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Long-term vegetation changes in experimentally grazed and ungrazed back-barrier marshes in the Wadden Sea

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Abstract. Vegetation succession in three back-barrier salt marshes in the Wadden Sea was studied using a data set comprising 25 years of vegetation development recorded at permanent quadrats. The effect of livestock grazing on succession was assessed by comparing quadrats where grazing was experimentally prevented or imposed. We studied changes at the species level as well as at the level of the plant community. Special attention is given to effects on plant species richness and community characteristics that are relevant for lagomorphs (hares and rabbits) and geese. Inundation frequency and grazing were most important in explaining the variation in species abundance data. The three marshes studied overlap in the occurrence of different plant communities and the observed patterns were consistent between them. Clear differences in frequency and abundance of plant species were observed related to grazing. Most plant species had a greater incidence in grazed treatments. Species richness increased with elevation, and was 1.5 to 2 × higher in the grazed salt marsh. Grazing negatively influenced *Atriplex portulacoides* and *Elymus athericus*, whereas *Puccinellia maritima* and *Festuca rubra* showed a positive response. The communities dominated by *Elymus athericus*, *Artemisia maritima* and *Atriplex portulacoides* were restricted to the ungrazed marsh. Communities dominated by *Puccinellia maritima, Juncus gerardi* and *Festuca rubra* predominantly occurred at grazed sites. As small vertebrate herbivores prefer these plants and communities for foraging, livestock grazing thus facilitates for them.

Keywords: Correspondence analysis; Exclosure; Goose; Hare; Livestock; Salt marsh; Species richness.

Nomenclature: van der Meijden (1990) and Schaminée et al. (1998).

Introduction

Vegetation succession in salt marshes has been described by various authors for many different marsh types (Ranwell 1968; Westhoff 1987; Adam 1990). Salt marshes are suitable systems for studying vegetation succession because they are relatively simple and species-poor. Understanding the patterns of development and the processes behind them helps to gain insight into the functioning of ecosystems in general and is relevant for the sustainable management of salt marshes.

Elevation and sedimentation

Elevation of the marsh plays an important role in structuring salt-marsh ecosystems, as it is directly related to inundation frequency and hence to sediment deposition, evaporation, aeration, nutrient status, temperature and salinity (Adam 1990). The distribution of salt-marsh plants is strongly related to the gradients in elevation (Sanchez et al. 1996; Olff et al. 1997). Sediment type also affects vegetation composition to a large extent and is influenced by the position of the marsh in the tidal basin. Back-barrier salt marshes, or barrier-connected marshes according to de Jong et al. (1999), have developed on top of a sandy substrate, show less sediment accretion and have soils with a thinner layer of clay than more sheltered mainland salt marshes (Dijkema 1983a). Olff et al. (1997) showed that the pool of nitrogen is positively related to the thickness of the clay layer. They studied a chronosequence on one of these back-barrier marshes and they concluded that succession there is caused mainly by the continual increase in nutrient availability. In back-barrier salt marshes, most elevational variation is caused by elevational differences in the sandy subsoil (van Wijnen & Bakker 1997), and each elevational position was shown to have its own characteristic successional sequence. The final stages on high and low marsh are characterized by tall-growing species (Olff et al. 1997), suggesting that light competition becomes more important with increasing nutrient availability. Similar conclusions were drawn from studies in which permanent quadrats have been studied for several years (Roozen & Westhoff 1985; Bakker 1985; Jensen 1985), though the study period is often short, relative to the speed of vegetation change.

Grazing with livestock

Grazing with livestock affects biotic and abiotic components of the marsh (Jensen 1985; van Wijnen et al. 1999). Empirical studies show that short plants characteristic of early succession are favoured by grazing (Kiehl et al. 1996; Aerts et al. 1996). Ungrazed high marshes tend to become dominated by tall *Elymus athericus* (Andresen et al. 1990; Olff et al. 1997), and tall *Atriplex portulacoides* becomes dominant on the low marsh (Bakker 1985; Jensen 1985; van der Wal et al. 2000b). Brackish marshes without grazing become covered with tall *Phragmites australis*. This happens, for example, in estuarine marshes such as the Dollard (Esselink et al. 2000) or close to large dune systems with seeping fresh water (Hobohus 1986; Neckermann 1987). The plant species richness is higher in grazed than in ungrazed high marsh (Bakker 1989) at the scale of 4 m^2.

Importance of marshes and their management by grazing

Salt marshes in the Wadden Sea are important spring staging habitat for waterfowl such as Brent geese (*Branta bernicla bernicla*) and Barnacle geese (*Branta leucopsis*) and a year-round habitat for lagomorphs, such as hares (*Lepus europaeus*). These small vertebrate herbivores forage on short plant species such as *Puccinellia maritima*, *Festuca rubra*, *Triglochin maritima* and *Plantago maritima* (Prop & Deerenberg 1991; van der Wal et al. 2000a). Natural succession of salt marshes has been shown to affect the occurrence of these plants, leading to a decline in the importance of the marsh as a habitat for these small herbivores (van de Koppel et al. 1996; van der Wal et al. 2000b).

From 600 BC onwards, salt marshes in the Wadden Sea have been grazed with livestock in summer (Behre 1985) and currently about half of the marsh area in the Wadden Sea is grazed (de Jong et al. 1999). Large areas of marsh have been taken out of grazing over the past 20 yr due to lack of interest from farmers (Dijkema 1983b) or for nature conservation purposes (Stock & Kiehl 2000). Grazing is still one of the most important and common management tools on salt marshes and therefore proper insight is required into effects of grazing on salt-marsh ecosystems. In this paper we describe vegetation development in different plant communities, where grazing with livestock was experimentally ceased or imposed. The goals of the analysis presented here were (1) generalization of effects of grazing management at back-barrier marshes in the Wadden Sea; (2) comparison of short-term and long-term experiments and (3) evaluation of effects of livestock grazing on plant species that are important for other herbivores such as geese and hare. The patterns of development between high and low marsh were compared using data from three back-barrier salt marshes over a period of more than 25 years.

Methods

Study sites and permanent quadrats

The study was performed at 6 study sites on the 2 Dutch Wadden Sea islands of Terschelling (53° 26' N, 5° 28' E), Schiermonnikoog (53° 30' N, 6° 10' E) and the Danish peninsula of Skallingen (55° 30' N, 8° 20' E), (App. 1; see AVS electronic archive at www.opuluspress.se). All these marshes are characterized by a sandy substrate and classified as back-barrier salt marshes (de Jong et al. 1999). Extensive parts of these marshes are grazed with livestock. On Skallingen ca. 1100 ha are grazed with 0.5 cow ha^{-1} and 0.5 sheep ha^{-1} (Jensen 1985). The western part of the Terschelling marsh (200 ha) is grazed with cattle at a stocking density of 0.5 cow ha^{-1} (State Forestry Service, pers. comm.). On Schiermonnikoog stocking rates decreased from 1.5 cow ha^{-1} in the 1970s to 0.5 cow ha^{-1} at 400 ha, from 1995 onwards. None of the marshes in our study are artificially drained. Tidal amplitude ranges from 1.5 m at Skallingen to 2.3 m at Schiermonnikoog (van Wijnen & Bakker 1997).

In the early 1970s, exclosures were erected and areas were fenced off at the 6 study sites (see App. 1). At Terschelling (sites 1 and 2) 2 exclosures of 30 m × 30 m were constructed in 1972 on the grazed marsh; observations started in 1976. At Schiermonnikoog (sites 4 and 5) 7 exclosures measuring 50 m × 12.5 m were built in 1974 and 1972 respectively, while observations had started 1 yr earlier. At Skallingen (site 6) 6 exclosures of 40 m × 60 m, constructed in 1972 (Jensen 1985), were studied from 1976 onwards. In addition, hitherto ungrazed areas were grazed anew in 1972 on Terschelling (site 3) and on Schiermonnikoog (site 5). All this resulted in 4 experimental treatments. Those quadrats on which grazing by livestock was stopped or imposed are referred to as ‘experimentally ungrazed’ and ‘experimentally grazed’, respectively. The other quadrats are classified as ‘control grazed’ and ‘control ungrazed’ because no experimental change in management took place.

Paired 2 m × 2 m quadrats were established inside and outside the grazing treatments. Vegetation relevés were made annually at Schiermonnikoog and every three years at Skallingen and Terschelling. The relevés were made in late summer, initially according to the scale of Braun-Blanquet (Westhoff & van der Maarel 1973), from 1976 onwards following the decimal scale of Londo (1976). The Braun-Blanquet data were transformed to percentage values as described by Bakker (1989). A total of 2596 recordings were used in the present study, up to and including 1998. The majority of these were made on Schiermonnikoog where 58 quadrats were studied for 26 yr. The total number of recordings was 72 for site 1 and site 2, while all other sites have more than 372. At each study island, the quadrats were positioned over the entire tidal range from low to high marsh. In 1999 clay thickness was measured in triplicate and averaged per quadrat. We measured elevation of each individual quadrat with respect to mean high tide (MHT). Subsequently, the inundation frequency was calculated following van Wijnen (1997).

Data analysis

We tested whether a linear or unimodal multivariate model should be used, and accepted the unimodal model. Then Canonical Correspondence Analysis (CCA; Jongman et al. 1995) was performed to obtain an overview of the major patterns in the 1989 data set. We chose for the year 1989, because after that year a number of quadrats was discarded and therefore this year yielded the largest variation. The vegetation data from the quadrats at the starting year and the end year were used to calculate the position of these recordings in the ordination diagram, without influencing the ordination. Species data were log-transformed and rare species were down-weighted to reduce their influence on the analysis. Inundation frequency, grazing status, thickness of the clay layer and site were entered as environmental variables. A Monte Carlo permutation test was used to test the significance of the environmental variables that were selected in the forward selection procedure.

Frequencies of occurrence per plant species were calculated for each treatment and site. The analysis of frequencies was restricted to quadrats that had a constant treatment for more than 20 yr. In this way bias caused by the fact that quadrats were in transition was minimized. Using a χ^2-test, we tested deviations from an even distribution in the untransformed frequencies.

For each relevé, the number of species present was counted. Differences in species number between grazing treatments per year were tested for statistical significance using a paired t-test. The effect of elevation on species number for quadrats in the year 1989 was determined using an Analysis of Covariance (ANCOVA) with elevation as a co-variable and grazing as a factor.

Species-specific responses for the 'experimentally ungrazed' and 'control grazed' treatments over time were analysed using the procedure described by Huisman et al. (1993). The best fitting significant model, from a predefined set of 5 hierarchical models, was selected for each species and treatment. The analysis was restricted to 7 species that have particular relevance for grazing by small vertebrate herbivores: *Puccinellia maritima*, *Festuca rubra*, *Triglochin maritima*, *Plantago maritima*, *Artemisia maritima*, *Atriplex portulacoides* and *Elymus athericus*. No extra data transformation took place. We analyzed the developments in the low and high marsh separately and restricted the analysis to quadrats that were followed over the entire experimental period. We separated low and high salt marsh at a level of 50 inundations per yr and assigned corresponding pairs of quadrats to these classes, based on the average inundation frequency of the pair. The boundary was arbitrarily drawn based upon the occurrence of plant communities in relation to inundation frequency in our data set. Other authors mention boundaries in the order of 100 inundations per yr (Gray & Scott 1967; Erchinger 1985). The models were tested per study island, to asses the generality of the patterns found.

All relevés were phytosociologically identified at the association level according to Schaminée et al. (1998), with support of the computer program Salt97 (de Jong et al. 1998). Vegetation change at the association level was then analyzed by summarizing the frequency of occurrence of each association in relation to grazing for the final year of study.

Results

Overview of the data set, interaction of grazing and abiotic conditions

The relevés were significantly separated along axes correlated to grazing status and inundation frequency in the CCA (Fig. 1A-F). The total variation explained by the first 4 hypothetical axes was 22% for the species data and 87% for the species-environment data. Vectors for the environmental variables inundation frequency, clay layer thickness, grazing status and site (Fig. 1B) yield information about their influence on the vegetation composition; the length of these vectors is a measure of the magnitude of this influence. Clay-layer thickness was positively related to inundation frequency. Inundation frequency (Permutation test: $F = 11.1$; $P < 0.005$; LambdaA = 0.29) and grazing status (Permutation test: $F = 8.7$; $P < 0.005$; LambdaA = 0.22) had the strongest correlations to the first and second canonical axes and were most important in explaining the observed variation. Grazing effects are independent from

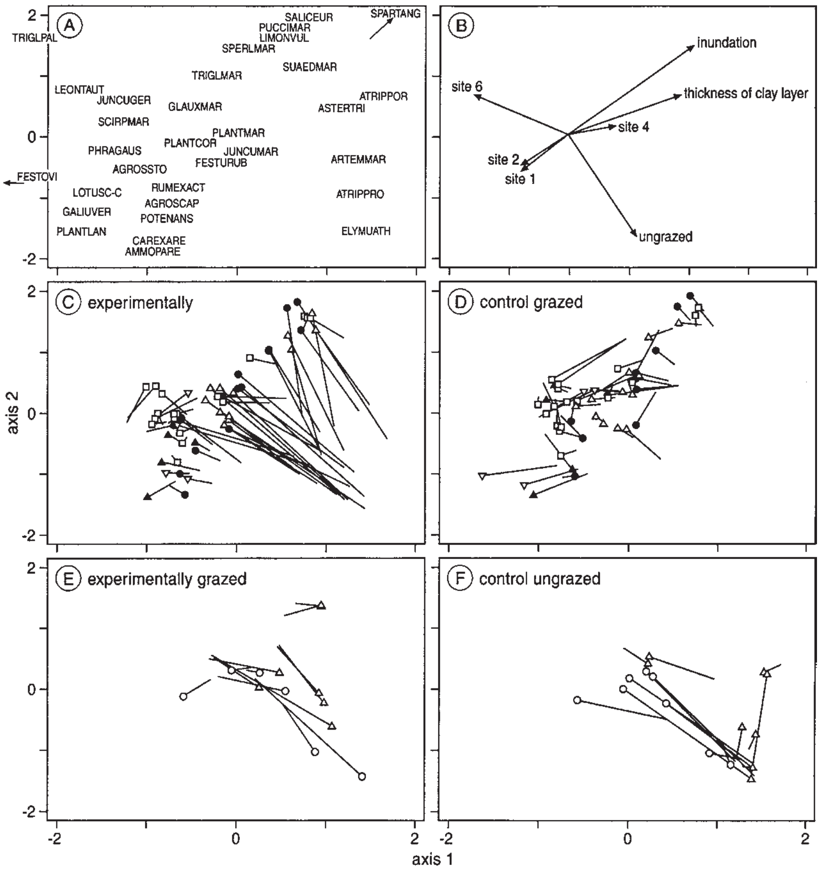

Fig. 1. Bi-plot of sample- and species-scores from the Canonical Correspondence Analysis (CCA). **A.** Relative positions of 36 characteristic species, along the first 2 canonical axes. Species are referred to by the first 5 letters of the species and the first 3 letters of the genus name. **B.** The vectors of the environmental variables that were significant. **C-F.** The change of position in the ordination diagram between the starting and the end year of quadrats in the 4 experimental treatments. **C.** experimentally ungrazed; **D.** control grazed, **E.** experimentally grazed and **F.** control ungrazed. The starting year of observations is indicated by a symbol that also refers to the study site that the quadrat belongs to: Skallingen (□, site 6); Schiermonnikoog (○, site 5) and (●, site 4); Terschelling (▲,site 2), (△, site 3) and (▽, site 1). The scale for Fig. 1B was multiplied by 5.

inundation frequency (the arrows in Fig. 1B are perpendicular). The identity of 4 of the sites significantly explained some of the variation (Fig. 1B, LambdaA ranges from 0.08 to 0.18). However, it is not surprising that vegetation composition differs between sites, as the quadrats were not selected at the start of the study to be equal in this respect. For the purpose of this paper it is important that the patterns in development can be compared.

The lower-right part of the ordination diagrams (Fig. 1A) is characterized by plants associated with the ungrazed marsh: *Elymus athericus, Atriplex prostrata* and *Artemisia maritima*. The plant species that occur at a higher elevation are found in the lower-left corner of the diagrams, e.g. *Festuca ovina* or *Galium verum* (Fig. 1A). *Spartina anglica*, *Puccinellia maritima* and *Atriplex portulacoides* are species of the low marsh, found in the upper-right corner of Fig. 1A. The quadrats at sites 1 and 2 at Terschelling and some of the quadrats at Skallingen and Schiermonnikoog were positioned at the transition to low dunes (lower left corners of Fig. 1B-F). At Skallingen and Terschelling, some quadrats harboured *Phragmites australis*, which was lacking in the Schiermonnikoog samples. *Elymus athericus* was never observed in the study quadrats at Skallingen, although the species was present at different locations on the peninsula. Quadrats at Skallingen also featured the occurrence of *Scirpus maritimus*, found in the upper left quadrant of the ordination diagram (Fig. 1A).

The impact of grazing is very apparent from the trajectories that quadrats followed in the ordination diagram between the start and the end of our observation period. Experimentally ungrazed quadrats (Fig. 1C) almost all moved to the lower right corner of the diagram, which is characterized by *Elymus athericus* and *Atriplex portulacoides*. Experimentally grazed quadrats (Fig. 1E) showed exactly the opposite pattern. The ungrazed treatments at Skallingen (Fig. 1C, open squares) differed in their development from those at Schiermonnikoog (open and closed circles) and at site 3 on Terschelling (open triangles), by the absence of *Elymus athericus*. Low marsh quadrats at Skallingen became dominated by *Atriplex portulacoides*, as occurred elsewhere, but were not invaded by *Elymus athericus* subsequently. At the upper ranges of elevation, the patterns of change were not obviously related to grazing, as quadrats in the lower left corner of Fig. 1C only moved short distances in an inconsistent direction. Some of the control ungrazed quadrats changed considerably over time (Fig. 1F), indicating that their development had not yet reached a stable state, when the observations started.

Table 1. Frequencies (%) of species occurrence per treatment for the 30 species occurring most frequently. All relevés are included except those in transition for less than 20 yr. Species are grouped according to their response to grazing; for the groups '>> ungrazed' and '>> grazed' the frequncies in grazed and ungrazed sites, respectively, deviate significantly from proportionality (χ^2-test, $P < 0.05$).

	Species	Grazed	Ungrazed
>> ungrazed	*Artemisia maritima*	43	65
	Atriplex prostrata	19	68
	Elymus athericus	26	52
	Atriplex portulacoides	14	25
No significant difference	*Festuca rubra*	78	85
	Juncus maritimus	9	10
	Lotus corniculatus	8	10
>> grazed	*Plantago maritima*	67	40
	Agrostis stolonifera	53	41
	Juncus gerardi	63	22
	Glaux maritima	58	22
	Triglochin maritima	49	23
	Armeria maritima	46	26
	Puccinellia maritima	43	23
	Spergularia maritima	43	10
	Limonium vulgare	39	12
	Trifolium repens	31	20
	Aster tripolium	36	15
	Poa pratensis	26	19
	Salicornia europaea	35	7
	Suaeda maritima	30	12
	Plantago coronopus	23	2
	Potentilla anserina	14	10
	Agrostis capillaris	15	6
	Carex arenaria	15	6
	Leontodon autumnalis	16	1
	Phragmites australis	14	3
	Plantago lanceolata	11	6
	Ammophila arenaria	10	6
	Spergularia salina	12	2

Grazing management and species richness

In total, 172 plant species were observed over the years. However, many species were only observed very infrequently. Ca. 80% of the species show a higher incidence at grazed than at ungrazed sites with constant treatment for more than 20 yr. Of the 30 most frequent species on salt marshes (Table 1) only *Artemisia maritima*, *Atriplex prostrata*, *Elymus athericus* and *Atriplex portulacoides* showed significantly greater incidence without grazing (χ^2-test, $P < 0.05$). The differences in species presence between treatments is due to species observed very rarely (i.e. less than 1% of the cases). Species only found in a single treatment were more often observed in the grazed than in the ungrazed quadrats (57× vs 16×). The total set of observed species in quadrats with constant treatment for more than 20 yr contains 21 Red List species, of which 11 do not occur in the ungrazed sites.

Plant species richness at the 2m × 2m scale was affected by succession and grazing (Fig. 2). Species number showed a downward trend over time in ungrazed quadrats, whereas it increased in grazed quadrats. In three years, the grazed quadrats had significantly greater species numbers than their paired ungrazed counterparts (Fig. 2, paired t-test, $P < 0.05$, $20 < n < 90$). With increasing elevation, species richness increased (Fig. 3, Ancova, $P < 0.001$, $n = 132$). Species richness benefited from grazing with livestock on both the lower and higher salt marsh.

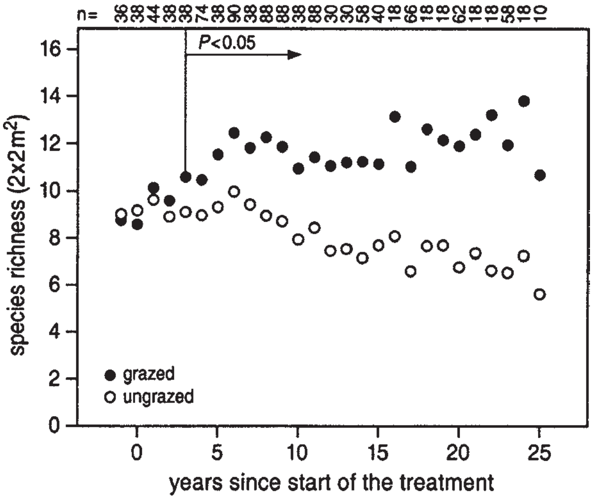

Fig. 2. The development of species richness over time in paired grazed and ungrazed permanent quadrats. Sample sizes (n) per year since the start of the treatment are indicated in the top of the diagram. After a period of 3 yr the differences between grazing treatments were significant, indicated by the arrow with text '$P < 0.05$'. Observations for sites 4 and 5 started 1 yr before the treatments were established.

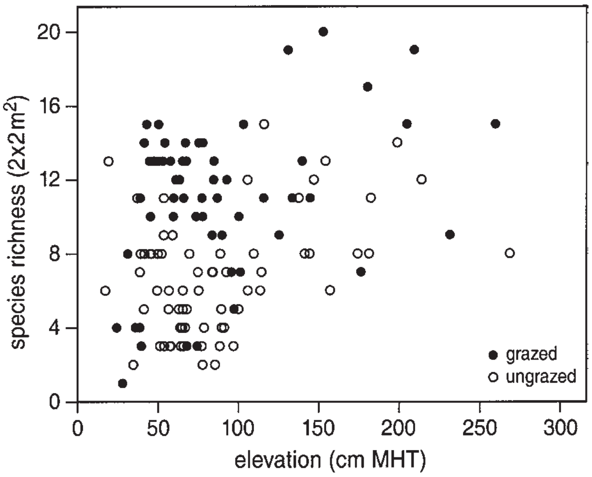

Fig. 3. Relationship between elevation with respect to Mean High Tide (MHT) and the species richness in grazed and ungrazed permanent quadrats for the year 1989 (ANCOVA, $df = 132$, $R^2 = 0.38$, $P < 0.01$ for the factors grazing and elevation).

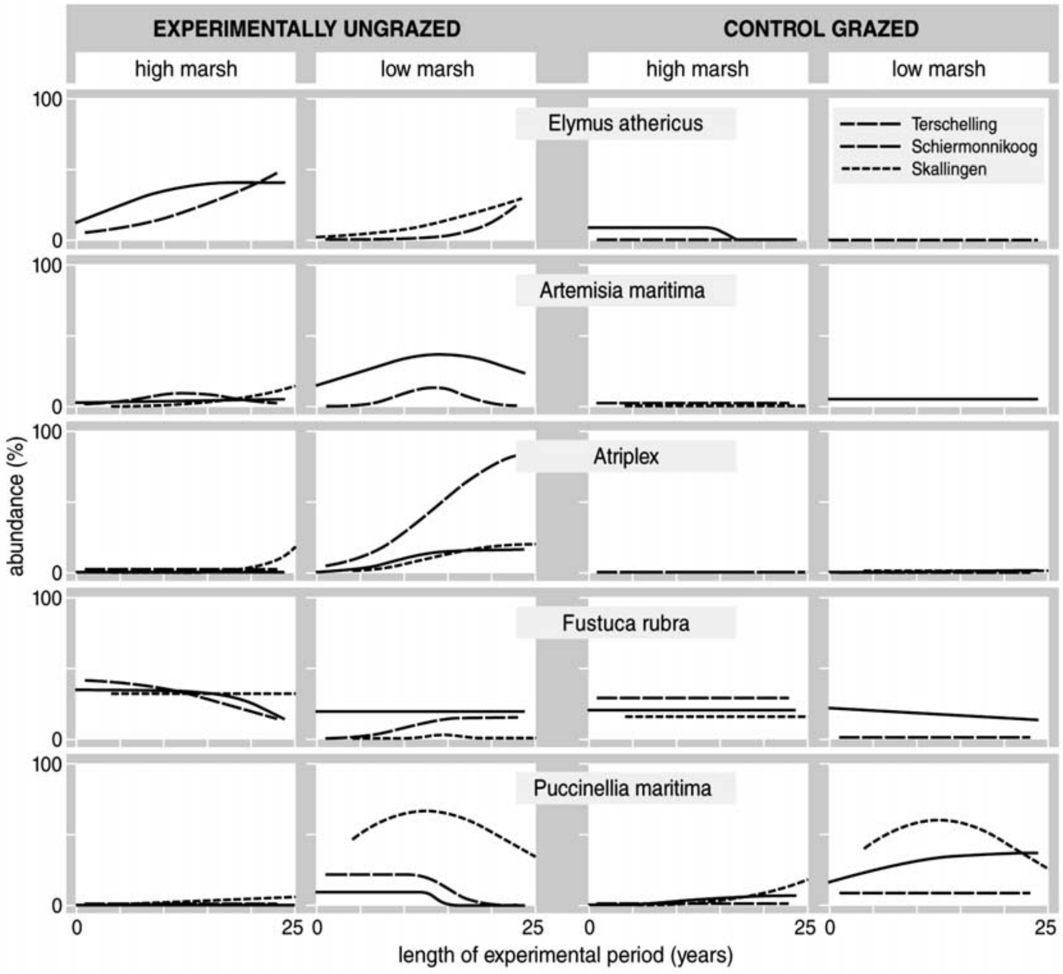

Fig. 4. Species response curves showing the abundance of a selection of 5 species in relation to the duration of each of the grazing treatments, per study island and per level of inundation. Associated models and sample sizes are given in App. 2.

Effects of changes in management on important species for geese and hare

Cessation of grazing led to an increased cover of *Elymus athericus* and *Atriplex portulacoides* and a decrease of *Puccinellia maritima* and *Festuca rubra* (Fig. 4). *Plantago maritima* and *Triglochin maritima* also showed negative trends in the ungrazed quadrats, but their cover was generally very low (App. 2; see the AVS electronic archive at www.opuluspress.se). *Artemisia maritima* at first benefitted from cessation of grazing on the low marsh, but later disappeared. Except for Skallingen, *Elymus athericus* quickly invaded the ungrazed high marsh. Even the low marsh of Terschelling and Schiermonnikoog was invaded by *Elymus athericus* after 15 yr. *Festuca rubra* significantly declined in the ungrazed high marsh at two of the study islands. Its increase at the ungrazed low marsh of Terschelling was not paralleled at Schiermonnikoog or Skallingen. Cover values for *Elymus athericus*, *Atriplex portulacoides* and *Artemisia maritima* remained constant and close to zero in the control grazed quadrats. However, at Skallingen, the cover of *Puccinellia maritima* initially increased and decreased again later, parallel to the development in the experimentally ungrazed marsh there. *Puccinellia maritima* increased in cover at the grazed low marsh of Schiermonnikoog. Species response curves over time (Fig. 4) showed essentially the same pattern for the three study islands. At Skallingen and at Terschelling, several of our exclosed quadrats became dominated by *Scirpus maritimus* and *Phragmites australis* (not shown).

Effects of grazing at plant community level

Seven plant associations, as defined by Schaminée et al. (1998) occurred more than twice in our data set in the final year (Table 2). The *Puccinellietum maritimae,* *Juncetum gerardi*, *Armerio-Festucetum*, *Atriplici-Agropyretum pungentis* and the *Lolio-Potentillion* occurred most frequently. The *Puccinellietum maritimae* and the *Juncetum gerardi* were found more frequently in the grazed situation (χ^2-test, $P < 0.05$) and the *Armerio-Festucetum* almost significantly so (χ^2-test, $P < 0.10$). The *Atriplici-Agropyretum pungentis*, the *Artemisietum maritimae* and the *Halimionetum portulacoides*, associations characterized by *Elymus athericus*, *Artemisia maritima* and *Atriplex portulacoides* were exclusively found in ungrazed treatments. Of our ungrazed quadrats 58% were classified to the latter associations.

Discussion

Developments in grazed and ungrazed salt marsh

Consistent with other studies (Dijkema 1983a; Roozen & Westhoff 1985; Jensen 1985; Andresen et al. 1990; Adam 1990), the ungrazed marsh became dominated by tall-growing plants. In all our study islands, *Atriplex portulacoides* cover increased in the ungrazed low marsh (Figs. 1 and 4). The ungrazed high marsh became dominated by *Elymus athericus* in many quadrats, except at site 6 (Skallingen) and site 2 (at Terschelling). Fresh water seepage from the dunes at site 2, and from an aquifer connected to the mainland at Skallingen (Christiansen pers. comm.), favoured the growth of *Phragmites australis* and *Scirpus maritimus* here. *Phragmites australis* may be a very important species locally. It covered up to 100% in some of the ungrazed quadrats there, but only 2% on average in the grazed marsh. The same phenomenon was described by Dijkema (1983a) and observed for brackish marshes (Adam 1990; Esselink et al. 2000). *Artemisia maritima* at first increased in abundance after cessation of grazing, but was displaced by *Elymus athericus* later on. Even on low salt-marsh quadrats *Elymus athericus* cover started to increase after 2 decades of not grazing (Fig. 4), emphasising the importance of long-term vegetation studies. *Puccinellia maritima*, *Triglochin maritima*, *Plantago maritima* and *Festuca rubra* generally declined in abundance in ungrazed quadrats. These results agree with many studies summarized in Jensen (1985) for *Puccinellia maritima*, *Triglochin palustris*, *Plantago maritima*, *Artemisia maritima* and *Atriplex portulacoides*. *Festuca rubra* however is often mentioned to be negatively affected by grazing, according to 12 studies cited in his overview. The adverse effect of grazing in these studies may in part be due to soil compaction due to treading, as was suggested by Jensen (1985). We found a negative effect of cessation of grazing, as it leads to the dominance of *Elymus athericus*, at the expense of *Festuca rubra*.

Plant communities

The changes at the individual level were reflected at the level of the community (Table 2). Grazing promotes the *Juncetum gerardii* (Gray & Scott 1967; Adam 1990), the *Puccinellietum maritimae* and the *Armerio-Festucetum* (Dijkema 1983b). Cessation of grazing led to an increase of communities dominated by *Elymus athericus*, *Artemisia maritima* and *Atriplex portulacoides* (see also Figs. 1C, 1F). However, not all of the quadrats studied turned into these communities. In particular the *Lolio-Potentillion* and the *Armerio-Festucetum* remain present in the ungrazed situation (Table 2). Using vegetation maps, Gettner et al. (2000) also observed increased cover of communities dominated by *Artemisia maritima* and *Atriplex portulacoides* at the mainland salt marshes along the coast of Schleswig-Holstein (Germany), after only 3-4 yr without grazing. Studies that compared vegetation maps for experiments with exclosures and different stocking rates of cattle and sheep, indicate that the *Elymus athericus* community can become dominant at natural as well as at artificial salt marshes (van Wijnen et al. 1997; Bakker et al. 2002). However, Kiehl et al. (2000a) argue that low sedimentation rates and waterlogging may hamper this development and lead to a mosaic of different communities in the ungrazed marsh.

Table 2. Occurrence of plant communities per treatment in the final year of study (1996-1998). Plant communities are grouped depending on their response to grazing; for the groups '>> ungrazed' and '>> grazed' the frequencies in grazed and ungrazed sites, respectively, deviate significantly from proportionality (χ^2-test, $P < 0.05$).

	Association	Grazed	Ungrazed
>> ungrazed	*Halimionetum portulacoides*		6
	Artemisietum maritimae		7
	Atriplici-Agropyretum pungentis		34
>> grazed	*Puccinellietum maritimae*	14	4
	Juncetum gerardii	19	3
No significant difference	*Armerio-Festucetum*	19	10
	Lolio-Potentillion	16	16
Not tested	Other	15	1

Species richness

As in other studies (Adam 1990) we found that the richness of species declined without grazing. However, none of the species characteristic of salt marshes occurred exclusively in only one of the grazing treatments. The differences in species presence between treatments is due to species observed very rarely, and is biased towards the grazed quadrats. This fact in itself may be of importance, because it indicates differences in opportunities for colonization and establishment. The identity of the species involved may however not be important, because such differences are much more likely to be caused by chance effects. Chaneton & Facelli (1991) and Kiehl (1997) point out that differences in species richness may be dependent on the scale of measurement. They argue that the structure of ungrazed vegetation is more coarse-grained, with larger patches dominated by individual species. However, the probability of finding an individual of a certain species increased for most of the plant species found under grazing in this study (Table 1), and the number of associations that occurred under grazed conditions was higher than under ungrazed circumstances (data not shown). It is therefore likely that, also at courser scales, species richness will be higher in fixed size quadrats under grazing at these intensities. This is furthermore supported by yet unpublished data on species richness up to a scale of 50 m × 50 m from a variety of marshes along the Dutch Wadden Sea coast (Bos unpubl.). Species richness increased with elevation and grazing positively affected richness at low as well as high marsh (Adam (1990), Fig. 3). This differs from results presented by Bakker (1989), who found lower species richness at the grazed low marsh, due to complete destruction of the top soil.

Goose, rabbit and hare grazing

Geese, hare and rabbits are the most obvious herbivores on marshes whose habitat is affected by changes in vegetation composition. However, by their own grazing, they may affect vegetation as well. Hare grazing, for example, affects plant species composition on salt marshes, but not to the same extent as livestock do (van der Wal et al. 2000b). According to the latter study, selective grazing on *Atriplex portulacoides* by hare may delay natural succession by ca. 40 yr, in the low parts of back-barrier marshes. Effects of geese on vegetation composition have been demonstrated for Lesser snow geese *Chen caerulescens caerulescens* in La Pérouse Bay, Canada (Bazely & Jefferies 1986; Kotanen & Jefferies 1997). In the marshes we studied , the impact of geese on succession appears to be low (van der Wal et al. 2000a), just like on the Hamburger Hallig, Germany (Kiehl et al. 2000b). The main colonizers of ungrazed salt marsh, *Atriplex portulacoides* and *Elymus athericus*, are unpalatable to geese and the geese are not present during the major part of the growing season (Adam 1990). Both plant species increase in abundance during natural succession, which negatively affects geese, hares and rabbits (van de Koppel et al. 1996). Due to natural vegetation succession, Brent geese were shown to loose high quality feeding habitat (van der Wal et al. 2000a). By grazing with livestock however, a suitable sward for foraging is maintained which facilitates the smaller herbivores (Cadwalladr et al. 1972; Olff et al. 1997; Stock & Hofeditz 2000).

Management implications

The stocking rate (Andresen et al. 1990), the timing of grazing (Adam 1990) and even the nature of the stock (Gray & Scott 1967; Jensen 1985) mediate the effects of the herbivory. Intensive grazing leads to an impoverishment of the vegetation according to Dijkema (1983b) and Schaminée et al. (1998). Kiehl et al. (1996) showed that *Atriplex portulacoides* is only very rarely found on intensively grazed marshes. Under extensive grazing though, a mosaic of closely grazed areas and lightly grazed patches develops (van den Bos & Bakker 1990). Depending on the amount of variation that is desired managers should vary the stocking rates (Bakker 1985). Differences between sheep and cattle grazing originate from different ways of grazing (Gettner et al. 2000). Cattle tear the grass from the sward, whereas sheep rather bite the grass and are also more selective. Adam (1990) even hypothesizes that differences in the response of *Atriplex portulacoides* to grazing, between marshes in west and southwest Britain, may be related to this. Marshes in southwest Britain are primarily cattle grazed, and *Atriplex portulacoides* is equally abundant in grazed and ungrazed areas here, whereas it is limited to areas with restricted access for grazing sheep on the west coast.

The grazing of back-barrier marshes with livestock in this study was shown to enhance the species number in small quadrats with a fixed size, and to promote those plant species and those plant communities that are important forage for waterfowl, rabbit and hare. Other studies demonstrated that the grazing management affects the composition of invertebrate assemblages (Andresen et al. 1990; Meyer et al. 1995) and those of the breeding birds (Stock et al. 1992; Norris et al. 1998; Eskildsen et al. 2000) via its impact on the vegetation. All of these aspects are relevant to the management of salt marshes, but in certain cases the management objectives are at odds with each other. The basic tenet of this discussion on grazing management, is that grazing or the cessation of grazing is a means to reach previously defined ecological targets, and that long-term ecological monitoring is a prerequisite to judge to which extent these targets are fulfilled (Dijkema 1983b; Stock & Kiehl 2000; Bakker et al. 2002).

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