

Long-term effects of sheep grazing in various densities on marsh properties and vegetation dynamics in two different salt-marsh zones

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Running title: Long-term grazing treatments on salt marshes

Abstract

We tested the hypothesis that long-term grazing management with different stocking densities results in plant communities with distinctively different plant species composition and vegetation structure. We analyzed data from two long-term experiments in a low clayey and a high sandy salt marsh with different stocking densities of sheep after 11, 15, 19 and 23 years after the start of the various treatments on the German Wadden Sea coast.

On the low salt marsh, continued high stocking density (10 sheep ha^{-1}) resulted locally in progressive succession from the *Puccinellia maritima* community to the late-successional *Atriplex portulacoides* community. On the high salt marsh, the *Festuca rubra* community maintained in all stocking densities during the first 11 years. Intermediate stocking densities (1.5, 3 or 4.5 sheep ha^{-1}) resulted in *P. maritima* sward interspersed with patches of *F. rubra* and tall *Elytrigia atherica* communities in both salt-marsh types. Cessation of grazing resulted in progressive succession to the *E. atherica* community in later years in both salt-marsh types. Intermediate stocking density resulted in a mosaic of tall vegetation and patches of sward, and revealed the highest variation from sward to tall vegetation. Continued grazing with high stocking density led to a high proportion of sward, whereas cessation of grazing led to a high proportion of tall vegetation.

Grazers affect abiotic conditions by reducing soil-redox-potential and surface elevation change, and thereby drive composition and structure of salt-marsh vegetation.

Keywords: long-term vegetation dynamics, plant-herbivore interaction, soil-redox potential, surface elevation, sward, tall vegetation

Introduction

The interaction between grazers and vegetation has traditionally been studied from the grazers' perspective: i.e. how animals select forage of different quality in various plant communities (Grant et al., 1985). The vegetation perspective, particularly how grazing and different grazing regimes affect both composition of plant communities over time and spatial variation in vegetation structure, has received considerably less attention (see, however, Rook et al., 2004). For conservation management, an important question is under which conditions large grazers induce compositional and structural variation in grassland plant communities, as this appears to be a prerequisite for high biodiversity (Milchunas, Sala, & Lauenroth, 1988). Answering this question may allow managers to apply adequate management tools for maintaining a high diversity of plants and animals.

Traditionally, effects of grazers on vegetation dynamics have been investigated by comparing the vegetation of grazed and ungrazed sites by excluding grazers from previously grazed plant communities. The general pattern of such long-term studies (4 – 40 years) is a higher above-ground standing crop with homogeneous tall vegetation in exclosures than in continuously grazed plots with sward under high grazing pressure (see review by Milchunas & Lauenroth, 1993). When, however, vegetation productivity is higher than utilization (i.e. biomass loss to both grazing and trampling) by grazers, spatial heterogeneity in vegetation properties may develop as a result of selective grazing. The grazers return to previously grazed areas thus locally maintaining sward. In areas that remain ungrazed for a longer period, vegetation harbours taller tillers and accumulates litter, and becomes less attractive to grazing animals. The structure of the vegetation may reveal sward alternated with patches of taller stand, thus featuring heterogeneous vegetation. This phenomenon has been demonstrated within a plant community at the plot scale (< 100 m^2) in a pasture in Argentina

(Cid & Brizuela, 1998). In the long run, when other species establish in such tall patches, the initial plant community may be replaced. It is currently unknown, however, which grazing conditions induce homogeneous or heterogeneous vegetation, and eventually different plant communities at the landscape scale.

Here, we tested the hypothesis that long-term grazing management with different stocking densities results in plant communities with distinctively different plant-species composition and vegetation structure. We focus on the effects of a range of stocking densities of sheep on salt marshes. Salt marshes represent excellent sites to examine this hypothesis as they represent ecosystems without agricultural history of ploughing and fertilizer application but have a long history of livestock grazing. Natural succession on salt marshes is characterized by the interaction of plants and sediment trapped during tidal inundation (Nolte et al., 2013). The resulting surface-elevation change drives succession from pioneer communities on intertidal flats via early-successional communities with the grass *Puccinellia maritima* to later-successional communities with the shrub *Atriplex portulacoides* on the low salt marsh and communities with the grass *Festuca rubra* to the *Elytrigia atherica* community on the high salt marsh. After several decades the late-successional community with the tall grass *E. atherica* occurs on most of the gradient from low to high salt marsh (Wanner et al., 2014). Surface elevation and soil-redox potential are independent important predictors for plant species distribution in ungrazed salt marshes (Davy, Brown, Mossmann, & Grant, 2011). Livestock grazing suppresses vegetation succession in salt marshes (Jensen, 1985, Olff et al., 1997). Davidson et al. (2017) published a meta-analysis on effects of livestock grazing in salt marshes. Positive effects were observed on soil bulk density, salinity and plant species richness, whereas negative effects were found on plant cover, above-ground biomass, soil-redox potential, litter biomass and canopy height. A negative relationship was found between stocking density and canopy height. Duration of grazing (varying between 1 and 100 years) negatively affected canopy height. In their meta-analysis, canopy height was recorded as average height, which does not take into account spatial heterogeneity. Certain stocking densities can, however, result in locally different grazing intensities within a paddock. Hence, there is a knowledge gap with respect to effects of intermediate stocking densities possibly resulting in a pattern of sward and tall vegetation.

In this study, we investigated the relation between abiotic conditions, stocking densities and vegetation heterogeneity on two salt marshes with long-term experiments on the German Wadden Sea coast. Both sites experienced different stocking densities for over 20 years. We studied (1) interaction effects of grazing and abiotic parameters surface elevation, and soil-redox potential, (2) vegetation dynamics, especially the establishment of the tall late-successional *Atriplex portulacoides* and *E. atherica* communities by repeated vegetation mapping, and (3) vegetation structure by recording canopy height. We predicted that increasing stocking density results in increasing bulk density, hence lower surface-elevation change, reduced soil-redox potential (as a result of reduced soil aeration), decreasing average canopy height with spatial variation in plant communities and canopy height at intermediate stocking density (Fig. 1).

Methods

Study area and experimental set up

The study was conducted in a low and a high salt marsh, >65 km apart with roughly the same tidal regime. Both salt marshes were developed from coastal-engineering works. Intensive sheep grazing (10 sheep ha^{-1}) between March and November occurred on approximately 95 % of the salt marshes along the northern Wadden Sea mainland coast of Germany, including the study sites. At both sites, five adjacent experimental paddocks (ranging from 6-19 ha) were established in 1988: a treatment with cessation of grazing, three paddocks with intermediate stocking densities of 1.5, 3, 4.5 sheep ha^{-1} and a paddock with continuation of the initial density of 10 sheep ha^{-1}. Paddocks were separated by an artificial creek or fence. Each paddock was subdivided by several collector drains that ran parallel to the seawall. Watering points were available close to the seawall.

The low salt-marsh site

The polder Sönke-Nissen-Koog was embanked in 1924. Thereafter, a new salt marsh developed, induced by the construction of sedimentation fields.(54°38'N 8°50'E) and will be referred to as 'low salt-marsh' (clay content 30%) in the remainder of the manuscript. Low salt marsh is defined as the area with flooding frequency > 100 times yr^{-1} (Erchinger et al., 1996). Here, it amounts to 80-200 times yr^{-1} (Kiehl et al., 1997). Surface elevation ranged from seawall to intertidal flats between 28-48 cm above MHT. Vegetation was dominated by *P. maritima* community (Kiehl et al., 1997). The marsh was intersected with deep collector drains 100 m apart that could not be crossed by sheep. The collector drains allowed high sediment input, resulting in an alternating pattern of elevated levees along the collector drains with depressions in between. Because of high sediment input, collector drains were refurbished regularly before the start of the experiment in 1988, and twice during the experiment. The main channels separating the paddocks were dug out in 2009. Ditching enhanced the elevation differences between levees and depressions. Two treatments with intermediate stocking densities were discontinued 15 years after the start experiment, but the 3 sheep ha^{-1} treatment was maintained.

The high salt-marsh site

The polder Friedrichskoog was embanked in 1854. Also here, a salt marsh started developing after embankment (54°02’N 8°54’E) and will be referred to as ‘high salt-marsh’ (clay content 10%) in the remainder of the manuscript. High salt marsh is defined as the area with flooding frequency < 100 times yr^{-1}. It amounts to 40-50 times yr^{-1}. Elevation ranges from seawall to intertidal flats between 44-84 cm above MHT. Vegetation was dominated by *F. rubra* community (Kiehl et al., 1997). Because of the low sediment input, maintenance of the collector drains was not carried at a regular interval before the start of the experiment. Differences in surface elevation between levees and depressions were small. The shallow collector drains in this site could easily be crossed by sheep. The intermediate grazing treatments could not be maintained until the end of our study period; the last (3 sheep ha^{-1}) was discontinued 17 years after the start of the experiment..

Surface elevation

Elevation at both sites was measured 17 years after the start of the experiment using a levelling instrument (Spectra precision® laser LL500 and laser receiver HR500 by Trimble). In both sites, in each of the five sections of each grazing treatment (sheep densities 0, 3 and 10 sheep ha^{-1}, in the high salt marsh 3 sheep ha^{-1} only partly), we measured elevation at equal distances from the creeks that separated the treatments.

Soil-redox potential

As a proxy for the saturation of oxygen in the soil, we determined soil-redox potential in September 2011, 23 years after the start of the experiment. Each set of measurements was composed of the average measurement of five electrodes with a platinum tip of 1 mm and a Ag/AgCl calomel reference electrode (Cole-Palmer®), all of which were connected to a Graphtec GL200 Datalogger (Graphtec GB) and were read out 2 min after the electrodes were placed. Measurements were taken at both salt-marsh sites, in stocking densities 0 and 10 sheep ha^{-1} at different depths (2, 5 and 10 cm depth). We took 10 sets of measurements, at spots at 10 m distance from the levees where oxygen content is generally higher. Instantaneous measurements on redox may not necessarily reflect absolute values but allow comparisons between treatments (Van Bochove, Beauchemin, & Theriault, 2002).

Vegetation dynamics

Vegetation dynamics were assessed by repeated vegetation mapping at 11 years, 15 years, 19 years and 23 years after the start of the two grazing experiments. Plant nomenclature follows Van der Meijden (2005). Plant communities were assigned according to the standardized typology of Trilateral Monitoring Assessment Programme (TMAP) (Petersen, Kers, & Stock, 2014) which was especially developed to monitor dunes and salt marshes in the Wadden Sea region. Surface areas of the different plant communities were assessed in ArcGIS, and subsequently converted to percentage cover.

V*egetation structure*

Vegetation structure was determined by recording canopy height in September 2001, 13 years after the start of the various treatments, and the last year that all five grazing treatments could be compared between both sites. Canopy height was recorded with a calibrated stick and a styrofoam disc (20 g, diameter 30 cm), once every two metres along transects from the watering point near the seawall to the fence at the very wet parts of the low salt marsh (Fig. 4), and to the intertidal flats at the high salt marsh (Fig. 5). Measurements were carried out along four to six transects (length between 350 and 600 m for each of the treatments. Within each paddock, individual transects were spaced at least 20 m apart.

Statistical analyses

Surface elevation

Elevation data at the start of the experiment did not match our detailed measurements. Hence, it was not possible to estimate surface-elevation change (SEC) with respect to MHT over the 17-years period since the start of the experiment. Differences in surface elevation between grazing regimes after 17 years were tested with a separate two-way ANOVA analyses with grazing (3 levels) and section (5 levels) as categorical predictors and distance as a continuous variable. A post-hoc Tukey test tested for differences between grazing treatments. Low and high salt marsh were analyzed separately. To meet assumptions of normality and homogeneity of variances, we tested for homogeneity of variances tested with the Bartlett Chi square test; normal distributions of residuals were tested using visual inspection (QQ-plot).

Soil-redox potential

Averages of the five platinum electrodes were used for graphs and statistics, after correction for reference electrode (+192 mV), temperature, and soil pH. To examine how grazing affected soil-redox condition, we ran a two way ANOVA, with soil-redox potential as a dependent variable and grazing treatment (grazed at highest density of 10 sheep ha^{-1} vs ungrazed) depth (2, 5, 10 cm) and electrode number (1-5) as categorical predictors.

Vegetation dynamics

Vegetation maps were processed in ArcGIS (ArcMap 10.3).

Canopy height

Differences in mean canopy height were tested using multiple pairwise comparisons of means adjusted for multiplicity with the Tukey-Kramer method. Differences in mean canopy height between grazing treatments were tested using multiple pairwise comparisons of means adjusted for multiplicity with the Tukey-Kramer method. To relate canopy height across the gradient from the watering point to the different stocking densities, we used a linear regression model that included canopy height every two metres from the watering point. This analysis was done both for the low and the high salt marsh. The model included linear and quadratic terms in stocking density and distance from watering point as continuous variables. Since the model contained both linear and quadratic terms in stocking density and distance from watering point, we used sequential F tests to account for the dependence of the quadratic or the linear term. The models were fit using ordinary least squares. The ungrazed paddock on the low salt marsh contained dense stands of the tall-growing grass species *E. atherica* that were flattened. As a result, low canopy heights were recorded that were considered to be not representative for the actual canopy height in this paddock. Hence, we only used the mean measured canopy height computed over all transects within one paddock in the analyses, and excluded the ungrazed paddocks in the statistical analyses on canopy height.

Results

Surface elevation

Grazing significantly affected surface elevation negatively, on both the low and the high salt marsh ($F_{(2, 64)} = 53.523$, $P < 0.001$ and $F_{(2,131)} = 22.6$, $P < 0.001$; Fig. 2). There was also a significant negative effect of distance to the nearest collector drain levee, but only on the low salt marsh ($F_{(5, 64)} = 23.979$, $P < 0.001$; Fig. 2). The ungrazed marsh had the highest surface elevation and the intermediate stocking density showed intermediate elevation 17 years after start of the experiment, but were not significantly different from each other on the low salt marsh (Tukey HSD; $P = 0.18$). Lack of replication on the high salt marsh did not allow us to test this for the intermediate treatment. On both salt-marsh types, we found the lowest surface elevation in the treatment with 10 sheep ha^{-1} compared to treatments with 3 and 0 sheep ha^{-1} (low salt marsh: Tukey HSD; $P < 0.001$, high salt-marsh: Tukey HSD; $P < 0.001$; Fig. 2). Differences in elevation between 10 sheep and 0 sheep ha^{-1} were larger on the low than on the high salt marsh. A sharp elevation decrease from the collector drain levees can be clearly distinguished on the low marsh but not on the high marsh (Fig. 2).

Soil-redox potential

Soil-redox potential in the grazed treatment was significantly lower, both for the low ($F = 2957$; $P < 0.0001$), and the high salt marsh ($F = 111.8$; $P < 0.0001$). Grazing had, however, a much stronger effect on the low than on the high salt marsh. There was no interaction effect between grazing and soil depth on the high salt marsh. Both grazed and ungrazed treatment showed a marked decrease in soil-redox potential at greater depth. However, on the low salt marsh stronger negative soil-redox potentials with depth were found only in the grazed treatment (P = 0.023) (Fig. 3).

Vegetation dynamics

The low salt-marsh site was initially dominated by the *P. maritima* community. The tall *A. portulacoides* community had established 11 years after cessation of grazing only at great distance from the watering point, whereas tall *E. atherica* community established over the entire paddock, and later succeeded the *A. portulacoides* community. This phenomenon also occurred at intermediate stocking densities, although the tall *E. atherica* community became less dominant, and the *P. maritima* community sward persisted longer. The *P. maritima* community maintained most optimally with stocking density of 10 sheep ha^{-1}. After 23 years this community was also succeeded by tall *A. portulacoides* and *E. atherica* communities, particularly further from the watering point (Figs 4 and 6, Table S1).

The high salt-marsh site was initially dominated by the *F. rubra* community. It became gradually overgrown by the tall *E. atherica* community after cessation of grazing. The *F. rubra* community maintained in the paddock with continued intensive grazing, although it became infiltrated by the sward of the *P. maritima* community near the watering point, particularly during later years. The tall *E. atherica* community did not establish. The *F. rubra* community maintained after 15 years of grazing with lower stocking density. Unfortunately, no data are available for the longer term effects of grazing (Figs 5 and 6, Table S1).

Vegetation structure

Canopy height revealed a striking pattern of regular peaks in the low salt marsh of the paddocks with intermediate stocking densities (Fig. 7). The peaks were situated just before the deep collector drains parallel to the seawall, which sheep could only pass close to the fence separating the treatments. Canopy heights showed a gradual increase to a peak before a creek, dropping to a lower height just after the creek. Such patterns of peaks in canopy height could not be detected in the high salt marsh with only shallow drains that were easily crossed by the sheep.

Mean canopy height was significantly higher ($P < 0.001$) in the low than in the high salt marsh, except for 3 sheep ha^{-1}. In the ungrazed paddock of the low salt marsh, the canopy height was lower due to the flattened stands of the tall-growing *E. atherica* compared to the paddock in the high salt marsh (Fig. 8).

Overall tall vegetation (> 20 cm) dominated at both the low and high salt marsh in the treatment where grazing was abandoned 13 years before. The treatments with intermediate stocking densities revealed the highest variation in height classes from sward to tall vegetation > 20 cm, except for the paddock in the high salt marsh with 4.5 sheep ha^{-1} Treatments with the highest stocking density had only 10% vegetation < 10 cm in the low salt marsh, whereas it was 50% in the high salt marsh (Fig. 9).

Stocking density and distance to watering point interactively affected canopy height in both low and high salt marsh but this effect varied among the two types of salt marsh (Table 1). Canopy height was higher and more sensitive to increasing stocking density on the low than on the high salt marsh. More specifically, canopy height peaked at a lower stocking density and decreased more steeply for each unit increase in stocking density in the low than the high salt marsh. Similarly, canopy height increased at a steeper rate for each unit increase in distance from watering point in the low than high salt marsh (Fig. 10). Overall, on both low and high salt marsh, stocking density seemed to exert a stronger influence on canopy height than distance to watering point (Table 1).

Discussion

The aim of this study was to determine to what extent long-term management with different stocking densities drives species abiotic conditions and composition and heterogeneity in vegetation structure. We predicted that increasing stocking density would result in increasing bulk density, hence lower surface elevation change, and reduced soil-redox potential, decreasing average canopy height with spatial variation in plant communities and canopy height at intermediate stocking density. Our results showed that grazed areas on both low and high salt marshes, which previously experienced high stocking densities (10 sheep ha^{-1}), can be transformed from homogeneous sward into heterogeneous vegetation, especially at intermediate stocking densities (1.5-4.5 sheep ha^{-1}). Cessation of grazing, however, resulted in tall, homogeneous vegetation, much in line with our predictions. Again, this effect was found on both the low and high salt marsh. The ecological mechanisms underlying the observed changes in vegetation were strongly affected by interactive effects of grazing and abiotic conditions at the various sites. These interactions will be addressed in greater detail below and are illustrated in Fig. 11.

Higher stocking densities result in lower surface elevational change

On both salt-marsh types, we found lower surface elevation with increasing stocking density, whereas canopy height decreased. In a previous study in our study site, the high salt marsh showed higher SEC for the period 1990-1993 close to the intertidal flats than close to the seawall in all treatments (Dierssen et al., 1994. Treatments without grazing revealed SEC of 14 cm close to the intertidal flats, and 6 cm close to the seawall, whereas it was 5 cm near the intertidal flats compared to 3 cm near the seawall in the grazing treatment with 10 sheep ha^{-1}. Intermediate stocking densities generally showed intermediate SEC values (Dierssen et al., 1994). Also during 1995, SEC was higher in ungrazed treatments (15 - 20 mm) than in grazed treatments (10 mm) in both our low and high salt marsh study sites (Neuhaus, Stelter, & Kiehl 1999). These differences had increased 17 years after the start of the experiment. Larger differences between 10 sheep and 0 sheep ha^{-1} on the low than on the high salt marsh might be related to the more clayey soil in the low salt marsh (Schrama et al., 2013).

In line with our results, a grazing trial in the Leybucht salt marsh, Germany, revealed SEC 16 mm yr^{-1} with 1 and 2 head of cattle ha^{-1}, 20 mm yr^{-1} with 0.5 head of cattle ha^{-1}, and 21 mm yr^{-1} in ungrazed treatment over the first five years after the start of the experiment (Erchinger et al., 1996).

Higher stocking densities associated with lower soil redox potentials

Our results indicate a significant decrease in soil-redox potential in the grazed versus the ungrazed treatments, likely reflecting differences in soil bulk density as a result of herbivore trampling. This is in line with measurements indicating that soil-shear strength increased with subsequent low soil-redox potential with increased stocking density in our low salt-marsh site (Zhang & Horn, 1996). Such changes in soil-redox potential affect vegetation composition

(Davy, Brown, Mossmann, & Grant, 2011). Higher bulk density and an associated decrease in soil oxygen as a result of grazing were previously reported for mainland salt marshes of the Wadden Sea region (Nolte et al., 2013; Chang et al., 2016), on the back-barrier salt marsh of Schiermonnikoog, the Netherlands (Schrama et al., 2013) and as well as in the meta-analysis by Davidson et al. (2017). Experimental soil compaction in a mainland salt marsh revealed increased bulk density and water logging, decreased soil aeration, soil-redox potential and cover of *E. atherica* after two years (Van Klink et al., 2015). Because *E. atherica* generally prefers oxygenated soils on ungrazed salt marshes (Davy, Brown, Mossmann, & Grant, 2011; Sullivan et al., 2018), soil compaction through trampling and a decreased soil-redox potential may therefore provide a mechanistic explanation for the low cover of *E. atherica* in grazed salt marshes (Schrama et al., 2013). In general these effects were stronger on the low than the high salt marsh, which may be a result of differences in clay content between marshes. The low soil-redox potential in the grazed low salt marsh was associated with high clay content whereas the higher soil-redox potential in the grazed high marsh was associated with low clay content, which is also in agreement with results in other salt marshes (Schrama et al., 2013). Overall, differences in soil-redox potential between high stocking density and ungrazed treatments revealed a strong effect of grazing on soils, and thereby likely reflect differences in belowground oxygen stress, potentially driving some of the observed changes in community compositions.

Effects of grazing on vegetation dynamics

Vegetation dynamics reported in the present study fit within large-scale studies on mainland salt marshes along the entire Wadden Sea coast of Germany. The higher number of plant communities in the low than the high salt marsh is in line with results in Wanner et al. (2014).

Distribution and range of *P. maritima* in the north coast and *F. rubra* in the south coast is related to the continuum of lower lying salt marshes in the north to higher elevated salt marshes in the south (Suchrow & Jensen, 2010). Establishment of the *E. atherica* community in mid- and higher elevated *F. rubra* communities occurred in the southern region. Persistence of the early successional *P. maritima* community in the salt marshes of the northern region suggests that large-scale gradients of salinity, inundation frequency and sedimentation lead to geographical variation in the pace of succession (Rupprecht, Wanner, Stock, & Jensen, 2015).

The negative relation between stocking density and the concomitant increase of *E. atherica* community in our study is in line with other salt marshes in the Wadden Sea area. At the mainland salt marsh of the Leybucht, Germany, spreading of *E. atherica* into a *F. rubra* community was observed already eight years after cessation of cattle grazing, whereas establishment in the *P. maritima* community started after 15 years and covered the entire elevational gradient after 20 years. Spread of *E. atherica* hardly occurred in the treatments with 1 or 2 head of cattle ha^{-1} whereas in the treatment with 0.5 head of cattle ha^{-1} a considerable spread of the *E. atherica* community into the low and the high salt was observed (Andresen, Bakker, Brongers, Heydemann, & Irmler, 1990; Bakker, Bos, & De Vries, 2003).

Retrogressive succession under grazing regimes on the high salt marsh such as observed in this study, for example the establishment of the *P. maritima* community in the *F. rubra* community, might be explained by intensive grazing and trampling near the watering points. Overall, these results provide support for out hypothesis that grazing regimes are a major determinant of the distribution of plant communities on the salt marsh.

Differences in stocking densities drive vegetation heterogeneity

At both the low and high salt marsh, mean canopy height decreased with increasing stocking density. Although this pattern was broadly similar between sites, it was more pronounced in the low than the high salt marsh. The negative relationship between herbivore density and mean canopy height accords with results of the meta-analysis by Davidson et al. (2017). It is also in line with higher soil shear strength near the seawall (Zhang & Horn 1996). Andresen, Bakker, Brongers, Heydemann, and Irmler (1990) found increasing canopy height of the *Aster tripolium* layer with increasing distance to the seawall on the mainland salt marsh of Leybucht, Germany.

Intermediate stocking densities revealed the highest variation in vegetation canopy height. These results coincide with a previous study in our high salt marsh-site that showed that high spatial variation between stands < 10 cm and ≥ 10 cm was found at scale of 10 m x 2 m in paddocks with intermediate stocking densities, especially 3 sheep ha^{-1} (Berg, Esselink, Groeneweg, & Kiehl, 1997).

Besides a strong effect of stocking density on vegetation structure, there was also a significant impact of the position of watering points on canopy height. Swards dominated by *P. maritima* and *F. rubra* increased closer to the watering point and with increasing stocking density. These species have a high sugar content, and therefore selectively grazed (Fokkema et al., 2016) and have a high regrowth potential (Kleyer et al., 2008). Tall vegetation dominated by superior light competitors such as *A. portulacoides* and *E. atherica* increased further away from the watering points, which is likely caused by lower grazing intensity further away from the watering point. Adler and Hall (2005) modelled the effects of watering points on canopy height with various stocking densities. According to this model, an increase in stocking density will increase the portion of the gradient affected by grazing, since animals will have to walk farther to meet their daily requirements. The significant interaction between stocking density and distance to watering point on canopy height in our study may thus indicate that sheep in higher stocking densities removed more biomass and grazed further away from the watering point to meet their requirements.

Implications for management

Abiotic conditions such as elevation and soil-redox potential are important predictors for the occurrence of salt-marsh plant species and characteristic plant communities. As we show in this study, grazers can modify these abiotic conditions. They decrease soil-redox potential and surface elevation by trampling. As such, grazers and abiotic conditions operate in concert. Our results suggest that, together they shape the ecological context of grazed and ungrazed salt marshes, with major implications for local diversity of plant communities. High stocking density results in homogeneous sward, whereas moderate stocking density creates salt marshes with heterogeneous vegetation including both sward and tall canopy. All plant communities, however, irrespective of being located on a low or high salt marsh, converge to a similar community dominated by *E. atherica* after cessation of grazing. Only high stocking density of 10 sheep ha^{-1} (this study), 2 cattle ha^{-1} (Bos & De Vries 2003) or 1 horse^{-1} ha (Van Klink et al. 2016) can prevent high coverage of late-successional tall *E. atherica*.

Long-term experiments, like the one described in this study, are necessary to obtain a clear picture of the effect of stocking densities, and indicate that management should take its time to evaluate changes in grazing management. Kiehl, Eischeid, Gettner, and Walter (1996) previously reported that canopy height showed the greatest variation in the treatment where grazing was discontinued after only four years of study on our low salt marsh. Our results covering 11 years revealed, however, very low variation in height classes in the ungrazed treatment compared to the various grazed treatments. Another salt marsh that was abandoned after it was previously intensively grazed, produced a wealth of flowering plants and attracted many invertebrates in the first few years after abandonment (Irmler & Heydemann, 1986). However, tall-growing plant species took in the ten years after abandonment over and outcompeted low-statured plants, apart from the treatments with high stocking density (Andresen, Bakker, Brongers, Heydemann, & Irmler, 1990).

A previous large-scale study covering the German Wadden Sea coast of Schleswig-Holstein revealed that moisture and elevation were the main factors affecting species richness on salt marshes (Suchrow, Stock, & Jensen, 2015). Total number of plant species at landscape scale did not differ between grazed and ungrazed salt marshes (Wanner et al., 2014). Grazing management did, however, affect plant species richness at the small scale. Sward in salt marshes harbours relatively high plant species richness at the plot scale compared to tall vegetation (Bos et al., 2002).

Other studies show effects of vegetation on fauna. Spring-staging geese are hardly found on long-term abandoned salt marshes (Bos et al., 2005). Some invertebrates (Pétillon et al., 2005), and some breeding birds (Norris et al., 1997) prefer, however, patches with taller canopy. Stocking density of livestock thus results in cascading effects (Evans et al., 2015; Van Klink et al., 2016). As species responses vary among taxa, managers should not use plant-species richness as a proxy for overall biodiversity on salt marshes (Davidson et al. 2017). To preserve an optimum species diversity at various scales, a large-scale mosaic of different grazing regimes (including no grazing), inducing a maximum variety of different plant communities, is advocated (Wanner et al., 2014; Stock & Maier, 2016; Van Klink et al., 2016).

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Authors' contributions

M.St. conceived the study, J.B., M.Sc. and R.V. designed the field sampling methodology, M.Sc., P.E., P.D., S.N., R.V., Y.V. and M.St. collected the data, N.B. analysed the data with input from P.D., M.Sc. and R.V., J.B. led the writing of the manuscript, all authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Data will be uploaded and available from the University of Groningen Data Repository DataverseNL Dataverse Network (https://dataverse.nl/dvn/dv/GELIFES, permanent handle: ………..).

Preview link: https://dataverse.nl/privateurl.xhtml?token=4156e6b5-a2ec-4a96-b176-eb307048a994

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Table 1 Estimated coefficients and their standard errors (SE) for the regression of canopy height on sheep stocking density and distance to the watering point in low and high salt marsh 13 years after the start of the grazing experiment. Data of the ungrazed treatments were excluded from the analysis.

Site	Effect	Estimate	SE	T	P>|T|
Low salt marsh	Intercept	13.389	0.509	26.323	< 0.0001
	Distance from watering point	0.241	0.252	0.957	0.339
	Stocking density	1.172	0.173	6.769	< 0.0001
	(Distance from watering point)^2	0.45	0.045	10.066	< 0.0001
	(Stocking density)^2	-0.162	0.013	-12.069	< 0.0001
	Stocking density × distance from watering point	-0.496	0.031	-16.186	< 0.0001
High salt marsh	Intercept	11.703	0.339	34.48	< 0.0001
	Distance from watering point	1.092	0.061	17.778	< 0.0001
	Stocking density	-0.977	0.174	-5.626	< 0.0001
	(Distance from watering point)^2	-0.001	0.002	-0.322	0.747
	(Stocking density)^2	0.037	0.016	2.342	0.019
	Stocking density × distance from watering point	-0.103	0.009	-11.658	< 0.0001

Fig. 1 Expected differences in ecological processes between salt marshes that are not grazed, grazed at intermediate and high stocking density

Fig. 2 Effect of different grazing treatments on surface elevation in (A) low and (B) high salt marsh in sections from seawall to intertidal flat, 17 years after the start of the grazing experiment. Statistics are mentioned in the text

Fig. 3 Effect of grazing treatment (stocking density 0 vs 10 sheep ha^{-1}) on soil-redox potentials in (A) the low and (B) the high salt marsh, 23 years after start of the grazing experiment. All measurements were conducted at levees along the collector drains. Different letters indicate significant differences at $P < 0.05$

Fig. 4 Vegetation map 11, 15, 19 and 23 years after the start of grazing treatments in the low salt marsh. Note that two treatments were discontinued after 15 years. The regular pattern of the vegetation is caused by deep collector drains which could only be passed by the sheep at one point along the fence. Grazed treatments had a watering point close to the seawall (Online version in colour)

Fig. 5 Vegetation map 11, 15, 19 and 23 years after the start of grazing treatments on the high salt marsh. Note that the three intermediate treatments were discontinued after 11 - 15 years. Grazed treatments had a watering point close to the seawall (Online version in colour)

Fig. 6 Cover percentage of plant communities in low and high salt marsh 11, 15, 19 and 23 years after the start of grazing treatments in 1988. Not all treatments could be maintained (Online version in colour)

Fig. 7 Mean (10 points pooled for stretches of 20 m) canopy height at different stocking densities from the seawall to the intertidal flats in (A) the low and (B) high salt marsh, 13 years after the start of the treatments. The vegetation at the ungrazed low salt marsh was flattened, hence the canopy height was lower than could be expected based on vegetation composition

Fig. 8 Mean canopy height with SE for different stocking densities in the low and the high salt marsh, 13 years after the start of the experiment. Different letters indicate significant differences at $P < 0.001$. Note: in the ungrazed low salt marsh, vegetation stands were flattened, and consequently canopy height was lower than could be expected based on vegetation composition

Fig. 9 Cover percentage of canopy heights per treatment in the low and high salt marsh, 13 years after the start of the experiment, expressed as percentages of total number of measurements (925 in low and 1420 in high salt marsh). Frequency class > 20 cm low salt marsh is lower than could be expected based on vegetation composition with flattened vegetation at the ungrazed low salt marsh (see Fig. 8)

Fig. 10 Expected mean canopy height (cm) for (A) low and (B) high salt marsh as functions of the distance to watering points and sheep stocking density based on predictions of the regression model

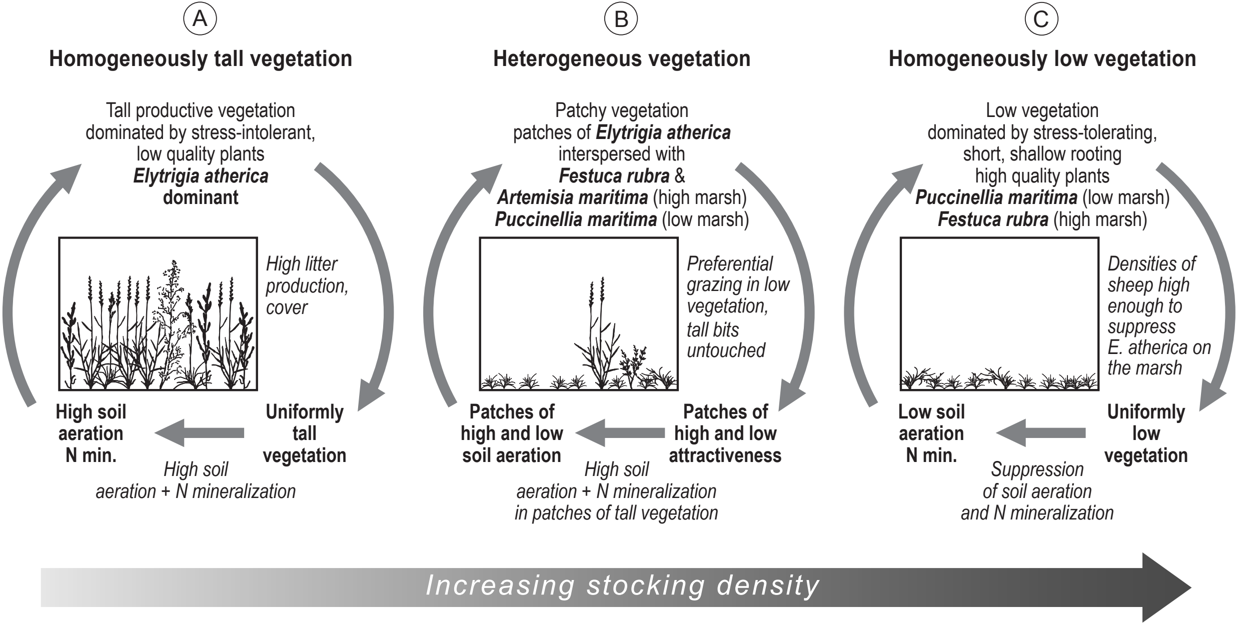
Fig. 11 Conceptual overview of the main ecological processes at play in high and low salt marsh that are grazed at different stocking densities after c. 15 years. The main variables include surface elevation, soil-redox conditions expressed as depth of aerobic layer, stocking density, spatial arrangement of plant communities, and their structural variation. Surface elevation change could not be quantified, because of insufficient data at the start of the experiment

Supplementary data S

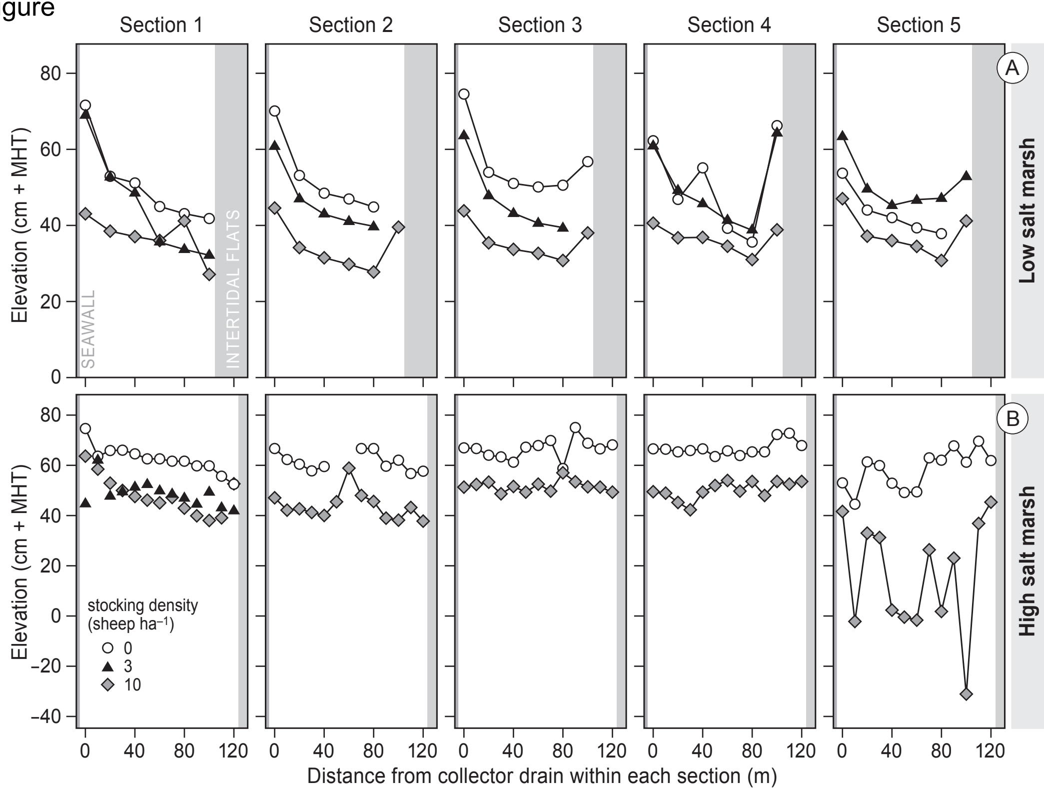
Table S1 Cover percentage of plant communities in low and high salt marsh since the start of the various treatments in 1988

Low salt marsh	**11 yr**					**15 yr**					**19 yr**					**23 yr**				
Sheep ha^{-1}	**0**	**1.5**	**3**	**4.5**	**10**	**0**	**1.5**	**3**	**4.5**	**10**	**0**	**1.5**	**3**	**4.5**	**10**	**0**	**1.5**	**3**	**4.5**	**10**
Artemisia maritima		3.5	3.6	4.1			0.5	2.7	2.0	2.9					1.7					3.0
Atriplex portulacoides	18.4	6.4	7.4	37.6		10.3	17.9	1.0	21.9	23.5	8.9		15.3		20.4	0.4		1.7		12.7
Elytrigia atherica	64.4	25.8	11.8	9.1		64.2	30.7	36.7	32.3	1.5	71.2		30.5		10.7	69.1		52.7		18.7
Festuca rubra	1.0	20.0	10.6			0.5	9.4	8.6	16.0	13.4			7.5		4.9			0.6		8.5
Puccinellia maritima	16.2	42.2	61.3	49.2	95.0	24.0	35.1	39.7	25.2	56.2	17.6		29.6		29.4	30.5		22.1		34.6
Salicornia spp.		1.8	4.2		4.2	1.0		2.8		1.7			1.7		30.1			3.9		5.9
Spartina anglica		0.3	1.0		0.8		6.3	8.4	2.5	0.8	2.3		6.8		1.7			18.9		8.3
bare soil													8.5		1.1					8.2

High salt marsh	**11 yr**					**15 yr**					**19 yr**					**23 yr**				
Sheep ha^{-1}	**0**	**1.5**	**3**	**4.5**	**10**	**0**	**1.5**	**3**	**4.5**	**10**	**0**	**1.5**	**3**	**4.5**	**10**	**0**	**1.5**	**3**	**4.5**	**10**
Agrostis stolonifera		1.4			0.6										0.8					0.5
Artemisia maritima			0.4																	
Elytrigia atherica	18.1	1.7	0.2			49.7					73.8					88.2				
Festuca rubra	75.0	76.0	77.7	86.3	86.6	48.6		89.7		99.8	25.0				31.7	6.8				80.3
Juncus gerardii								0.5												
Lolium perenne				1.2																0.4
Puccinellia maritima	6.7	14.4	18.7	10.8	4.2	0.6		9.8		0.2	0.4				58.4	1.8				17.7
Salicornia spp.		5.8	1.7	1.3	8.7										1.7					
Spartina anglica	0.2	0.7	1.3	0.3		0.2					0.3				5.3	2.5				
bare soil						0.9					0.4				2.1	0.7				1.0


A
Homogeneously tall vegetation
Tall productive vegetation dominated by stress-intolerant, low quality plants
Elytrigia atherica dominant
High litter production, cover
Uniformly tall vegetation
High soil aeration + N mineralization
High soil aeration N min.
B
Heterogeneous vegetation
Patchy vegetation patches of Elytrigia atherica interspersed with Festuca rubra & Artemisia maritima (high marsh) Puccinellia maritima (low marsh)
Preferential grazing in low vegetation, tall bits untouched
Patches of high and low attractiveness
High soil aeration + N mineralization in patches of tall vegetation
Patches of high and low soil aeration
C
Homogeneously low vegetation
Low vegetation dominated by stress-tolerating, short, shallow rooting high quality plants
Puccinellia maritima (low marsh)
Festuca rubra (high marsh)
Densities of sheep high enough to suppress E. atherica on the marsh
Uniformly low vegetation
Suppression of soil aeration and N mineralization
Low soil aeration N min.
Increasing stocking density

Figure



Section 1
Section 2
Section 3
Section 4
Section 5
A
B
Low salt marsh
High salt marsh
SEAWALL
INTERTIDAL FLATS
Elevation (cm + MHT)
stocking density
(sheep ha−1)
0
3
10
Distance from collector drain within each section (m)

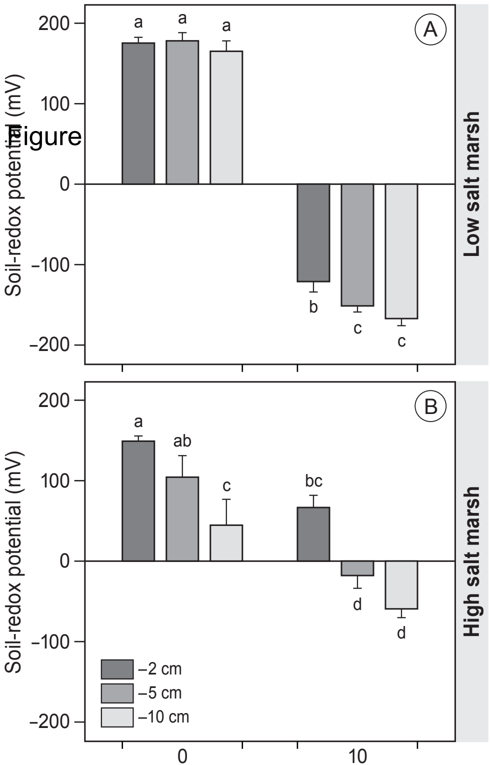
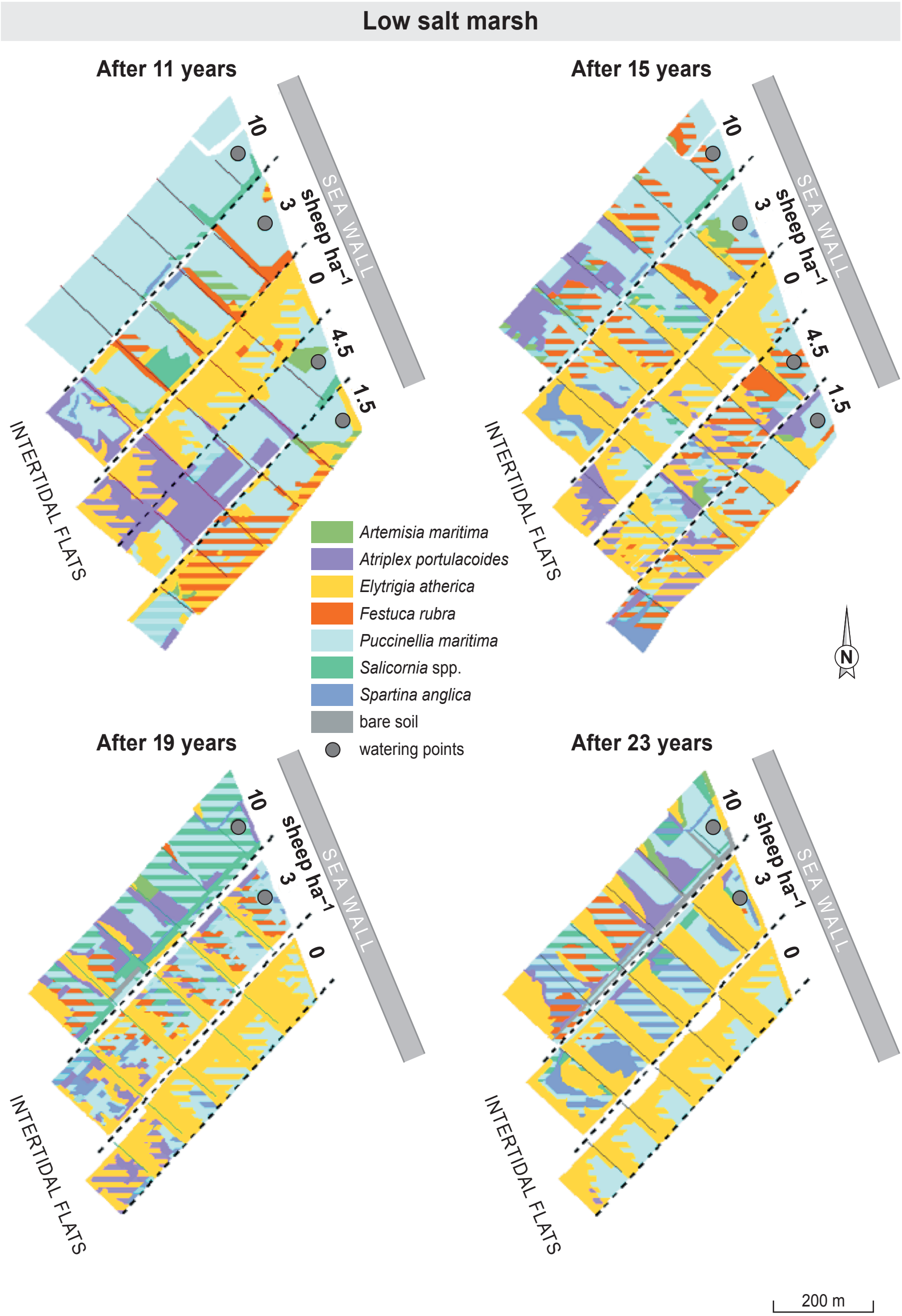
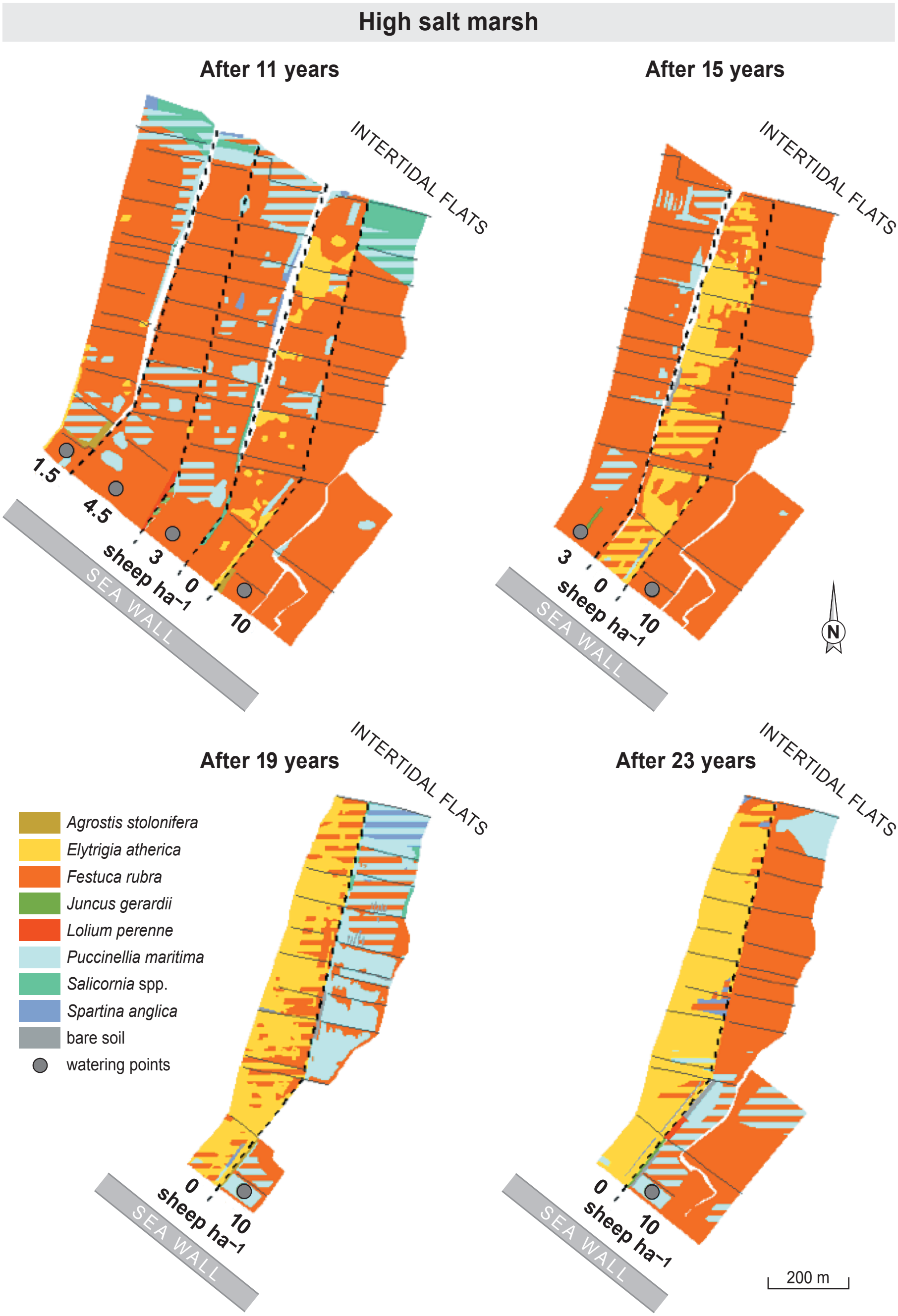


Figure
Soil-redox potential (mV)
200
100
0
-100
-200
a
a
a
b
c
c
A
Low salt marsh
B
High salt marsh
a
ab
c
bc
d
d
−2 cm
−5 cm
−10 cm
0
10
Number of sheep ha−1

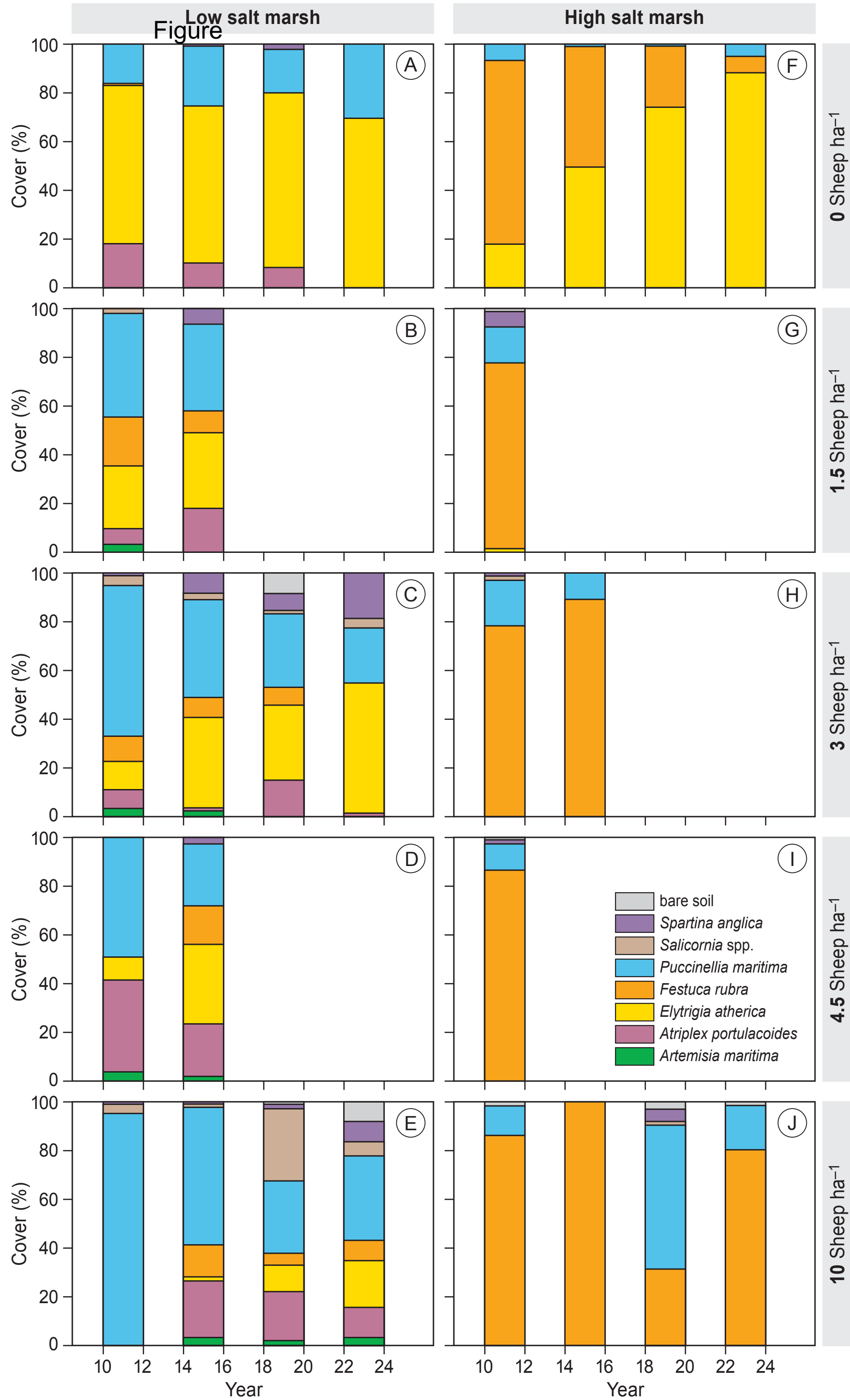
Figure


Low salt marsh
After 11 years
After 15 years
After 19 years
After 23 years
SEA WALL
INTERTIDAL FLATS
sheep ha⁻¹
10
3
0
4.5
1.5
Artemisia maritima
Atriplex portulacoides
Elytrigia atherica
Festuca rubra
Puccinellia maritima
Salicornia spp.
Spartina anglica
bare soil
watering points
N
200 m



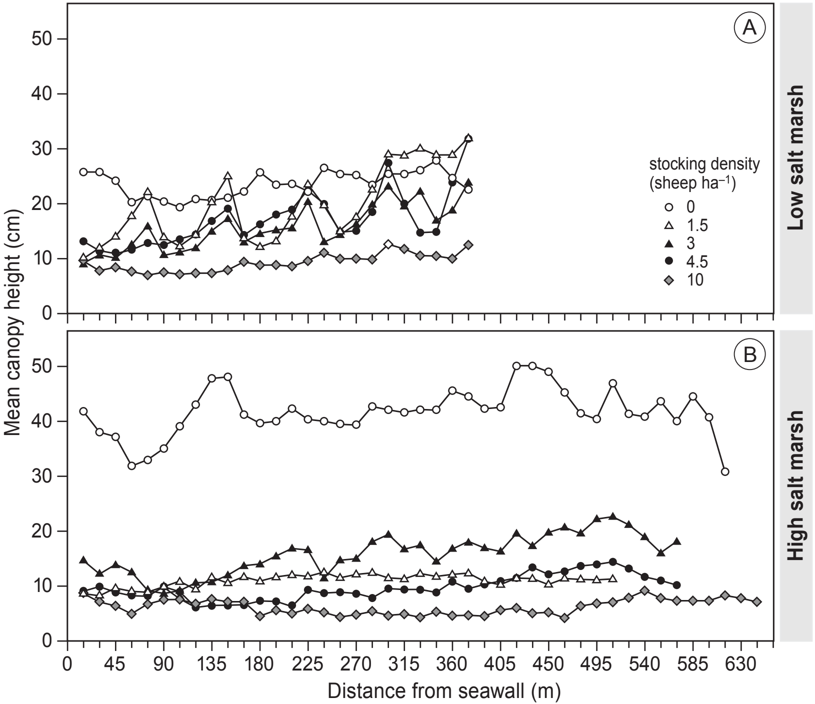
High salt marsh
After 11 years
After 15 years
After 19 years
After 23 years
INTERTIDAL FLATS
SEA WALL
1.5
4.5
3
0
10
sheep ha-1
Agrostis stolonifera
Elytrigia atherica
Festuca rubra
Juncus gerardii
Lolium perenne
Puccinellia maritima
Salicornia spp.
Spartina anglica
bare soil
watering points
N
200 m

Figure



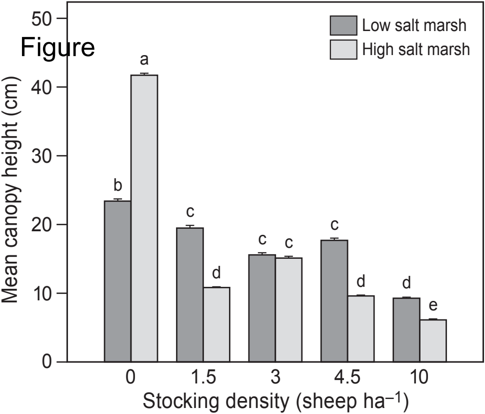
Low salt marsh
High salt marsh
0 Sheep ha⁻¹
1.5 Sheep ha⁻¹
3 Sheep ha⁻¹
4.5 Sheep ha⁻¹
10 Sheep ha⁻¹
Cover (%)
Year
A
B
C
D
E
F
G
H
I
J
bare soil
Spartina anglica
Salicornia spp.
Puccinellia maritima
Festuca rubra
Elytrigia atherica
Atriplex portulacoides
Artemisia maritima

Figure



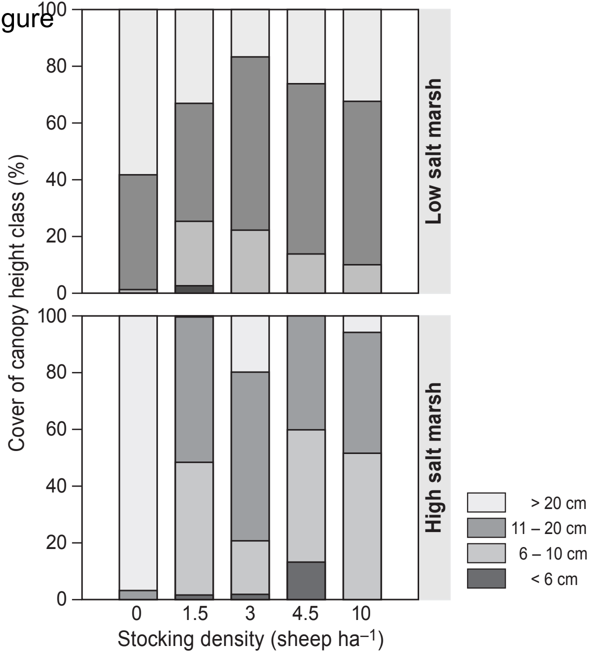
A
B
Low salt marsh
High salt marsh
stocking density
(sheep ha–1)
0
1.5
3
4.5
10
Mean canopy height (cm)
Distance from seawall (m)
0
10
20
30
40
50
0
45
90
135
180
225
270
315
360
405
450
495
540
585
630

Figure

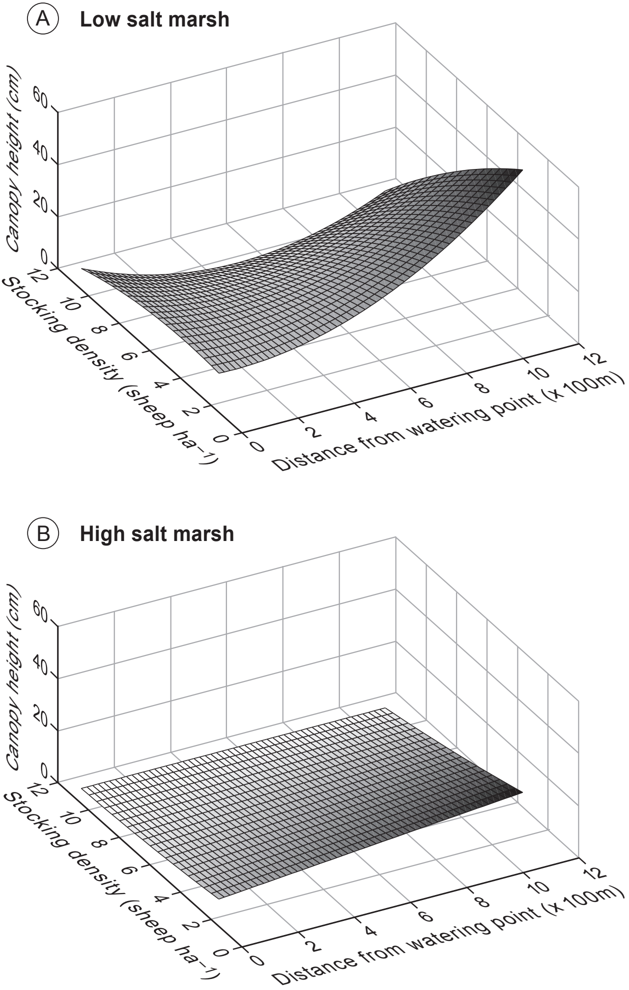


Low salt marsh
High salt marsh
Mean canopy height (cm)
50
40
30
20
10
0
a
b
c
d
c
c
c
d
d
e
0
1.5
3
4.5
10
Stocking density (sheep ha–1)

Figure

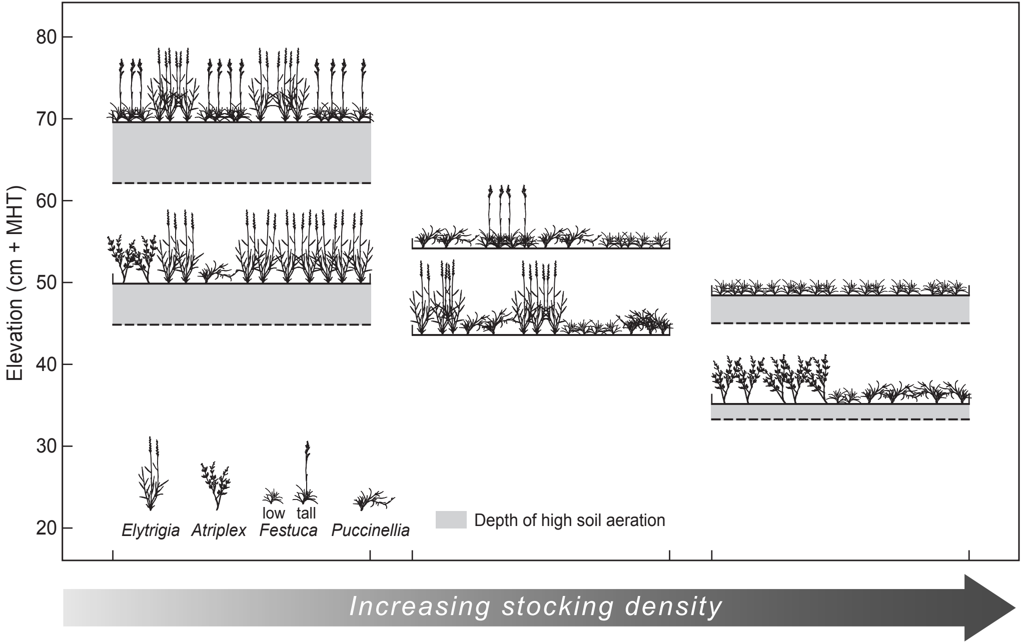


Cover of canopy height class (%)
100
80
60
40
20
0
Low salt marsh
High salt marsh
0
1.5
3
4.5
10
Stocking density (sheep ha–1)
> 20 cm
11 – 20 cm
6 – 10 cm
< 6 cm



A
Low salt marsh
Canopy height (cm)
0
20
40
60
Stocking density (sheep ha−1)
0
2
4
6
8
10
12
Distance from watering point (x 100m)
0
2
4
6
8
10
12
B
High salt marsh
Canopy height (cm)
0
20
40
60
Stocking density (sheep ha−1)
0
2
4
6
8
10
12
Distance from watering point (x 100m)
0
2
4
6
8
10
12

Figure



80
70
60
50
40
30
20
Elevation (cm + MHT)
Elytrigia
Atriplex
low
tall
Festuca
Puccinellia
Depth of high soil aeration
Increasing stocking density