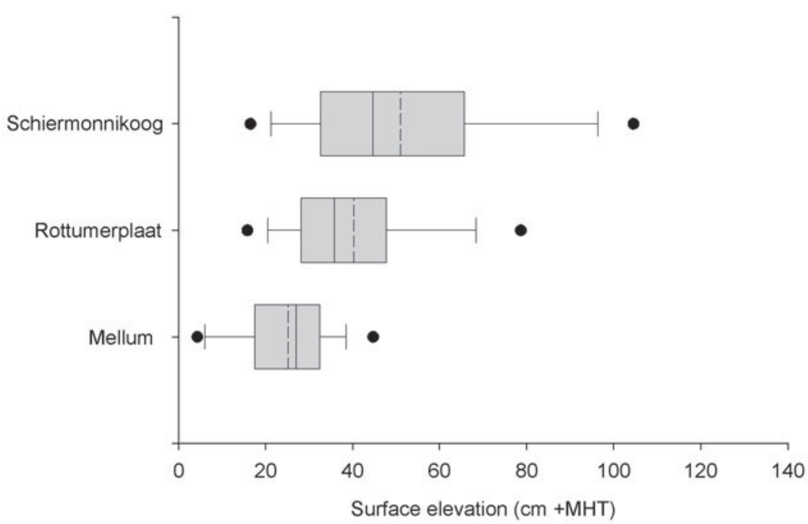

Fig. 3. Box plots showing the distribution of the surface elevation data (cm + Mean High Tide) measured at Schiermonnikoog, Rottumerplaat and Mellum. The boundaries of the box mark the 25th and 75th percentiles, the solid line within the box shows the median, and the dotted line shows the average. Whiskers indicate the 10th and 90th percentiles and points indicate the 5th and 95th percentiles.

Results

Elevation and clay layers

The areas that were selected on the three islands showed a large overlap in their surface elevation (Fig. 3). The greatest proportion of data points at each site was below 70 cm +MHT (75 % at Schiermonnikoog, 90% at Rottumerplaat and 100 % at Mellum). However, the distribution of the data points over the elevation gradient was different between sites. The larger proportion of the data that was obtained at higher surface elevation at Rottumerplaat and Schiermonnikoog, was caused by the presence of sand dunes in the areas. At Schiermonnikoog elevations up to 130 cm +MHT were measured. The average and median of all elevations recorded were therefore higher at Rottumerplaat and Schiermonnikoog compared with those at Mellum.

The thickest layers of clay were found at low elevations and they tended to decrease towards sites at high elevation (Fig. 4). At the low elevations there was a considerable overlap in the thickness of the clay layer between the three islands. This indicated similar sedimentation rates. Rottumerplaat had a thicker clay layer over a large part of the elevation gradient and it decreased only at the highest end of the gradient.

Vegetation types

All sites showed a clear gradient of vegetation types characteristic of the pioneer zone, low salt marsh, middle-high to the high salt marsh (Table 1). The variety of vegetation types that was found was larger at Schiermonnikoog (20 different types) compared to Rottumerplaat (9 types) and Mellum (8 types). Vegetation with more than 50% cover of *Atriplex portulacoides* (Ph5), was more abundant at Rottumerplaat and Mellum that at Schiermonnikoog. Vegetation types where *Festuca rubra* was the dominant or co-dominant plant species (Jfl, Jf, Jfz) were more abundant at Schiermonnikoog. The high salt marsh was characterised by vegetation types with a high cover (>25 %) of *Elymus athericus* (Xy5 and Xy3) at all the three sites. However, the area covered by vegetation with more than 50 % *Elymus athericus* (Xy5) was higher at Rottumerplaat and Mellum that at Schiermonnikoog. These differences in the area covered by vegetation types may simply be the result of the different distributions of sample points over the elevation gradient. Therefore, we looked at the abundances of individual plant species over this elevational gradient.

Table 1. The percentage of the total area of the transects (100 m × 1000 m) that is covered by the different salt-marsh vegetation types at Schiermonnikoog, Rottumerplaat and Mellum. The vegetation types are described according to de Jong et al. (1998). The dominant plant species or their minimal visual cover gives a short characterisation of each vegetation type.The vegetation types have been divided in the zones of salt marsh where they occur (de Jong et al. 1998).

Zone of salt marsh	Vegetation type	Short characterization	Cover (%) Schier	Cover (%) Rottum	Cover (%) Mellum
Pioneer	Ss3	*Spartina anglica* 5-50%	0.25	6.24	1.40
	Qq0	*Salicornia* ssp. <5%	1.30		
	Qq3	*Salicornia* ssp. >5%	7.45	4.73	1.26
	Qq3/Pl3		3.00		
Low marsh	Pl3	*Limonium vulgare* dominant, >25%	6.22	19.59	18.73
	P	*Puccinellia maritima*, sparse vegetation	0.43		
	Ph5	*Atriplex portulacoides* >50%	0.25	37.71	22.53
	Jfl/P/Pl3		0.89		
	Jfl/Pl3		18.30		
Middle high marsh	Jfl	*Festuca rubra* and *Limonium vulgare* codominant	7.78	5.06	
	Jf/Jjl	*Festuca rubra*, *Juncus gerardii* and *Limonium vulgare* codominant	1.06		
	Jj	*Juncus gerardii* dominant	0.89		
	Jf	*Festuca rubra* dominant	11.30	0.56	8.32
	Jfz	*Artemisia maritima* dominant	3.95		
High marsh	Ph3/Xy5				12.95
	Xy3	*Elymus athericus* codominant	4.22		
	Xy5	*Elymus athericus* dominant, >50%	8.39	15.56	22.34
	Xy3/Xy5		12.21		
	Cr	*Centaurium littorale* and *Sagina nodosa* present	3.33		
	R	Rest group, no salt-marsh vegetation type	0.83	1.43	
Remainder	Water		4.29	9.11	12.08
	Bare soil		3.66		0.40

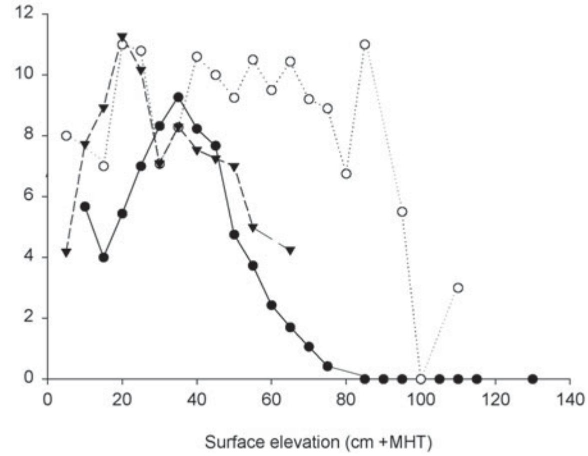

Fig. 4. Average thickness of the clay layer at different marsh surface elevation classes (cm + Mean High Tide) for Schiermonnikoog (●), Rottumerplaat (○) and Mellum (▼).

Cover of plant species

The cover of individual plant species showed clear differences between sites. We focused on three typical young to mid-successional species, which are important food plants for hares and geese, and two typical late successional plant species. Plant species which are preferred as food plant species by geese, *Plantago maritima* and *Puccinellia maritima*, occurred at a similar surface elevation with higher cover at Schiermonnikoog compared to those at Rottumerplaat and Mellum (Fig. 5). *Plantago maritima* was rarely found at Rottumerplaat and Mellum. *Festuca rubra*, a preferred food plant for both geese and hares, occurred over a large part of the elevation gradient at Schiermonnikoog, whereas it was found at only a small part of the gradient at Rottumerplaat and Mellum. The typical late successional species of the lower salt marsh *Atriplex portulacoides,* dominated the lower elevations at both Rottumerplaat and Mellum, whereas it contributed a low amount of cover at Schiermonnikoog (Fig. 6). *Elymus athericus,* as a typical late successional species of the high marsh, occurred with higher cover at both low and high elevations on Rottumerplaat and Mellum compared to that on Schiermonnikoog (Fig. 6). At the upper part of the elevation gradient at Rottumerplaat and Mellum, almost no other species were found with *Elymus athericus* which constituted nearly 100 % of the vegetation. In contrast, on Schiermonnikoog this species did not reach higher cover values than 70 %.

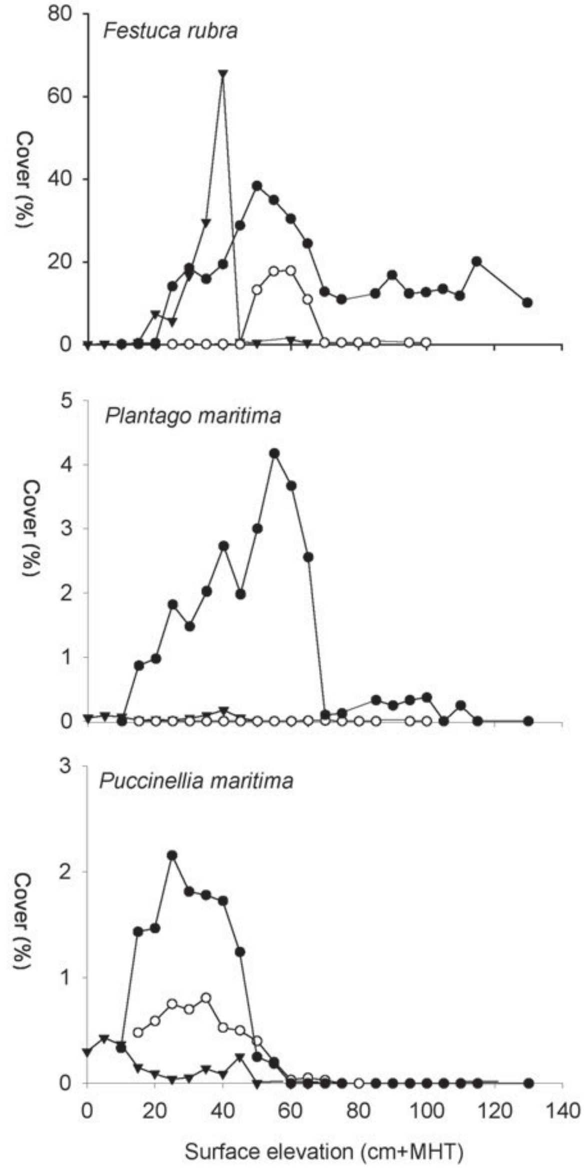

Fig. 5. Mean cover of important food plant species for hares and geese; *Festuca rubra, Plantago maritima* and *Puccinellia maritima*, at different marsh surface elevation (cm + Mean High Tide) for Schiermonnikoog (cm + Mean High Tide) for Schiermonnikoog (●), Rottumerplaat (○) and Mellum (▼).

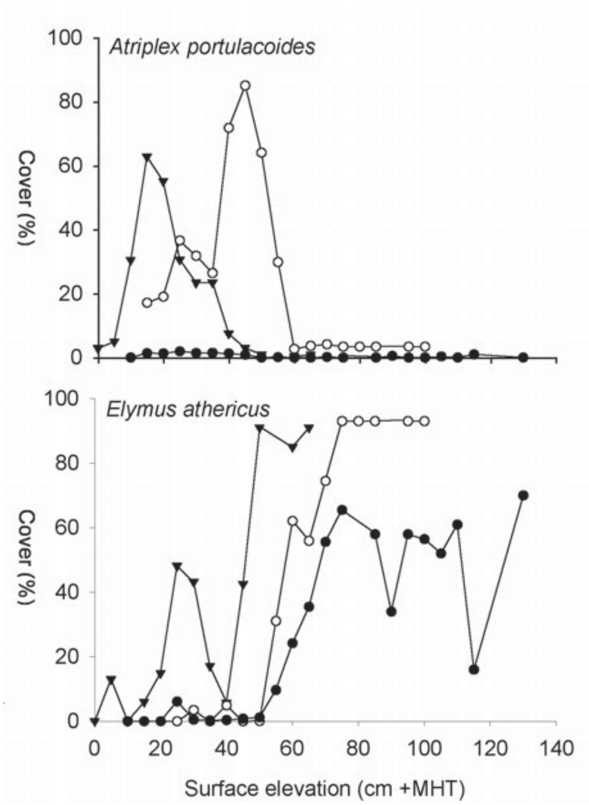

Fig. 6. Mean cover of typical late successional plant species; *Elymus athericus* and *Atriplex portulacoides*, at different marsh surface elevation (cm + Mean High Tide) for Schiermonnikoog (cm + Mean High Tide) for Schiermonnikoog (●), Rottumerplaat (○) and Mellum (▼).

Discussion

Interpretation of the differences in vegetation development, is difficult as numerous factors influence the plant assemblages. Due to the geographical locations, abiotic conditions will differ between sites. For instance, Mellum is located near the mouth of the River Weser. Although the salinity extremes around Mellum are in the range of 25 - 35 ‰ (Meyer & Michaelis 1980), and therefore hardly different from those reported for Schiermonnikoog and Rottumerplaat (Abrahamse et al. 1977), the type of sediment, sediment load of the water, the concentration of solubles in the water etc. might differ. Despite these differences, all three islands have important similarities in their development. Salt-marsh development started in the same period and proceeded after the formation of a sand dune. Besides, none of the areas has been grazed by livestock. As most salt marshes in the Wadden Sea have a history of grazing by livestock (Bakker et al. 2003) increasing the sample size with more islands with a similar pattern of salt-marsh development is impossible. We are aware of the limitations imposed by this study, but despite their different locations the two islands without hares, showed a very similar pattern of vegetation development.

Next to hares, rabbits can have a major impact on the vegetation, but at present only effects have been observed in dune vegetation (ten Harkel & van der Meulen 1996; Kiffe 1989; Zeevalking & Fresco 1977). As rabbits mainly graze in close proximity to their burrows (Palomares & Delibes 1997), their effect on salt-marsh vegetation would be expected to be low. Dropping counts at Rottumerplaat showed that no grazing occurred further than 100 m from the sand dike (pers. obs.). Moreover, rabbits were not present on Mellum so the difference in development between on one hand Rottumerplaat and Mellum compared with Schiermonnikoog on the other, cannot be explained by rabbit grazing. Brent geese occur in high numbers on each island in spring. Barnacle geese are only present at Schiermonnikoog. Both goose species show large overlap in their choice of habitat and diet (Stahl et al. 2002; van der Wal et al. 1998; Prins & Ydenberg 1985) and differential effects of grazing between the two goose species do not seem likely. Therefore, we think that the differences in vegetation development between Rottumerplaat and Mellum on one hand and Schiermonnikoog on the other, can mainly be explained by the effects of hare grazing.

Vegetation succession with and without hares

Plant productivity in European temperate coastal marshes is mainly nitrogen-limited (van Wijnen & Bakker 1997; Kiehl et al. 1997). The amount of nitrogen in the soil is correlated with the thickness of the clay layer (Olff et al. 1997). The input of clay by means of continuous flooding of the sea, has been regarded therefore as the major factor driving salt-marsh succession (Olff et al. 1997).

At the higher elevations Rottumerplaat showed a greater thickness of clay compared to the other sites. A difference in the spatial heterogeneity of the salt marsh (Bockelmann et al. 2002), for example in the orientation of the creek drainage system, may largely explain this greater thickness of clay. A similar thickness of the clay layer was found at the lower marsh elevations at the three sites. A maximum of 9 to 11 cm of clay was deposited. From aerial photographs it was observed that salt-marsh vegetation was first established on the three islands in the early 1970s Thus, we have investigated about 30 years of vegetation succession at each site. As the sedimentation of clay in this period is very similar between the sites, the rate of nitrogen input in the system is expected to be similar. As a consequence, the speed of vegetation succession is predicted to be comparable between the sites. Thirty years of vegetation succession in the absence of hares (and livestock) grazing, resulted in a high cover of typical late successional species. Both Rottumerplaat and Mellum featured a high dominance of *Atriplex portulacoides* in the low salt marsh and *Elymus athericus* in the high marsh. At Schiermonnikoog, *A. portulacoides* was present but occurred only with a low cover, whereas *E. athericus* never formed the dense stands that were found at Rottumerplaat and Mellum. At Rottumerplaat and Mellum a sharp boundary existed between the *A. portulacoides* dominated low marsh and an *E. athericus* dominated high marsh. As a consequence, plant species which are highly selected as food plants by geese, such as *Plantago maritima* and *Puccinellia maritima* (Prop & Deerenberg 1991; Prins & Ydenberg 1985) showed a lower abundance on the hare-free islands. This is in line with earlier studies which show that hares facilitate the food supply for geese by preventing the dominance of *Atriplex portulacoides* (van der Wal et al. 2000b). In addition, the most important food plant for hares, *Festuca rubra* (van der Wal et al. 1998), occurs along only a small part of the elevational gradient at Rottumerplaat and Mellum, whereas it was found along the entire gradient at Schiermonnikoog.

Vegetation types typical of the middle salt marsh dominated by *Festuca rubra* are rare on the two hare-free islands. Earlier observations on Rottumerplaat (de Meulmeester & Janssen 1997; Horsthuis et al. 1996) or the vegetation map that was made in 1986 (by Rijkswaterstaat, Directie Groningen) did not report that large areas with these middle salt-marsh vegetation types occurred. In 1986, the area where the present measurements were taken was dominated by *Salicornia*-type vegetation in the low marsh, *Limonium*-type vegetation in the middle and *Juncus gerardii* and *Elymus athericus*-type vegetation in the highest parts of the marsh. Observations at Mellum, since the early 1970s, also show that these middle salt-marsh vegetation types never occurred in large abundance (Kuhbier 1987). These observations suggest that typical late successional species like *Atriplex portulacoides* and *Elymus athericus* will invade and dominate the vegetation during the early stages of succession when no hares are present. Their early dominance might prevent a stage developing where there is a high abundance of important food plant species for geese and hares.

The recorded vegetation development at Rottumerplaat and Mellum is consistent with the results of small-scale experiments at Schiermonnikoog. Excluding hares on young marshes lead to an increase in cover of typical late successional species such as *A. portulacoides* on the low marsh and *E. athericus* on the high marsh (van der Wal 2000b; Kuijper et al. in prep.). These experiments at Schiermonnikoog are not only applicable to understanding the local effects of hare grazing but are relevant to the set of salt-marsh systems on the Dutch and German Wadden Sea islands.

Consequences for conservation

Grazing by large herbivores, such as cattle and sheep, has large effects on salt-marsh vegetation (Andresen et al. 1990). Hence, livestock grazing is widely used as a management tool to prevent the dominance of single tall-growing species (Bakker et al. 1993). The potential effects of natural small herbivores, such as hares, are often neglected by managers. However, experiments at Schiermonnikoog showed that grazing by hares does affect species composition (van der Wal et al. 2000b) at a small scale (80 m^2), and the present study showed that we can scale-up these effects to 9 - 10 ha. By retarding vegetation succession, hares create a spatially heterogeneous vegetation with a higher diversity of plant species. The cover of species that are selected as food plant species by both hares and geese is higher in hare-grazed areas. Hare grazing thus facilitates food supplies for geese (van der Wal et al. 2000b). Although hares can retard vegetation succession for approximately 30 years (van der Wal et al. 2000b), they are not able to stop vegetation succession, and eventually late successional species dominate the marsh (Olff et al. 1997; Roozen & Westhoff 1985). At old, and hence productive, marshes, livestock grazing is needed to set back the successional clock. At the young stages of salt-marsh development small herbivores can have large long-lasting effects on the vegetation succession by preventing the establishment of late successional species that results in a relatively high plant diversity.

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