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Grazing as a nature-management tool

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Grazing as a nature-management tool

The effect of different livestock species and stocking densities on salt-marsh vegetation and accretion

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Grazing as a nature-management tool

The effect of different livestock species and stocking densities on salt-marsh vegetation and accretion

PhD thesis

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the decision by the College of Deans.

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Friday 24 January 2014 at 14.30 hrs.

by

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Chapter one

1

The past and present of using livestock grazing as a nature-management tool in salt marshes – An introduction

Stefanie Nolte

Salt marshes

Coastal salt marshes may be defined as areas which are subject to periodic flooding (tidal and non-tidal) as a result of fluctuations in the level of the adjacent saline-water bodies and are vegetated by herbs, grasses or low shrubs (Adam 1990). Along the coast of the Wadden Sea we can classify these into mainland, estuarine and back-barrier-island marshes (Adam 2002). As a result of the regular exposure to sea water these areas are dominated by a number of salt-tolerant plants (Allen 2000). These plants are often specialists and restricted to these ecosystems (Westhoff et al. 1993). Therefore the protection of salt marshes plays an important role in the conservation of biodiversity in Northwest Europe. In addition to the characteristic plant species, salt marshes are an important habitat for many bird species (Norris et al. 1997) and

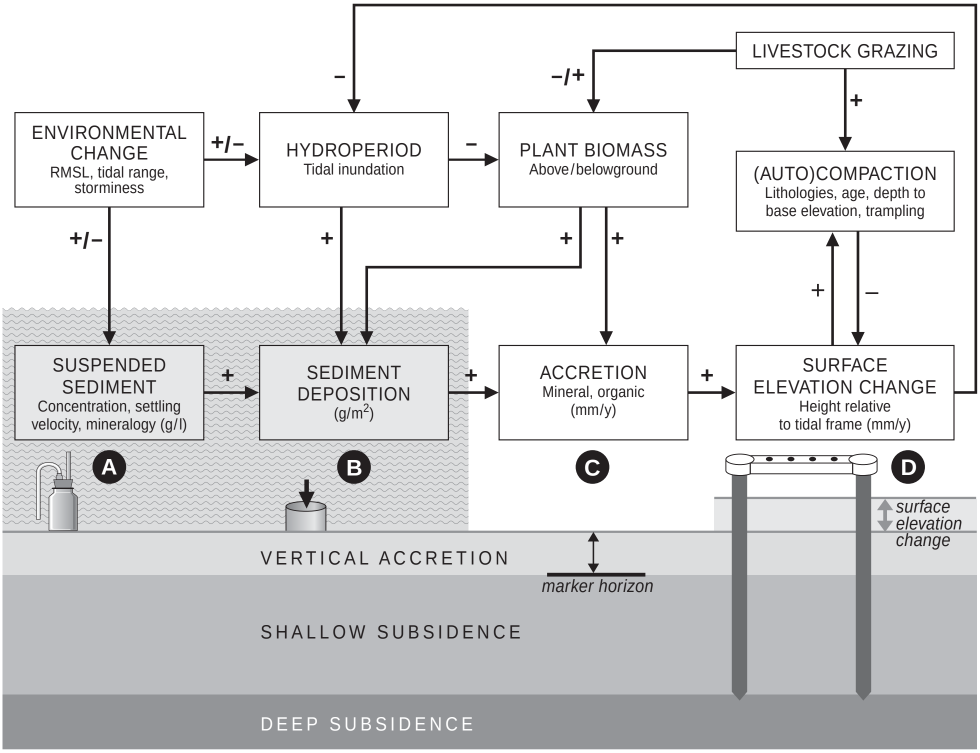


Figure 1.1 Factors affecting sediment dynamics in salt marshes after Allen (2000) and Cahoon et al. (2002a). The processes can be differentiated into the deposition of sediment (**B**) onto the marsh surface in g/m^2, the accretion (**C**) containing both deposited mineral sediments and organic particles in mm/yr, and the resulting surface elevation change (**D**) with respect to a fixed ordnance datum. These processes are influenced by a variety of variables such as the suspended sediment concentration (**A**) in the inundating water.

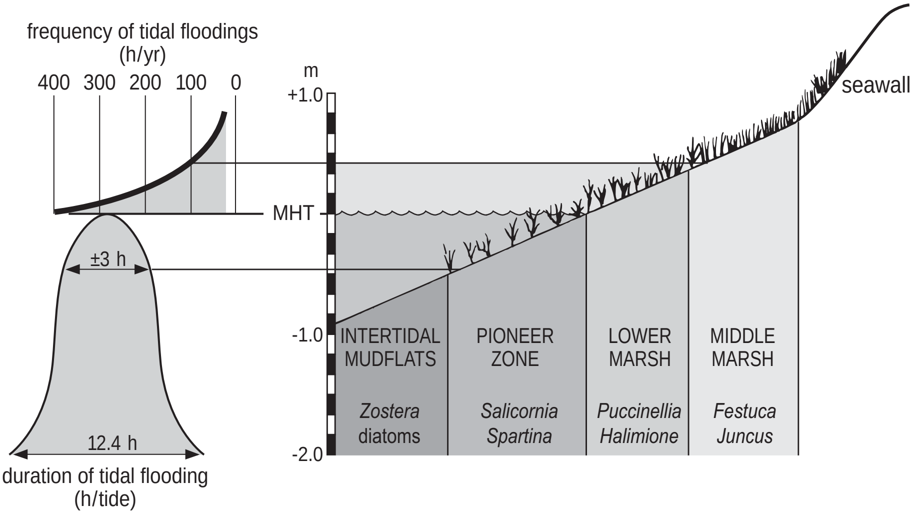


Figure 1.2 Zonation of mainland salt marshes in relation to duration and frequency of tidal floodings (Erchinger 1985).

invertebrate species (*e.g.* Pétillon et al. 2005, Rickert et al. 2012), and play an essential role in coastal protection (Borsje et al. 2011).

Salt marshes develop because of the interplay of physical factors such as current and biological factors such as vegetation (Allen 2000; Fig. 1.1). Regular inundations bring suspended sediment to the marsh, which settles on the surface and leads to an increased surface elevation. Back-barrier salt marshes develop naturally with respect to sedimentation and drainage by meandering creeks. On most mainland marshes sedimentation is facilitated by sedimentation fields. Brushwood groynes reduce the energy of the waves and thus enhance sedimentation. Drainage of the soil was traditionally enhanced by intensive ditching. When surface elevation and drainage are sufficient to allow periods of soil aeration the growth of pioneer vegetation is possible. A further rise in surface elevation then enables other halophytic plants to grow. The plants in salt marshes generally form a distinct zonation, which represents the elevation gradient of the marsh and therefore the flooding frequency (Adam 2002; Fig. 1.2) and the amount of oxygen in the soil (Bockelmann and Neuhaus 1999, Davy et al. 2011). The regular addition of sediments increases elevation and adds nitrogen to the system which leads to a vegetation succession as shown on a back-barrier-island marsh by Olff et al. (1997). During undisturbed succession, *i.e.* without livestock grazing, plant species with a low stature (*e.g. Puccinellia maritima*) are outcompeted on back-barrier and mainland marshes by tall-growing species such as *Elytrigia atherica* (Olff et al. 1997) which form species-poor mono-specific stands. In brackish marshes like the Dollard, a spread of the tall species *Phragmites australis* in place of *Elytrigia atherica* was observed (Esselink et al. 2000).

To graze or not to graze?

The tall growing grass *Elytrigia atherica* is a late-successional species of the high-elevated marsh zone which was rapidly increasing during the last decades on natural aging back-barrier-island salt marshes (Veeneklaas et al. 2013). On mainland marshes this increase coincided with a change in management regime in many salt-marsh areas (Esselink et al. 2009). Until recently most salt marshes were used for intensive livestock grazing. Livestock grazing had a long tradition along the Wadden Sea coast (Esselink et al. 2000), which had been agriculturally exploited for centuries (Zeiler 2006, Esselink et al. 2009). A reduction of stocking rates or abandonment was caused in large areas by the establishment of nature conservation areas, especially in Germany where the National Park policy is to reduce all human interference (Bakker et al. 2003, Esselink et al. 2009). In the Netherlands abandonment of mainland marshes took place when livestock grazing became no longer economically feasible for farmers. It resulted in a strong increase of *Elytrigia atherica* (Esselink et al. 2009). This development led to the question for salt-marsh management 'to graze or not to graze?' (Bakker et al. 2003), and to the establishment of a number of grazing experiments on German mainland marshes (*e.g.* Andresen et al. 1990, Kiehl et al. 1996). As a result of some of these grazing experiments a further cessation of grazing in salt marshes was advocated as the dominance of single species, mainly *Elytrigia atherica* in the high marsh and *Atriplex portulacoides* in the low marsh, could not be detected (Kiehl et al. 1996). However, these results were based on a five year study and did therefore not quantify long-term effects (Bakker et al. 1996). Studies investigating the effect of cessation after nine, ten and eleven years found *Elytrigia* to invade the high marsh which might lead to a future loss of species richness (Schröder et al. 2002, Gettner 2003, Kiehl et al. 2007). It is, however, argued that the neglect of drainage ditches will lead to a higher groundwater table and prevent both *Atriplex* and *Elytrigia* to become dominant in soils with poor drainage (Kiehl et al. 2007) and that an increase in spatial diversity will create areas with favourable conditions for other plant species than *Elytrigia* in ungrazed marshes (Stock and Kiehl 2000, Gettner 2003). In contrast, a recommendation for grazing in low densities is given by other authors for both back-barrier-island (Bos et al. 2002, Bakker et al. 2003) and mainland marshes (Andresen et al. 1990, Bouchard et al. 2003). An invasion of *Elytrigia*, which is likely going to lead to dominance, was described by Tessier et al. (2003) after eight years at the Mont Saint Michel bay. Dominance of *Elytrigia* in combination with a decreasing species number was also found after nine years (Andresen et al. 1990) and ten years (Bouchard et al. 2003). Even though a repressing effect of a high groundwater table on *Elytrigia* was described by Kleyer et al. (2003) after 11 years of cessation, the authors recommend a low stocking density rather than no grazing.

How to graze?

We can summarize that *Elytrigia* is invading the high-marsh and even the low-marsh zone (Veeneklaas et al. 2013) in many marshes after approximately ten years (Bakker et al. 2003), and that the spread of this species leads to a decrease in the number of plant species (Andresen et al. 1990, Kleyer et al. 2003, Bouchard et al. 2003, Bakker et al. 2003). Therefore low stocking densities have been adopted as a strategy for nature management in salt marshes (Adam 2002), and are recommended by the Trilateral Monitoring Assessment Programme TMAP (Bakker et al. 2003, Esselink et al. 2009). The question 'to graze or not to graze' should thus be replaced by 'what targets is conservation management aiming at and how to reach these?' (Adam 2002, Bakker et al. 2003). To address this question a grazing experiment is required, comparing the effect of both different stocking densities and livestock species on the ecosystem (Bakker et al. 2003). The importance of stocking density for nature conservation was investigated in various systems (Hickman and Hartnett 2002, Dumont et al. 2007a, Scimone et al. 2007, Dumont et al. 2009). For salt marshes different authors recommend a variation of stocking densities to reach a high structural diversity (Berg et al. 1997) and plant biodiversity (Bakker at al. 2002, Andresen et al. 1990, Kleyer et al. 2003). However, not only the stocking density, also the livestock species should be considered when choosing an adequate grazing management (Rook et al. 2004). Livestock species differ in their physiology and morphology. Differences in their digestive systems for example lead to a higher daily forage intake of horses compared to cattle, because cattle as ruminants are able to extract more nutrients from their forage (Duncan et al. 1990). These differences between livestock species will influence their behaviour namely diet choice, activity and spatial distribution; leading to dissimilarities in their influence on vegetation.

Another option for nature management in grasslands might be a rotational grazing regime, in which years of grazing are followed by years without grazing. In years without grazing grazing-sensitive plant species could be able to produce flowers and seeds. Moreover, invertebrates would profit from the flowers, seeds and the taller vegetation (Irmler and Heydemann 1986). Before tall competitive species such as *Elytrigia atherica* can spread, renewed grazing completes the rotational regime and supresses their spread. The aim of this study is to investigate different grazing regimes with respect to stocking density, livestock species and rotational grazing and investigate the effect on plants and sediment dynamics to answer the question 'how to graze?'.

The grazing experiment

To investigate the differential effects of two livestock species in two densities on vegetation and sediment dynamics a large-scale grazing experiment is installed in the research area 'Noord-Friesland Buitendijks' (NFB) (53°20'11", 5°43'40"). The research area has developed from sedimentation fields and is situated at the Dutch mainland Wadden Sea coast. The yearly average precipitation is 820 mm and average yearly temperature is 9.5°C (data Royal Netherlands Meteorological Institute). On average the area lies 58 cm above mean high tide (MHT) and the local tidal amplitude is 2.1 m. Typical for man-made mainland marshes the morphology of the area is characterised by an evenly distribution of small drainage ditches, which silted up after maintenance stopped in 2000 (van Duin et al. 2007).

The experimental setup includes three blocks of approximately 55 ha (Fig. 1.3),

Figure 1.3 Map of the experimental setup at Noord Friesland Buitendijks including the three blocks ('West', 'Mid', East'). The grazing treatments are indicated by a number giving the stocking density and a letter representing the livestock species (H = horse, C = cattle, R = rotational grazing, N = ungrazed). The freshwater source situated at the southern end of each paddock is marked with a white dot.

which are named ‘West’, ‘Mid’ and ‘East’ with respect to their situation. Blocks are orientated perpendicular to the summerbank and include vegetation types of the high marsh, low marsh, and in one case also of the pioneer zone. In each of these blocks the following grazing treatments are applied in paddocks of *ca.* 11 ha: grazing with horses at stocking densities of 0.5 animal/ha and 1.0 animal/ha and grazing with cattle at stocking densities of 0.5 animal/ha and 1.0 animal/ha. Grazing treatments started in 2010. Additionally, a rotational treatment is applied, in which a year without grazing (2010, 2012) is followed by a year of cattle grazing with 1.0 animal/ha (2011). Treatments are randomly assigned to paddocks with the only constriction that horse grazing treatments are not to be placed in neighbouring paddocks. As horses are very social animals, we otherwise expect the animals in two neighbouring paddocks to interact and therefore influence the results. Livestock is obtained from local farmers and grazing takes place from May until October. Livestock has access to a freshwater source in the high marsh close to the southern end of each of the paddocks. Prior to the experiment the blocks Mid and East were grazed intensively by livestock (cattle or horses), while the West block was ungrazed for approximately the last 30 years (Esselink et al. 2009). Before the start of the experiment livestock was introduced to the West block to approximate similar starting conditions in all three blocks.

Thesis outline

To explain the effect of the different grazing treatments on the vegetation it is crucial to understand the driver of potential changes (de Bello et al. 2010). In our case, the driver will be behavioural differences between the grazers. We expect cattle and horses and animals in the two stocking densities to differ with respect to diet choice, activity and spatial distribution. In **chapter 2** we, therefore, perform focal observations and study the animal’s behaviour in detail, to be able to relate these to other results presented in the following chapters, *e.g.* with respect to vegetation. In general, the effect of management on the biodiversity can be monitored in a variety of approaches as outlined by de Bello et al. (2010). Among these approaches are the monitoring of single species, of species diversity indices (*e.g.* number of species per area), and of functional indicators (*e.g.* canopy height) (Fig. 1.4). The monitoring of a single species has the advantage that it can give a deeper insight into the species phenology and status. This status of the plant can have a strong effect on the ecosystem, as for example flower visiting insects only benefit from their host plants if these are able to produce flowers. Therefore, we monitor the effect of the grazing treatments on the flower production of the target plant species *Aster tripolium* (**chapter 3**). Furthermore, we apply the classical approach of monitoring an index of plant species diversity by recording the number of plant species in permanent plots

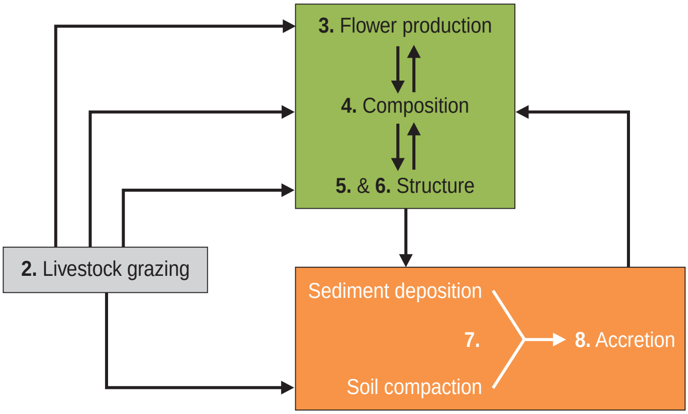


Figure 1.4 Behavioural differences between livestock species (**chapter 2**) are likely leading to differential effects of grazing treatments on the vegetation. Vegetation can be directly affected by a reduction of flower production (**chapter 3**), a change in plant species composition (**chapter 4**) and an alteration of vegetation structure (**chapter 5** and **6**). These aspects of vegetation are again interacting as *e.g.* a reduced seed set or altered light-competition conditions lead to changes in species composition. Vegetation structure is also likely to influence sediment deposition and thus reducing accretion rates. Accretion rates might further be reduced by livestock grazing, as grazing might increase compaction (**chapter 7** and **8**).

(**chapter 4**). In addition to the number of species per area we also investigate the effect of grazing treatments on the vegetation composition change in these permanent plots. Although the monitoring of species number in a given area (permanent plots) has a long standing tradition, the plant species diversity might be affected differently on various spatial scales (de Bello et al. 2010). Therefore, we additionally count the number of plant species on various spatial scales in the grazing experiment and calculate species-area curves (**Box 1**). To investigate what effect different stocking densities have on species diversity after a longer time period, similar measurements are carried out in the German experimental sites Friedrichskoog (FK) and Sönke-Nissen-Koog (SNK). In these areas we also investigate the long-term effect of different stocking densities on the vegetation structure (canopy height) on a large scale (**chapter 5**). The structure of the canopy is likely to be altered by grazing (Berg et al. 1997) and can have effects on other functional groups in the ecosystem. Breeding birds, for example, prefer a certain vegetation structure for their nest sites (Bakker et al. 1993, Norris et al. 1997) and geese were found to choose vegetation with a short canopy for grazing (Olff et al. 1997, Bos et al. 2005). Small-scale structural diversity is furthermore likely to increase the biodiversity, as patches of tall and short vegetation provide niches for a variety of plant and invertebrate species (Olofsson et al. 2008). Therefore, we investigate the effect of the grazing treatments in the experiment on small-scale vegetation-structure patchiness (**chapter 6**). In addition to its effects on diversity of different groups, the vegetation structure was also found to be an important factor in sediment dynamics (*e.g.* Bouma et al. 2005, Baustian et al. 2012, Fig. 1.1). Sediment dynamics can be differentiated into several mechanisms as outlined in **chapter 7** (Fig. 1.1). The sediment which is suspended in the inundating water is trapped by the vegetation and settles on the marsh surface and forms the mineral part of accretion. The organic part of accretion is made of dead plant material such as litter and roots. Autocompaction of the soil, caused by the soil's own weight, leads to a reduction of total accretion. However, compaction might also be increased by grazing through trampling (Schrama et al. 2013). Furthermore grazing might alter vegetation structure which was found to increase sediment deposition rates. These two processes, namely increased compaction and reduced sediment deposition, might lead to a reduced total accretion rate in grazed marshes. Whether this is the case and whether the resulting accretion rate in grazed marshes is sufficient for marshes to outpace sea-level rise is investigated in **chapter 8**. Finally, **chapter 9** contains a synthesis integrating the effect of different grazing management schemes on the various aspects of vegetation, such as flower production of target species, plant-species diversity and structural diversity, and on accretion in salt marshes.

Chapter two

2

Diet choice, activity and spatial distribution of horses and cattle at two grazing densities in a coastal salt marsh

Stefanie Nolte, Christa van der Weyde, Peter Esselink,
Christian Smit, Sip van Wieren, Jan P. Bakker

Submitted to Grass and Forage Science

Abstract

To preserve species-rich semi-natural grasslands, grazing with livestock has become a common tool in nature management. However, management effects on these grasslands are likely to vary depending on the species of livestock and stocking density. Thus, we studied the behaviour of two livestock species (horses and cattle) at two stocking densities (0.5 and 1.0 animal per ha) in a coastal grassland by using focal observations. This study focused on behaviours linked to diet choice, activity and spatial distribution. Livestock species shared a high overlap in diet choice, although horses preferred forage species with high-fibre content, such as the low-marsh species, *Puccinellia maritima*. Furthermore, horses were more active and spent more time grazing than cattle. Spatial distribution of both species was related to vegetation type. Both species preferred high-marsh vegetation types but horses spent more time in the low marsh compared to cattle. Additionally, at the high stocking density, both livestock species spent more time in the low marsh. Cattle formed a grazing gradient with respect to distance to the freshwater source. Knowledge of behavioural differences between livestock species and stocking densities will allow managers to apply optimal grazing regimes for conservation goals as discussed in this paper.

Introduction

Many semi-natural grasslands in Europe are at risk of being abandoned because livestock grazing with large herbivores for agricultural purposes is no longer economically feasible (*e.g.* Poschlod and WallisDeVries 2002). The value of these often traditionally grazed areas for biodiversity conservation has led to the now common practice of livestock grazing as a tool in nature management (*e.g.* Bos et al. 2002, Sammul et al. 2012). Few studies, however, have compared the behaviour of different species of livestock at various stocking densities and whether this might affect management goals.

Grazing by livestock influences the vegetation by slowing down succession and preserving earlier, more species-rich successional stages. Livestock grazing also affects the ecosystem by increasing seed dispersal (Bakker et al. 2008) and soil compaction (Schrama et al. 2013), slowing down the establishment of shrubs and trees (Smit and Ruifrok 2011) and redistributing nutrients (van Uytvanck et al. 2010). Additionally, grazing may induce patchiness of vegetation and structural heterogeneity, which leads to increased biodiversity (Adler et al. 2001, Rook et al. 2004). However, behavioural differences between livestock species or breeds at different stocking densities are likely to influence the strength of these effects. These behavioural differences can be divided into three different categories: diet choice, activity and spatial distribution.

Diet choice of different livestock species, such as horses and cattle, are likely to greatly overlap (Vulink 2001). Nevertheless, some differences in the relative importance of plant species in the diet might be caused by characteristics of the digestive system, mouth anatomy and nutritional requirements. Horses require a higher food intake than cattle due to their digestive system and have been found to consume more high-fibre forage such as fibrous grasses (Gordon 1989, Duncan et al. 1990, Vulink 2001, Menard et al. 2002). Horses also have two sets of incisors and are able to graze closer to the ground by biting off parts of plants, whereas cattle use their tongue to rip off plants. Thus, horses are able to graze on very short tillers, which explains their selection of much shorter swards than cattle (Gordon 1989). Diet choice by wild herbivores, including wild-ranging livestock, has been shown to be generally based on maximizing energy intake (Belovsky 1986, Vulink and Drost 1991, Vulink 2001). However, several studies have shown that forage quality is also an important factor determining herbivore selectivity, especially when nutritional differences in quality between plant species are large (Arnold 1987, Bakker 1989). We expect horses and cattle to differ in their mineral requirements and thus mineral content of plants should explain the preference for certain plant species.

Differences in digestive systems among large herbivores partly determine their patterns of activity. Ruminants, such as cattle, possess a fermentation chamber in the foregut where food is retained longer in contrast to hind-gut fermenters, such as horses (Duncan et al. 1990). Therefore, ruminants can extract more nutrients from their forage than hind-gut fermenters. The latter generally compensate for this by having a higher daily food intake (Duncan et al. 1990). Higher food intake leads to longer grazing times, and thus to a higher general activity of horses compared to cattle.

Spatial distribution of herbivores within the available space is often linked to their dietary choice because animals frequently revisit areas with a high abundance of favoured plant species (*e.g.* Jensen 1985, Rook et al. 2004). Additionally, herbivores frequently revisit previously grazed areas with a short canopy of re-growing vegetation that is rich in proteins and has a low stem to leaf ratio (Ydenberg and Prins 1981, McNaughton 1984, Dumont et al. 2007b). Another factor influencing spatial distribution of herbivores might be distance to a freshwater source. Grazing intensity often decreases with distance to the freshwater source as summarized by Adler et al. (2001) for wild and domestic animals in terrestrial grazing systems. The same effect was found in salt marshes for both sheep (Kiehl et al. 1996) and cattle (Esselink et al. 2002).

In addition to differences between livestock species, stocking density is also likely to influence diet choice, activity and spatial distribution. At high stocking densities, availability of preferred food plants might decrease and animals would have to include less preferred species in their diet (Crawley 1983, Augustine and McNaughton 1998). The depletion of preferred food plants might then also lead to increased activity as animals are forced to search for plants. This search for food plants will then affect spatial distribution.

There are many reasons to assume that these morphological and behavioural differences among grazer species and at different stocking densities will result in distinctive impacts on ecosystems. Yet, surprisingly few studies have investigated these differences with regard to effects on biodiversity. We conducted this study in coastal semi-natural grassland (salt marsh) because land abandonment is a common phenomenon both in the Wadden Sea (Esselink et al. 2009) and the Baltic Sea area (Sammul et al. 2012). Apart from the natural absence of trees, these grasslands are very comparable to other semi-natural habitats with a long history of human influence. The survival of these grassland habitats is important in order to preserve biodiversity in Western Europe (Adam 1990). To achieve this goal, nature management often applies grazing in these areas. Grazing with livestock in intermediate stocking densities has a positive effect on plant-species richness in salt marshes as it prevents dominance of one or a few plant species *e.g.* the tall grass *Elytrigia atherica* (Bakker et al. 1993, Bakker et al. 2003, Bos et al. 2002), or *Phragmites australis* in brackish marshes (Esselink et al. 2002, Sammul et al. 2012). Also, grazing has a positive effect on migratory waterfowl (van der Graaf et al. 2002) and ground breeding birds (Bakker et al. 1993). However, there is a gap in knowledge on the differential effects of different livestock species or stocking densities on the biodiversity of salt marshes. We studied grazing behaviour of horses and cattle under two different stocking densities, focusing on diet choice, activity, and spatial distribution. We predict that:

1) Diet choice will differ between livestock species and between different stocking densities.
2) Habitat selection will differ between livestock species and between stocking densities. Animals will tend to visit vegetation types dominated by preferred food plants more often irrespective of the abundance of these vegetation types.
3) Horses will have a bias towards food plants with high-fibre concentration in their diet compared to cattle, especially at higher densities when availability of short high-quality swards is limited.
4) Horses will be more active than cattle in that they will travel further distances within the study area and will spend more time grazing to fulfil their comparatively higher need for forage.
5) Horses will distribute more randomly over the available area, because of their higher activity, while cattle will cluster more in their distribution.
6) The spatial distribution of animals will be affected by their preference for certain food plants and the vegetation types in which these plants are common.

Material and methods

Study site

The research area, 'Noord-Friesland Buitendijks' (NFB) (53°20'11", 5°43'40"), is a temperate salt marsh located on the north coast of The Netherlands. Average yearly precipitation is 820 mm and average yearly temperature is 9.5°C. Salt marshes are intertidal areas that include an elevational gradient from intertidal flats to the seawall with a characteristic vegetation zonation. NFB is of anthropogenic origin because its development was facilitated by ditching and the construction of sedimentation fields. Thus, it is characterized by an evenly distributed drainage pattern and rather flat relief. This leads to relatively small abiotic variation and is therefore ideal for a large experimental setup as experimental areas will be abiotically comparable.

The experimental treatments, consisting of four different grazing regimes within two replicate blocks (Fig. 2.1), were established in the spring of 2010. Before the start of the experiment, the site had been subject to intensive grazing during the summer months (Esselink et al. 2009). Each block was subdivided into five paddocks (*ca.* 11 ha each). Each paddock includes an elevational gradient from North to South and is comprised of both high and low marshes. For analysis, the paddocks were further subdivided into a grid of 24 cells each. The following grazing regimes were applied within each block: cattle grazing (0.5 and 1.0 animal per ha), horse grazing (0.5 and 1.0 animal per ha), and no grazing. The application of treatments in each block was

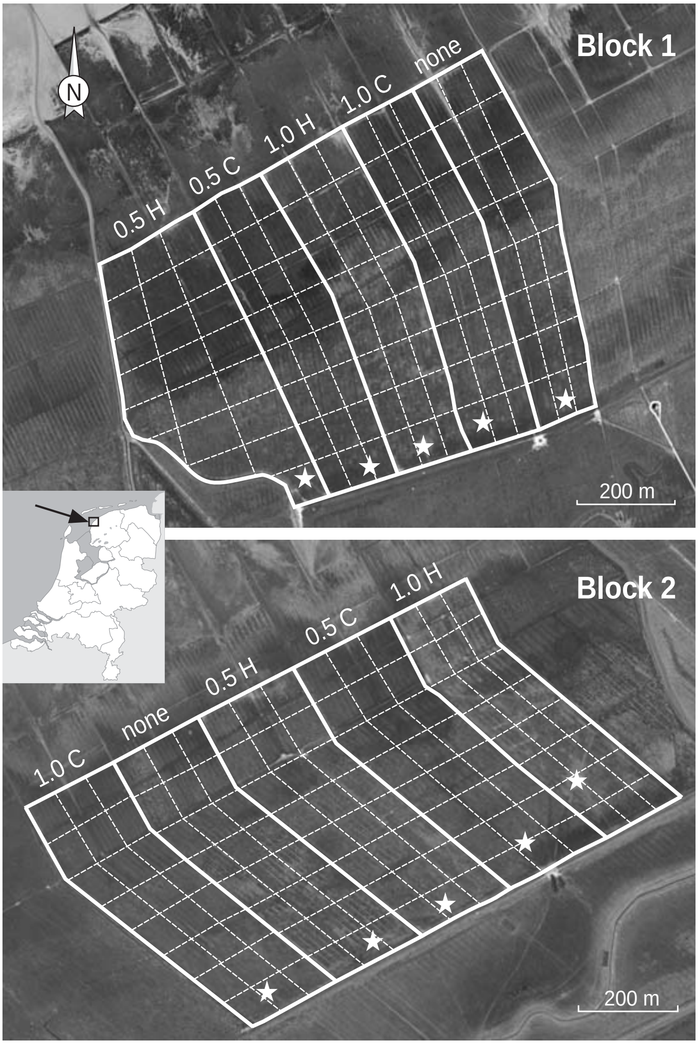


Figure 2.1 Experimental setup with paddocks (white line), grid cells (dashed line) and freshwater source (★). The grazing treatments are indicated by a number giving the stocking density and a letter representing the livestock species (H = horse, C = cattle). One paddock per block remained ungrazed.

randomized with one exception. The placing of treatments with horses next to each other was avoided in order to prevent these very social animals from interacting with the group in the adjacent paddock. Animals were obtained from local farmers and remained in the paddocks from June to October. Access to a freshwater source was always given in the southern end of each paddock.

Focal observations

We recorded diet choice, activity, grazing time and spatial distribution of the livestock during 24h-observation sessions in August and September 2010 as follows (Esselink et al. 2000). Four observation sessions per block were carried out, resulting in a total number of eight observation sessions per grazing regime. Every session started at noon and ended at noon the following day excluding the night hours. This procedure was followed to account for diurnal differences in the behaviour of animals such as Rutter et al. (2004) found for cattle and sheep. The animals were approached as closely as possible without disturbing them (Dumont et al. 2007a). The behaviour of the animals (grazing, walking, resting, drinking) and their position was recorded every hour using a GPS with 5m accuracy. If the animals were grazing, we noted the plant species of the third bite for each individual animal. This was done to avoid a bias towards easily identifiable plant species (Dumont et al. 2007a). Nomenclature follows van der Meijden (2005). Number of hourly scans decreased from 16 at the beginning of August to 13 by the end of September because of the shortening of the day-light period.

Forage quality

We collected samples of all plant species available to the grazers in the area for chemical analysis. Samples were collected at the beginning of September, representing the peak of the growing season for salt marshes and also the season in which the animal observations were conducted. We haphazardly collected 'bite'-samples of the above-ground biomass of several individuals. To test for possible chemical differences associated with small-scale abiotic variations and between stocking densities, samples were taken from all cattle-grazed paddocks ($n = 4$). It was impossible to analyse samples for all species from all treatments because of time constraints. All samples were dried at 70°C within one day after collection, then ground, sieved (1-mm sieve) and analysed for neutral detergent fibre (NDF in % of dry matter weight) (van Soest et al. 1991). NDF includes cellulose, hemicellulose and lignin as major components and is the preferred measure for digestibility of ruminant feed (van Soest et al. 1991). Furthermore samples were analysed for N, P, K, Ca, Mg and Na.

Spatial distribution in relation to freshwater source and vegetation types

To study the spatial distribution of livestock, we used the 24 grid cells per paddock described earlier, which were approximately 0.5 ha in size. For each grid cell, we calculated distance of the central point (centroid) to the freshwater source, which was used as an explanatory variable. Additionally, the most abundant vegetation type was assigned to each grid cell using a vegetation map of the area, which had been created in 2009 (Nolte, unpubl. data). Vegetation types in the map were classified according to the TMAP typology key for Wadden Sea salt marshes (Esselink et al. 2009). In order to investigate whether diet choice was driven by availability of plant species, the total area of each vegetation type was calculated for each paddock using the same vegetation map. A geographic information system (ArcGIS 10) was used for digitizing the map and calculating distances and areas.

Statistical analyses

Diet choice

We performed a Canonical Correspondence Analysis (CCA) to investigate differences in diet choice between horses and cattle (prediction 1). We combined plant species chosen by all individuals within one paddock and focal observations to obtain the diet choice of the group. The diet choice then consists of a percentage value for each plant species. Thus, if for example two out of ten horses in the group in one focal observation chose the plant species *Aster tripolium*, this species would represent 20% of the diet choice of the group. The diet compositions of each focal observation were used as species response variables in the CCA. As explanatory variables, we included livestock species and stocking density. The following covariables were used: block, vegetation type in which the animal was observed, and time of day. Covariables were selected using the forward selection procedure.

Habitat selection

The experimental site can be subdivided into several vegetation types dominated or characterized by certain plant species. It was investigated whether choices of different livestock species and stocking densities for certain vegetation types significantly differed (prediction 2) or whether these simply reflected dissimilarities in abundance of vegetation types between paddocks. Abundance of vegetation types for each paddock was assessed by calculating the proportion of vegetation types on the vegetation map. Ivlev's electivity index E (Jacobs 1974) was calculated according to Equation 1:

$$E_i = \frac{(d_i - a_i)}{(d_i + a_i)} \qquad \text{(Eq. 1)}$$

where d_i represents percentage of time spent in vegetation type i and a_i represents percentage area of vegetation type *i*. The values of *E* range between -1 to 1, where negative values indicate avoidance of a particular vegetation type, and positive values indicate selection for that vegetation type.

Forage quality

We calculated the average percentage of dietary NDF of dry matter weight for cattle and horses per observation session (prediction 3). First, the average NDF percentage of plant species was multiplied by the number of times the species was recorded per observation session. Results were summed up and divided by the total number of species occurring in the diet to obtain an index for the mean NDF. This mean NDF value was used as the predicted variable in a model containing livestock species, stocking density, and their interaction term. We detected heterogeneity of variance with a greater spread of residuals in cattle compared to horses, and in lower stocking densities compared to higher stocking densities. Therefore, a generalized least squares model (GLS) was used to include a variance structure for both livestock species and stocking density (Zuur et al. 2009) using the nlme package (Pinheiro et al. 2013) for R 2.15.2.

Activity

We digitized the position of the group of animals within each paddock with GPS-coordinates during each observation session using ArcGIS 10. Distance between the two coordinates of each chronological pair of observations during the observation session was used to estimate the minimum distance the animals moved in one hour (*e.g.* Pépin et al. 2009). We used this measure as an index for the general activity of the animals (prediction 4) (*e.g.* Elizalde-Arellano et al. 2012). The difference between treatments was analysed using a generalized linear model (GLM) approach with a Poisson distribution. Overdispersion was detected and thus standard errors were corrected using a quasi-GLM model (Zuur et al. 2009). The analysis was performed using the AED package (Zuur et al. 2009) for R 2.15.2. The full model included livestock species, stocking density and their interaction effect.

The difference in proportion of time the different livestock species spent grazing was analysed with a GLM, assuming a binomial distribution. We started with a full model including livestock species, stocking density and the interaction effect.

Spatial distribution

We compared the spatial distribution of animals in their paddock (prediction 5) with random distributions using the Average Nearest Neighbour Distance tool in ArcGIS 10. The position of the group at each focal observation is represented by a point. The Average Nearest Neighbour Distance tool measures the distance between each of these points and their nearest neighbouring point. It was then tested whether NN-ratio of the spatial distribution of points differed significantly from the NN-ratio of a random spatial distribution with the same characteristics (number of points and available area) (Ebdon 1977). A ratio of observed to expected average nearest neighbour distance (NN-ratio) smaller than 1 indicates clustered points, whereas a ratio greater than 1, indicates dispersed points.

A GLM was applied to investigate which grid-cell characteristics affected the spatial distribution of animals (prediction 6). The predicted variable was “count of animals per grid cell of each observation session”. This count is a proportion of the highest number of animals that could be present in the grid cell. Thus, the highest possible number of animals per grid cell was included as an offset variable. Due to this proportionality, a negative binomial distribution was assumed to account for overdispersion (*e.g.* Zuur et al. 2009). The full model contained livestock species, stocking density, vegetation type, distance to the freshwater source, and coordinates of the grid cells centroid (x,y). The coordinates of the grid cells were included to account for possible spatial autocorrelation among adjacent cells. The interaction effects between livestock species, stocking density and vegetation type were also included. Moreover, we included the interaction effects, livestock species*distance and stocking density*distance, in order to detect possible gradients from the freshwater source. We used a stepwise backwards model selection based on AIC values (Zuur et al. 2009).

Results

Diet choice

The diet choice of horses and cattle showed a large overlap (Fig. 2.2). However, the diet choice of horses contained a remarkable proportion of *Puccinellia maritima* (low-marsh species), especially at high stocking densities. Cattle stocked at low densities had a high proportion of *Aster tripolium* in their diet compared to all other grazing regimes. As preferred food plants become sparse with higher stocking density, livestock might be switching to less preferred species (horses to *Puccinellia maritima*, cattle to *Agrostis stolonifera*).

In the CCA, we found 8.6% of variation in the diet choice data (prediction 1) was explained by the first two axes (Fig. 2.3). The model was significant with $P < 0.05$ (F-ratio 4.295), indicating significant differences between the diet choice of livestock species and at different stocking densities. The diet of horses and animals in high densities frequently contained *Cirsium* spp., *Potentilla anserina* and *Puccinellia maritima* (Fig. 2.3). In comparison, in the diet of cattle and under low stocking densities *Aster tripolium*, *Festuca rubra*, *Spartina anglica* and *Triglochin maritima* were found more often.

The electivity index (prediction 2) indicated that at both stocking densities, animals showed a positive selection for typical high-marsh vegetation types. These typical high-marsh vegetation types are the brackish flooded grassland dominated by *Agrostis stolonifera* and the *Elytrigia repens* type. In contrast, vegetation types typical for the low marsh had a negative score on the electivity index, such as the *Suaeda/Salicornia* type and the *Spartina* type (Fig. 2.4 C-D). Horses showed lower avoidance of these vegetation types in the low marsh than cattle, especially at higher stocking densities (Fig. 2.4).

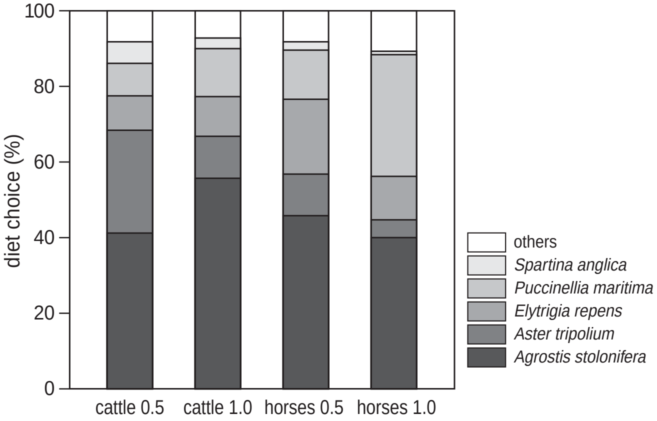


Figure 2.2 Average diet choice of horses and cattle within different stocking densities measured in percent time spent grazing on a plant species. *P. maritima* played a remarkably large role in the diet composition of horses at high densities. Cattle stocked at low densities had a high proportion of *A. tripolium* in their diet compared to all other treatments.

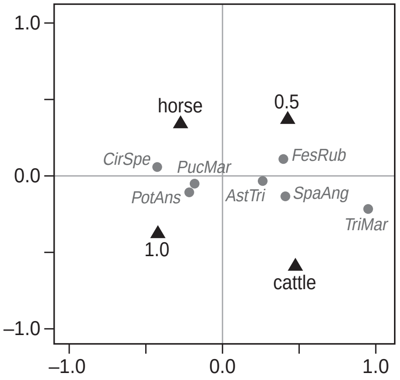


Figure 2.3 Biplot of CCA showing differences between the diet choice of cattle and horses at different stocking densities. Cattle showed a preference for *Aster tripolium*, *Festuca rubra*, *Triglochin maritimum*, and *Spartina anglica*, whereas the diet of horses more often contained *Potentilla anserina*, *Puccinellia maritima* and *Cirsium* spp. Species with species-fit-ranges under 1% are not plotted in this graph to improve readability. Eigenvalues: 0.075 (first axis), 0.011 (second axis), 0.415 (third axis), 0.373 (fourth axis). Monte Carlo Permutation F-ratio = 0.075 (first axis), P-value = 0.02.

Forage quality

No differences were found between samples from different treatments, so all samples of the same species were pooled. Average NDF percentage was higher in the diet of horses (63%) than of cattle (60%). In the GLS model, livestock species was a significant factor (DF = 1, F-value = 20.62, $P < 0.001$), whereas stocking density did not have an effect.

Activity and Grazing Time

Horses were more active than cattle (prediction 4), as indicated by the larger distance between two successive observations (mean distance horses = 152 m, SD = 124; Cattle = 121 m, SD = 99). The GLM explaining minimum distance that livestock travelled between observations contained only livestock species (t-value 2.83, $P < 0.001$) as an explanatory variable. Horses spent more time grazing than cattle (mean grazing time horses = 82.5 %, SD = 10.6; Cattle = 48.2 %, SD = 9.3) (Df 1, $P < 0.001$), whereas stocking density did not have an effect on grazing time in the second GLM. The average length of daylight period of the day during the study was 14.5 hours. Thus, horses spent on average 12 hours and cattle, 7 hours, per day grazing.

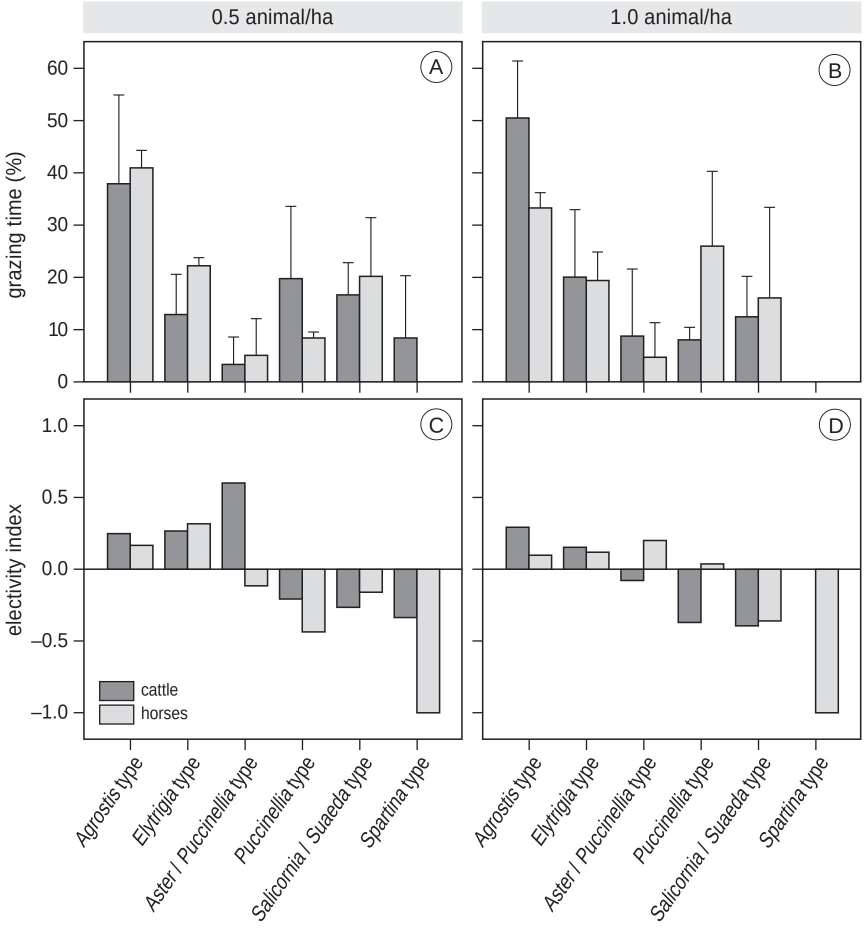
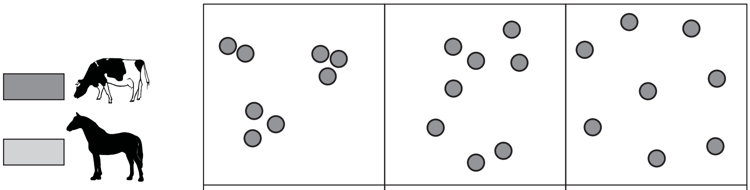


Figure 2.4 Comparison of allocation of grazing time among vegetation types at low (**A**) and high (**B**) stocking densities. Preference (electivity index >0) and avoidance (electivity index <0) based on allocation of grazing time and the availability of vegetation types for vegetation types at low (**C**) and high (**D**) stocking density for cattle (dark grey) and horses (light grey).

Spatial distribution

The results of the average nearest neighbour analysis (prediction 5) indicate that three out of four horse paddocks showed a random spatial distribution of animals. Horses neither clustered together nor dispersed evenly over these paddocks as indicated by the NN-ratio close to 1 (Fig. 2.5). Only one of the horse-grazed paddocks was characterized by a high NN-ratio and a distribution that was significantly different from random. This indicates that in this paddock, the horses spread evenly over the whole paddock. Cattle on the contrary, had a significantly clustered distribution in three out of four paddocks, as indicated by a NN-ratio <1. In the fourth paddock, cattle showed a trend towards clustering but this was not significant.

Vegetation type seemed to be the main factor explaining the spatial distribution of animals (Df $=1$, $P<0.001$) in the GLM applied to investigate which grid-cell characteristics affected spatial distribution of animals (prediction 6). Especially vegetation types dominated by *Agrostis stolonifera* and *Elytrigia repens* in the high marsh seemed to be preferred (Fig. 2.6). We could not discover any direct significant effect of livestock species, stocking density or distance from the freshwater source. The interaction, however, between livestock species and distance from the freshwater source was significant. This significant interaction effect indicates that cattle and horses distributed differently with respect to the distance to the freshwater source (Fig. 2.6). Cattle showed a grazing gradient, as expected, while horses were spread more evenly over the available area.



						Clustered			Random			Dispersed		
Livestock	Density	Block	NN ratio	Z score	p value	0.001 -2.58	0.05 -1.90	0.1 -1.65				0.1 1.65	0.05 1.96	0.01 2.58
Cattle	1.0	2	0.735	-3.656	0.000	▓								
Cattle	1.0	1	0.776	-3.178	0.001	▓								
Cattle	0.5	2	0.874	-1.754	0.079			▓						
Cattle	0.5	1	0.777	-3.158	0.002	▓								
Horses	1.0	2	0.954	-0.637	0.524					░				
Horses	1.0	1	1.002	0.023	0.981					░				
Horses	0.5	2	0.947	0.750	0.453					░				
Horses	0.5	1	1.151	2.145	0.032									░

Figure 2.5 Average nearest-neighbour distance between positions of livestock groups obtained by pooling all observations from all observation sessions. In three cases, the cattle had a highly significant clustered distribution (negative Z score, P-value <0.001), whereas horses were randomly distributed.

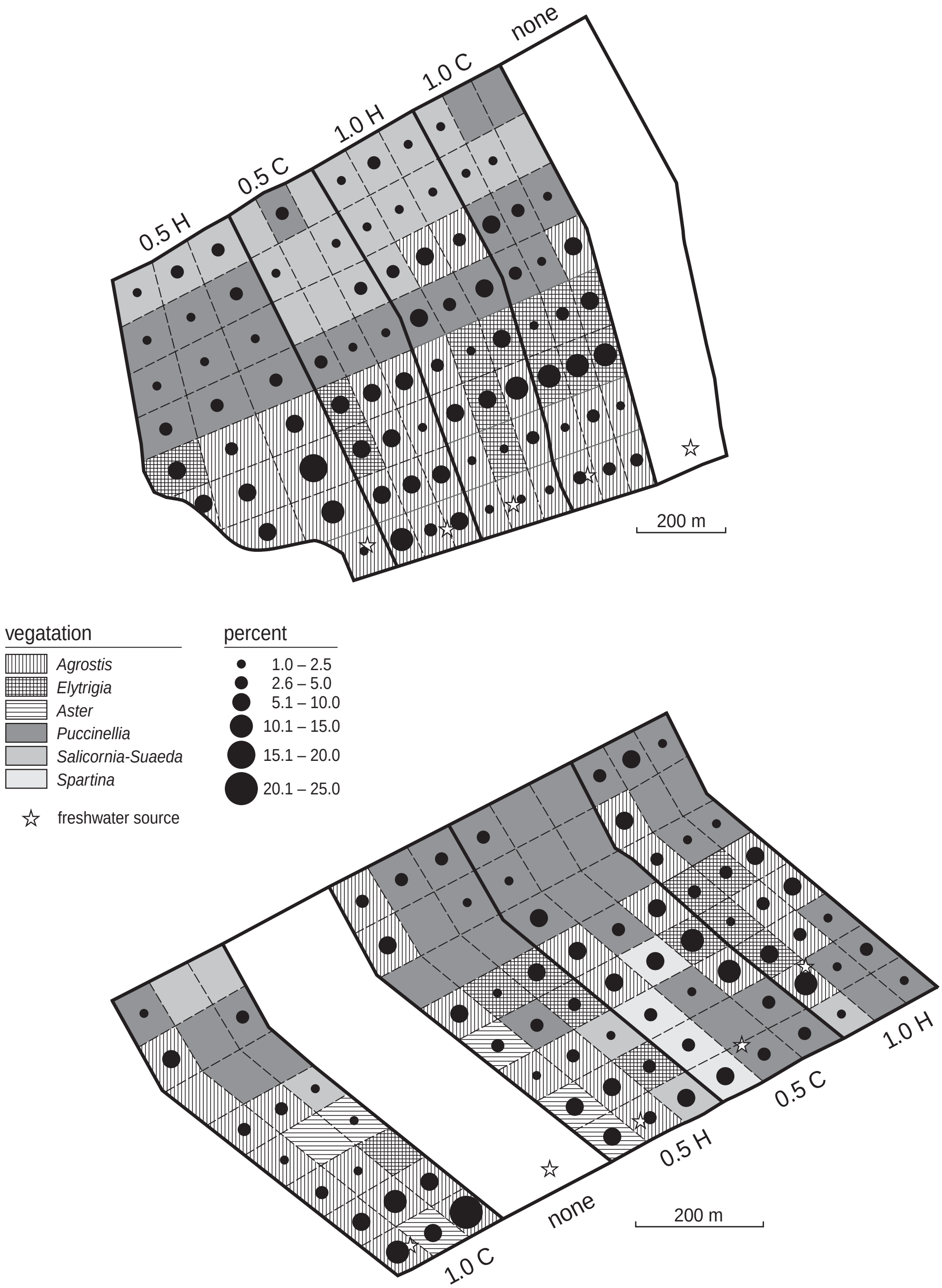


Figure 2.6 Spatial distribution of animals (% time spent per grid cell) including vegetation type. Cattle seemed to prefer high-marsh vegetation types (*Agrostis* and *Elytrigia*) and stayed close to the freshwater source. Horses spent more time in low-marsh types (*Puccinellia*), and were spread more over the entire available area.

Discussion

Behavioural differences were found between livestock species and between stocking densities with respect to diet choice, activity and spatial distribution. These differences were likely due to physiological and morphological differences between cattle (ruminants) and horses (hind-gut fermenters).

Diet choice

Despite the generally high overlap, diet choice of horses and cattle clearly differed. Fibre content seemed to be an important factor determining these differences. While horses are better able to tolerate high-fibre forage, cattle are more selective for forage with lower fibre content (*e.g.* Gordon 1989). In this study, horses grazed more often on *Puccinellia maritima*, which had a relatively high NDF content (64.4% DM), whereas cattle grazed more frequently on *Aster tripolium*, which had a much lower NDF content (43.3% DM). *Puccinellia maritima* was also found to be avoided by cattle in an earlier study on the island of Schiermonnikoog (Bakker 1989). Average fibre content of the diet of horses was higher than that of cattle, as expected. In addition, horses are less able to tolerate secondary metabolites than cattle (Krysl et al. 1984, Menard et al. 2002). These secondary metabolites are more common in dicotyledonous plants. Thus, the presence of secondary metabolites might be a reason for horses to avoid these plants. No information is available, however, on the amount of secondary components in dicotyledonous plants in the study area. Analysis did not indicate any effect of any other mineral component (data not shown). This suggests that horses and cattle were not limited by the analysed nutrients, or that differences between food plants were too small for animals to discriminate (Crawley 1983). With respect to vegetation types, the preference of the animals for certain types could not be explained only by their abundance (Fig. 2.4CD). When comparing different stocking densities, we found a tendency for animals at higher densities to include more food plants in their diet that were avoided at lower densities. This shift might be caused by depletion of more palatable plant species at higher stocking densities (Crawley 1983, Augustine and McNaughton 1998). Interference between animals has also been found to result in animals being less selective at higher densities, even when preferred species were abundant (Crawley 1983). Dumont et al. (2007a) found, in a study comparing different stocking densities of sheep and cattle, that differences in diet composition observed between densities were not the consequence of differences in diet choice but could be directly related to differences in plant availability. However, the study only differentiated between grasses, legumes and forbs, and between short and tall vegetation, and did not investigate the preference for single plant species. We can conclude that there are differences in the diet choice between livestock species and stocking densities. These differences are probably caused by the horses' ability to tolerate food plants with higher fibre content and the depletion of preferred food plants at higher stocking densities.

Activity

Horses spent a greater part of the day foraging than cattle because of the higher amount of low quality forage in their diet. Additionally horses were more active; covering greater distances over the area. Horses require more time foraging because hind-gut fermenters are less efficient in extracting nutrients from their forage compared to ruminants (Duncan et al. 1990). Thus, horses are forced to spend more time grazing. These longer grazing periods also cause horses to travel longer distances compared to cattle. Cattle in contrast to horses spend a large part of their time ruminating and during these periods only travel very short distances or remain in the same position. Our results are supported by other studies, which found horses and other equids to forage 50% longer than ruminants such as cattle (Duncan et al. 1990, Menard et al. 2002). The daily food intake in a study in the Camargue was 63% higher for horses (Menard et al. 2002). As a result of the higher activity of horses, Mandema et al. (2013) found a higher probability of artificial bird nests being trampled in horse-grazed compared to cattle-grazed treatments in the same experimental setup used in this study.

Spatial distribution

The results of a generally higher activity of horses are consistent with the results of the spatial distribution of the animals. We found horses to be distributed more randomly over the marsh, whereas cattle tended to be more clustered and remained longer at the same spot. This behaviour can be explained by the physiological differences between their digestive systems, which force horses to spend more time grazing. Distance to the freshwater source plays an important role in explaining the spatial distribution of cattle. Cattle were found, in this study, to show a grazing gradient and spent more time close to the freshwater source. This finding is in line with results of Esselink et al. (2002). Also Mandema et al. (2013) observed artificial bird nests to have a higher probability of being trampled close to the freshwater source. The distribution of horses, however, appeared not to be affected by the distance to the freshwater source, and horses utilized the available area more randomly. The horses' spatial distribution might be caused by other behaviour such as the avoidance of areas with a high number of biting insects (Duncan 1983). Cattle might be less affected by biting insects as they lie down to ruminate for parts of day, and as summarized by Hart (1992), lying down is also a mechanism animals use to avoid parasites. However, we observed horses to move to the low marsh even in cold weather when the number of biting insects was generally low (Nolte, pers. observation).

The spatial distribution of the animals was mainly explained by vegetation type, with both livestock species preferring *Agrostis* and *Elytrigia* types. Similar behaviour was found by Loucougaray et al. (2004). They showed that horses and cattle were highly selective between the three different available vegetation types dependent on their nutritional value. The interaction of livestock species and vegetation was not significant in our model, which suggests that horses and cattle did not differ in their main choice of vegetation type. We did, however, find that horses mostly used the *Elytrigia*-type for grazing (93% grazing behaviour of encounters in *Elytrigia* type; N = 231), whereas cattle used these areas more for resting and ruminating (34% grazing behaviour of encounters in *Elytrigia* type; N = 248), probably because these areas are situated at a higher elevation and are thus dry. This would explain why cattle spent a large part of the day in an area with low quality food plants (NDF of *Elytrigia repens*, 68.07% DM, and *Elytrigia atherica*, 62.55% DM).

We conclude that both livestock species at both stocking densities mainly preferred to be in *Agrostis*- and *Elytrigia*-type vegetation. We also found a grazing gradient for cattle, which suggests that horses spent more time in the areas further away from the freshwater source in the low marsh, whereas cattle concentrated around the freshwater source. Unfortunately, the gradient to the freshwater source was correlated with the distribution of the vegetation types and thus, it is not possible to distinguish whether animals stayed in the high marsh because of a preference for the vegetation type or proximity to the freshwater source. Furthermore, we do not know whether horses went to the low marsh zone specifically to forage in a preferred vegetation type, or whether they went to the low marsh for some other reasons and then consumed the dominant plant species because it was present there. For example, one of the reasons explaining the distribution of horses in a study in the Camargue was the abundance of biting flies (Duncan 1983). We did not measure the abundance of biting flies but did observe horses to spend the most time in the low marsh even when weather conditions were unfavourable for biting insects.

A limitation of our study might be missing observations during the night but these were technically difficult to perform (Dumont et al. 2007a). A study on the grazing behaviour of cattle showed that grazing at night only represented 10% of the total daily eating time (Rutter et al. 2004) and can thus be neglected. Grazing at night, however, is known to play an important role for horses (*e.g.* Boyd et al. 1988). In a study by Berger et al. (1999), activity of Przewalski horses was higher during night time only on hot summer days in July. Thus, the differences we found in activity between horses and cattle would only be strengthened if night grazing would have been included.

Implications for management

The differences we found in diet choice, activity and spatial distribution of horses and cattle are likely to have differential effects on the ecosystem. Firstly, we expect preferred food plants to be at greater risk of damage through defoliation. Secondly, the higher activity and grazing intensity in horse-grazed paddocks are likely to result in a higher pressure on all plant species compared to cattle grazing (Holmes 1980). The local grazing intensity is also very different and might lead to ungrazed patches in the low marsh of the cattle-grazed area. This will not only affect plants but also ground-breeding birds, for example, which were found to have a lower nest-trampling risk in cattle-grazed areas and further away from the freshwater source in the same study area (Mandema et al. 2013). Both distribution and species composition of plant communities will also be affected by the different grazing regimes over the long term. This study provides a baseline for connecting a thorough knowledge of the different behaviour of horses and cattle under different stocking densities as a cause for changes observed in the ecosystem. Based on further research, the choice of livestock should be considered carefully to reach the desired outcome of nature conservation policies. If the area should be grazed evenly, with removal of low-quality plant species as a goal, our results lead to a recommendation of horses. If the goal is also to provide undisturbed refuges for other organisms, such as ground-breeding birds, cattle would be recommended. The recommended stocking density depends on the grassland productivity and its status. If late-successional stages dominate the area or if the area has a high productivity, a slightly higher but still intermediate stocking density would be recommended. These general results are likely to be transferable to other grassland types, although it should be taken into account that stocking densities need to be adapted for grasslands of different productivity (Bakker et al. 2006).

Acknowledgements

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Chapter three

3

Flower production of *Aster tripolium* is affected by behavioural differences in livestock species and stocking densities – The role of activity and selectivity

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Abstract

Semi-natural grasslands are an important habitat for endangered plant and animal species. In grasslands low-intensity livestock grazing is frequently applied as a tool for nature conservation. We aim to investigate how different livestock species in various densities influence the state and flower production of a single plant species by selective defoliation and/or trampling. We hypothesized that (1) moderate stocking densities would cause more damage than low, and that (2) horses would cause more damage than cattle due to their higher activity. The experiment took place in a salt marsh in The Netherlands where grazing treatments with horses and cattle in two stocking densities were installed. Damage to individual *Aster tripolium* plants and number of flowerheads were recorded at the end of the grazing season in late September. We found (1) more damage and fewer flowerheads in moderate stocking densities compared low densities. However, a reduction of flowerheads by higher stocking densities was less clear with cattle. No clear difference (2) between livestock species was found, due to opposite trends in moderate and low densities. At low stocking densities, cattle caused more damage by selective defoliation. At moderate densities, horses caused more damage, because of their higher mobility which led to damage by trampling. We conclude that the response of *Aster* to grazing is strongly affected by behavioural differences between livestock species. Grazing experiments and management schemes for semi-natural grasslands should therefore not only consider stocking densities, but also livestock species to reach desired conservation goals.

Introduction

Semi-natural grasslands have been recognized as important for the conservation of rare and endangered species of plants and animals (Metera et al. 2010). Many grasslands which were traditionally used for livestock grazing are now abandoned, because their exploitation is no longer economically feasible for farmers (*e.g.* Poschlod and WallisDeVries 2002). After abandonment, succession generally leads to an increase of tall-growing plant species, the disappearance of rare species, and a decrease in biodiversity (Metera et al. 2010). To maintain these species-rich habitats, livestock grazing has been applied successfully as a management tool to slow down succession by reducing the expansion of tall-growing species (Bos et al. 2002). Effects of livestock grazing on the ecosystem have mainly been studied either on an area level by mapping plant communities, or on the level of plant communities by recording permanent plots (*e.g.* Bakker et al. 2003). So far, studies on the fecundity (or performance) of individual species as a response to grazing are limited (but see Damhoureyeh and Hartnett 2002, Reece et al. 2004, Wu et al. 2010, Axelsson and Stenberg 2012), and were mostly performed where the protection of a single species was the study aim (*e.g.* Mysterud and Østbye 2004, Pisanu et al. 2012). Yet, single plant species may be of great importance for a large number of animal species in an ecosystem context (*e.g.* Machado and Sazima 2008, Watson and Herring 2012). These different animal species occupy and use various parts of the plant. Herbivorous insects, for example, feed on different parts of the plants like leaves and stems, while pollinators are flower visitors (Meyer et al. 1995). Meanwhile the production of flowers is likely to be reduced or inhibited by livestock grazing (Kiehl et al. 1996, Piqueras 1999). Therefore the effect of livestock grazing on vegetation should be investigated not only on the basis of plant species presence and absence, but also the plants performance should be taken into account.

The choice of livestock species and stocking density for nature management schemes should be made carefully, as various livestock species and densities are likely to affect the state and phenology of the plant differently. However, most studies only investigate the influence of different stocking densities (*e.g.* Evju et al. 2011) and found a reduction of flowers in higher stocking densities (Kiehl et al. 1996). Yet, because of their anatomy and physiology, animals of different herbivore species are likely to vary in factors such as diet composition, food intake and spatial distribution. Horses, for example, were found to include a higher percentage of high-fibre forage such as fibrous grasses in their diet (Gordon 1989, Duncan et al. 1990, Menard et al. 2002). Additionally, horses were found to have a higher general food intake and mobility in comparison to cattle (*e.g.* Duncan et al. 1990, Menard et al. 2002). The mobility of animals might also influence their spatial distribution in addition to other factors such as the availability of resources, *e.g.* freshwater. With decreasing distance to the freshwater source, the local grazing intensity has been found to decrease both in systems with wild herbivores (*e.g.* Hopcraft et al. 2012) and domestic animals (*e.g.* Nash et al 1999). This decrease in local grazing intensity leads to an increase in canopy height with increasing distance to the freshwater source (Adler and Hall 2005). A study by Bakker et al. (chapter 5) shows the herbivore density to affect the distance up to which herbivores influence canopy height. It is very likely, that livestock species also differ in their spatial distribution with respect to the freshwater source.

These behavioural differences are key factors in understanding how severely and in which way plants are damaged. The two main types of plant damage which may occur are (a) defoliation and (b) trampling. In this study we define defoliation as the removal of aboveground biomass by grazing. This may include the removal of leaves as well as stems and flowers. The occurrence of defoliation will mainly depend on the livestock's selectivity, while the occurrence of trampling mainly depends on the livestock's mobility. These two types of damage may have different effects on the plant's ability to compensate for the loss of biomass (McNaughton 1979, Crawley 1983, Paige and Whitham 1987) and to reproduce (Oom et al. 2008).

The aim of this study was to investigate the effect of both different livestock species and stocking densities on the target plant species *Aster tripolium* L., henceforth only called *Aster*. We conducted the experiment in a coastal salt marsh, with horses and cattle at two stocking densities each, and studied the response of the target species. *Aster* is a key species in the salt-marsh ecosystem and supports a wide variety of herbivorous and sometimes monophagous invertebrates compared to other salt-marsh plants (Meyer et al. 1995, Rickert 2011). Among these invertebrates are butterflies, flies, weevils, and leaf beetles, which compete with the livestock for this high quality plant species.

Aster was found to be negatively affected by higher sheep densities (Kiehl et al. 1996). Therefore we expect (H1) more damage and fewer flowers, as well as fewer individuals and flowers per square metre in moderate compared to low density treatments. The diet choice differed between horses and cattle in the study area (chapter 2), with cattle including a higher percentage of *Aster* in their diet and thus probably showing a higher selectivity for *Aster*. Yet, horses were found to have a much higher food intake (*e.g.* Duncan et al. 1990, Menard et al. 2002) and will thus probably consume a higher amount of *Aster* even without being selective. With respect to livestock species we therefore expect (H2) more damage and less flowers, and fewer individuals and flowers per square metre in the horse-grazed treatments. Furthermore we expect the spatial distribution of animals, and therefore the local grazing intensity, to be affected by the position of the freshwater source. Thus, (H3) the distance of plants to the freshwater source will have an effect on damage and number of flowers per individual, as well as the number of individuals and flowers per square metre. Because of the aforementioned differences in diet choice, food intake and mobility between livestock species we expect (H4) more damage by defoliation in the cattle-grazed compared to horse-grazed paddocks and more damage by trampling under moderate stocking densities compared to low stocking densities.

Materials and Methods

Grazing experiment

The study area 'Noord-Friesland Buitendijks' is situated on the northern mainland coast of The Netherlands (53°20'11", 5°43'40"). It is a temperate salt marsh and part of the UNESCO world heritage site Wadden Sea. Salt marshes are regularly inundated by sea water and are therefore dominated by plants which are able to tolerate high salt concentrations and water-logged soils. Most salt marshes show an elevation gradient (Adam 2002). This elevation gradient in combination with the amount of oxygen in the soil leads to a clear vegetation zonation in most marshes (*e.g.* Bockelmann and Neuhaus 1999, Davy et al. 2011), with halophytes in the low and frequently inundated areas and an increasing amount of glycophytes in the higher, seldom inundated areas (Bakker et al. 1985). However, under grazed conditions halophytes can also dominate the high marsh (Bakker et al. 1985).

Recently large parts of the study area have been acquired by the NGO 'It Fryske Gea' for nature conservation purposes. The salt marsh has evolved from coastal engineering, *i.e.* by enhancement of natural sedimentation processes by the construction of sedimentation fields with brushwood groynes (Dijkema et al. 2011). The area was previously grazed intensively (Esselink et al. 2009) and maintenance of the drainage ditches stopped in 2000 (van Duin et al. 2007) which led to the filling of the drainage ditches. The neglect of drainage ditches was found to generally decrease soil aeration and leads to an increase of halophytic species (Esselink et al. 2002).

In 2010 a large-scale grazing experiment with four different grazing treatments and an ungrazed control was installed in the area, consisting of five paddocks of approximately 11ha to study the short-term effects of grazing. Each paddock included plant communities of the three salt-marsh zones along an elevation gradient from the seaward pioneer zone, over the low marsh up to a landward high-marsh zone. A freshwater source was available in each paddock in the high marsh (Fig. 3.1). The following four grazing treatments were applied: grazing with horses in two densities (low 0.5 animal/ha, moderate 1.0 animal/ha), grazing with cattle in two densities (low 0.5 animal/ha, moderate 1.0 animal/ha) and a 1-year short-term ungrazed control. Grazing took place from May to October. The exact length of the grazing period varied between treatments (12 – 16 weeks) due to problems obtaining the livestock. The moderate density horses and low density cattle paddocks were both grazed for the full 16 weeks, while the moderate density cattle paddock experienced 15 weeks, and the low density horses area only 12 weeks of grazing.

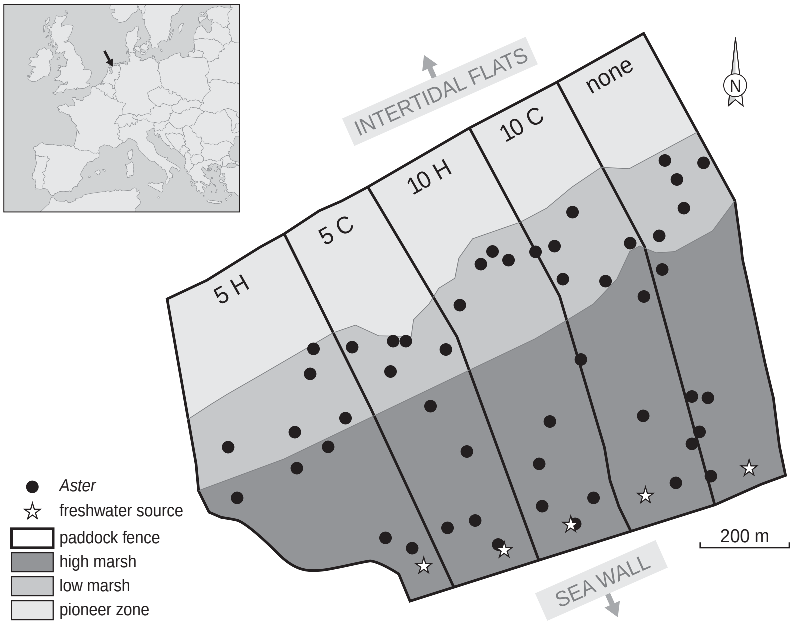

Figure 3.1 Experimental setup showing the position of the paddocks with their appointed grazing treatments (5H = low density horses, 5C = low density cattle, 10H = moderate density horses, 10C = moderate density cattle, none = one-year ungrazed) as well as the position of the *Aster* sampling locations (black dot) and the freshwater source (star).

Aster sampling locations

Aster tripolium L. is a perennial plant species (van der Wal and Herman 2012) common in salt-marshes, with slightly succulent leaves and a height of 5 – 90 cm (van der Meijden 2005). It is a common species of the low marsh and middle marsh, but under grazed conditions it is also very common in the high marsh (Bakker et al. 1985). *Aster* is able to tolerate waterlogged conditions with a redox potential as low as -100 mV (Davy et al. 2011), probably due to its aerenchyma, which was even found to increase when mycorrhizal fungi were absent (Scheloske et al. 2004).

In June 2010 we randomly positioned 50 sampling locations in the study area, with ten sampling locations in each grazing treatment (five in low-marsh zone and five in high-marsh zone). Marsh zone represents the distance to the freshwater source, as sampling locations in the high marsh are closer to the freshwater source than sampling locations in the low marsh. No sampling locations were placed in the pioneer zone, as *Aster* is not common in this zone. Coordinates were selected randomly using a vegetation map of the study area and the program ArcGIS 9. The centre of the sampling location was marked with a metal pin, which enabled us to find sampling locations with a metal detector. Within a radius of 5 m around the metal pin, 10 previously undamaged individuals of *Aster* were randomly selected, tagged and the initial height of the plant was measured as the distance from the ground to the highest expanded leaf. We used initial height as a variable as plants ability to produce flowers might strongly depend on their initial size in spring (Crawley 1983). In two cases, we found less than 20 individuals at the random sampling location, therefore the sampling location was rejected and another random sampling location used. In September, we estimated the damage to the plant in per cent visually by using classes of 5% steps (Piqueras 1999) (Fig. 3.2). One hundred per cent damage represented dead individuals. Different damage types (defoliation, trampling, both defoliation and trampling, unknown) were distinguished and recorded. Damage was assumed to be caused by defoliation if biomass (leaves, stem and/or flowers) was removed and bite-marks were visible, and by trampling if stems or leaves were bent down or snapped off without removal of biomass (Fig. 3.2). Additionally, the number of flowerheads per individual, henceforth referred to as 'flowers', was recorded. At the same time we counted the number of individuals within one square metre for every sampling location.

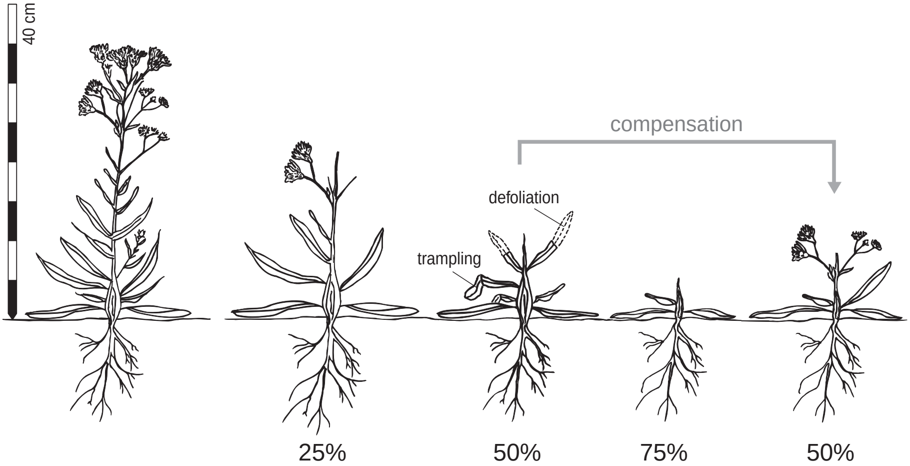

Figure 3.2 Comparison of a healthy *Aster* plant with three damaged individuals and an individual showing compensatory growth. The damage of each plant was estimated visually in percentages. Two different types of damage (defoliation, trampling) were distinguished if possible. Plants damaged early in the season were sometimes able to compensate for the loss of flower buds as indicated in the right plant.

Statistical analysis

In order to correct for the differences in the length of the grazing period per treatment, a correction factor was applied on the percentage of damage and the number of flowers (Eqs 1 and 2). Thereafter, the following analyses were performed on the corrected values. The damage values were classified in the same way after correction.

$$\textit{Corrected damage}\ [\%] = \frac{\textit{Damage}\ [\%]}{\left(\frac{\textit{weeks}}{\textit{total weeks}}\right)} \qquad \text{(Eq. 1)}$$

$$\textit{Corrected flowers} = \textit{number of flowers} * \left(\frac{\textit{weeks}}{\textit{total weeks}}\right) \qquad \text{(Eq. 2)}$$

We applied generalized estimation equation models (GEE) to analyse (a) the effect of grazing in general compared to the ungrazed control, and (b) the effect of the four grazing treatments (0.5 cattle, 1.0 cattle, 0.5 horses, 1.0 horses) on damage and number of flowers (Liang and Zeger 1986). We had to perform two analyses, because the ungrazed control could not be included in a model using livestock species and stocking density as factors, as *e.g.* the combination between the density 0 (ungrazed treatment) and the livestock species horses was not available in our experimental design. Therefore the general effect of grazing was studied by randomly selecting one hundred individuals out of the total of 400 measured individuals of the sampling locations in the four grazing treatments (0.5 cattle, 1.0 cattle, 0.5 horses, 1.0 horses) and comparing them to the one hundred individuals which were ungrazed. Whether an individual was from the ungrazed or one of the four grazed treatments was indicated by creating the categorical variable 'grazing'. The random selection for individuals in this analysis was only restricted by selecting an equal number of individuals from the high and low marsh as we expected the distance of the individual to the freshwater source to have on effect on the chance for being damaged.

In all GEE models the sampling location ID was used as a grouping variable and the exchangeable correlation structure was chosen. There is no reliable way to perform a post-hoc test on GEE models. Model selection was performed by dropping each term in turn and comparing the resulting models with the full model using ANOVA. The least significant term was dropped and the procedure repeated. All GEEs were performed using the package 'geepack' (Højsgaard et al. 2006) for the Statistical Software R version 2.15.0 (R Development Core Team 2012).

The first two analyses were performed to investigate which factors influence the amount of damage. To analyse the effect of grazing in general compared to the ungrazed control we constructed a GEE model including damage as a response variable and the term 'grazing'. To compare the effect of the four different grazing treatments (0.5 cattle, 1.0 cattle, 0.5 horses, 1.0 horses) the second model included (H1) stocking density, (H2) livestock species and (H3) marsh zone as explanatory variables. All two-way interaction effects were included. We used a value of 100% as the highest possible damage as an offset variable.

To answer the question how the grazing treatments influence the number of flowers per individual, we performed two more GEE models. Dead individuals were included into this analysis with zero flowers. The first model compares the ungrazed treatment to all grazed treatments by including the categorical term grazing as the predictor for the number of flowers. The marsh zone was included to investigate whether the zone has a direct effect on the number of flowers. The second model comparing the different treatments then included (H1) stocking density, (H2) livestock species, (H3) marsh zone and the height of the plant at first measurement (initial height), as well as all two-way interaction effects.

To see whether grazing leads to a reduced number of *Aster* individuals per square metre we built two generalized linear models (GLM) assuming a Poisson distribution (Zuur et al. 2009). The first model included the number of individuals per square metre as the output variable and the categorical variable grazing as the predictor. Instead of grazing, the second model included (H1) livestock species and (H2) stocking density to investigate the influence of the different grazing treatments. Another two GLM models including the same factors were used to analyse the influence of grazing and of the different treatments on the number of flowers per square metre. The number of flowers per square metre was estimated by multiplying the number of individual *Aster* plants per square metre with the mean number of flowers of living plants in the plot.

The question whether the type of damage (H4) differs between livestock species and stocking densities was analysed by using two separate analyses for defoliation and trampling as damage type. This procedure was necessary because a large proportion of the plants showed signs of both defoliation and trampling. For the first analysis, we combined the individuals that showed defoliation signs only with the ones with both types of damage, and accordingly for the second analysis, the trampled individuals were combined with the ones that had been both trampled and grazed. The predicted variable is the probability with which an individual is damaged by each of the two damage types. Both full GEE models included livestock species and stocking density, as well as the interaction term.

Results

Damage of plants

We found, on the one hand, that stocking density (H1) had a strong effect on damage (Table 3.1) with generally more damage in moderate density treatments (Fig. 3.3). Livestock species (H2) on the other hand, did not have any significant effect. When comparing grazed and ungrazed treatments the effect of grazing on the amount of damage in comparison to the ungrazed control was very high, with very little damage occurring in the ungrazed control, where the damage was probably caused by defoliation by hare. The model showed grazing to be a highly significant predictor of damage. The final model comparing the different grazing treatments included

Table 3.1 Model results of the GEEs comparing the influence of grazing and the different treatments on damage and the number of flowers and comparing the occurrence of damage types between treatments. Model results of GLMs comparing the number of plants and the number of flowers per square metre between treatments. A p-value is given if results were significant, 'n.s.' indicates non-significant results and '-' indicates factors which were not included in the full model.

	Damage		Flowers		Individual plants / sqm		Flowers / sqm		Defoliation		Trampling	
	χ^2	P	χ^2	P	z	P	z	P	χ^2	P	χ^2	P
grazed vs. ungrazed:												
grazing	40	<0.001	49.2	<0.001	-2,433	<0.05	-80,28	<0.001	-	-	-	-
marsh zone	-	-	6.9	<0.01	-	-	-	-	-	-	-	-
grazing * marsh zone	-	-	4.1	<0.05	-	-	-	-	-	-	-	-
treatments:												
stocking density	27.53	<0.001	4.3	<0.05	2,514	<0.05	45,086	<0.001	n.s.	n.s.	8.03	<0.01
livestock species	n.s.	n.s.	7.3	<0.01	n.s.	n.s.	5,122	<0.001	11.9	<0.001	n.s.	n.s.
marsh zone	5.07	<0.05	n.s.	n.s.	-	-	-	-	-	-	-	-
livestock species * stocking density	3.06	0.080	4.9	<0.05	-2,528	<0.05	-34,429	<0.001	n.s.	n.s.	n.s.	n.s.
livestock species * marsh zone	n.s.	n.s.	n.s.	n.s.	-	-	-	-	-	-	-	-
stocking density * marsh zone	5.95	< 0.05	n.s.	n.s.	-	-	-	-	-	-	-	-
initial height	-	-	85.8	< 0.001	-	-	-	-	-	-	-	-

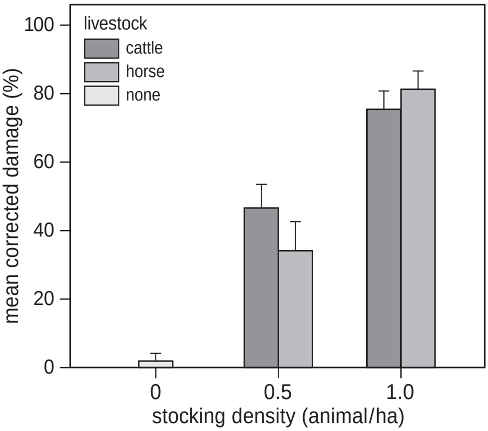

Figure 3.3 The mean corrected damage in the ungrazed control and under different grazing treatments. Different livestock species are represented by different coloured bars in the graph. Error bars indicate standard error.

stocking density and salt-marsh zone (H3), as well as the interaction term stocking density*salt-marsh zone (Fig. 3.4). Under low stocking densities more damage occurred in the high marsh than in the low marsh. The amount of damage in the low marsh, however, increased under moderate densities compared to lower densities. The interaction term livestock species*stocking density was not significant and thus dropped from the model. We found, however, the following trend. Cattle seem to cause more damage than horses in low density treatments, whereas this pattern is reversed in the moderate density treatments. Here horses caused slightly more damage.

Flowers per plant

The number of flowers per individual plant was found to be mainly influenced by initial height, which is the height of the plant in spring, but also by livestock species (H1) and stocking density (H2). We found a considerably higher number of flowers per plant in the ungrazed treatment compared to all others (Fig. 3.5). This finding was confirmed by the model, which showed a significant negative effect of grazing on the number of flowers (Table 3.1). We also found fewer flowers in the low marsh compared to the high marsh (H3). There is a significant interaction effect of grazing and zone. We found a stronger reduction of flowers by grazing in the high marsh compared to the low marsh.

The second model comparing the treatment effect on the number of flowers per individual plant confirmed a significant effect of stocking density (H1), livestock species (H2), initial height of the plant and the interaction term livestock species*stocking density (Table 3.1). When comparing the livestock species, we found

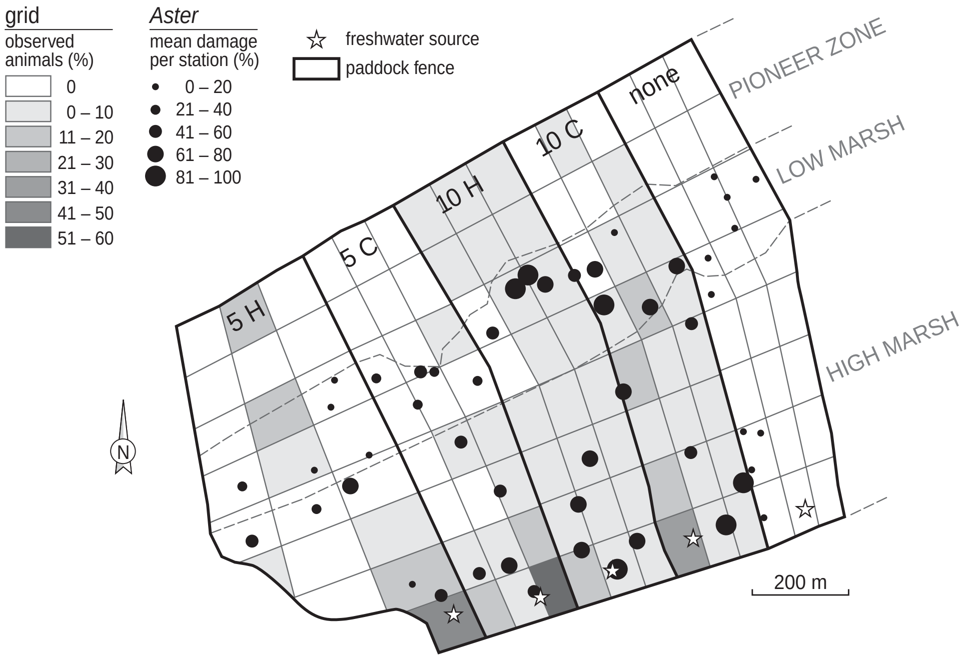

Figure 3.4 The map shows the effect of salt marsh zone on the amount of damage. The size of dots represents the mean corrected damage in per cent per sampling location. The colours indicate the average spatial distribution of animals during focal observations (chapter 2). 5H = low density horses, 5C = low density cattle, 10H = moderate density horses, 10C = moderate density cattle, none = one-year ungrazed

a clear effect in low densities with more flowers per individual plant in horse- compared to cattle grazed treatments (Fig. 3.5). Yet, in moderate densities no difference between livestock species could be detected. When comparing the stocking densities, we found a clear effect of fewer flowers in moderate densities in horse-grazed treatments, while in the cattle-grazed treatments we found a similar number of flowers per individual in both stocking densities.

Number of plants and flowers per square metre

Finally we investigated whether grazing and the different treatments have an effect on the number of individual *Aster* plants and the number of flowers per square metre. Grazing was found to reduce the number of individual plants and flowers per square metre significantly (Table 3.1). When comparing the treatments with respect to the number of plants per square metre we found that stocking density and the interaction term livestock species*stocking density was significant (Fig. 3.6A.). We found fewer individuals in moderate densities, but the livestock species had differential effects under different densities. In the GLM comparing the number of flowers

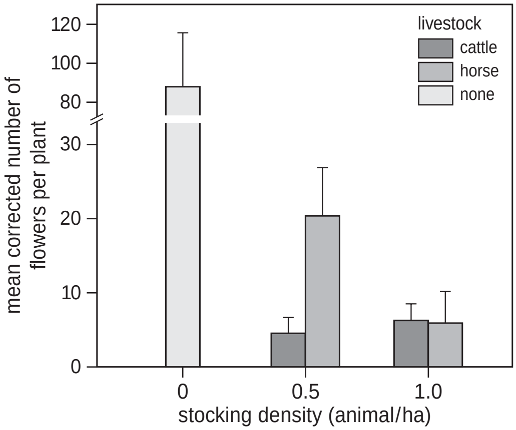

Figure 3.5 The mean number of flowers per individual plant in the ungrazed control and under different grazing treatments. Different livestock species are represented by different coloured bars in the graph. Error bars indicate standard error.

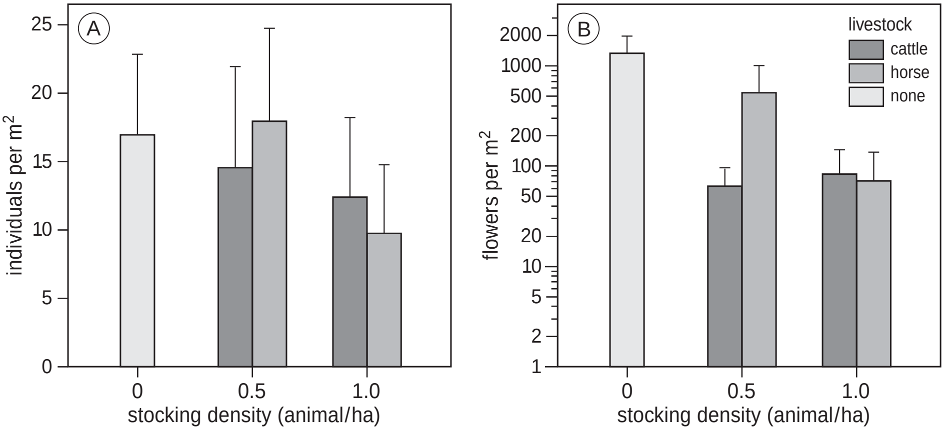

Figure 3.6 The impact of different grazing treatments on (**A**) the number of individuals per square metre and (**B**) the number of flowers per square metre. Different livestock species are represented by different coloured bars in the graph. Error bars indicate standard error.

per square metre between treatments all terms were significant. We found a higher number of flowers per square metre especially in the low density horse-grazed treatment (Fig. 3.6B).

Damage types

The results of the comparison of the proportion of damage types (H4) between treatments showed livestock species to be a significant predictor of defoliation and

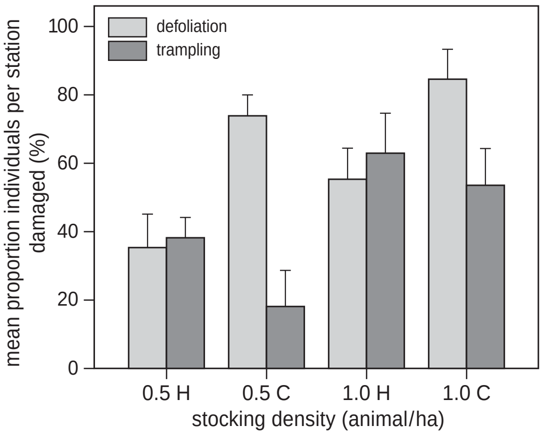

Figure 3.7 The proportion of damage by defoliation (light grey bar) or trampling (dark grey bar) as found in the different grazing treatments (0.5H = low density horses, 0.5C = low density cattle, 1.0H = moderate density horses, 1.0C = moderate density cattle). Error bars indicate standard error.

stocking density to be a significant predictor of trampling (Table 3.1). There was a higher proportion of individuals per sampling location showing signs of defoliation in the cattle-grazed treatments compared to the horse-grazed treatments in both densities (Fig. 3.7). The result for trampling as damage type was less clear. In the low densities, there seems to be more trampling in the horse-grazed treatment, whereas we found no strong trend in the moderate densities.

Discussion

We saw that grazing by two livestock species in different stocking densities might lead to contrasting results with respect to the effects on *Aster*. In general, grazing by livestock drastically increases damage of *Aster* plants and reduces the number of flowers per plant (Kiehl et al. 1996). Higher stocking densities cause generally more damage, although this does not always lead to a smaller number of flowers as seen in the cattle-grazed treatments. In higher densities, the more random effect of trampling plays a more important role and thus differences between livestock species become smaller. However, the effect of livestock species on damage and number of flowers per individual varied in different stocking densities. This is related to the varying importance of selective defoliation and more random trampling. Selective defoliation plays an important role in lower stocking densities, as it causes more damage than random trampling of plants, leading to the observed differences between cattle and horses.

Stocking density

The stocking density (H1) had a strong impact on the amount of damage, but a weaker effect on the number of flowers per individual plant and the number of individuals per square metre. We found more damage and fewer flowers with moderate stocking densities, as previously described for sheep grazing (Kiehl et al. 1996). This is also in line with results of a study on P*olygonum viviparum*, where stem height and aboveground mass of plants decreased significantly with increasing grazing pressure (Zhu et al. 2008). Contrastingly, Evju et al. (2011) found no effect of increased sheep densities on the population dynamics of the herb *Geranium sylvaticum*. In our study on *Aster* the reduction of flowers per individual plant and per square metre at moderate densities was clearly found in horse-grazed treatments. In cattle-grazed treatments, however, moderate stocking densities did not lead to a reduction of flowers. This outcome might be explained by the observation that cattle often damage a plant, but these plants seldom died (plant mortality in moderate density horses 64% versus moderate density cattle 10%). Plants that were damaged by cattle are most often damaged by defoliation as cattle selectively only removed parts of the plants. Thus, if defoliation is not severe and not repeated too often (Martínez-Ramos et al. 2009), compensatory growth and late production of flowers is still possible (Crawley 1983) (Fig. 3.2). Compensatory growth was also observed in some (*e.g.* Huhta et al. 2009, Olejniczak 2011), but not all studies (*e.g.* Li et al. 2004). To explain this discrepancy the limiting resource model was proposed (Wise and Abrahamson 2005) and found to be a good predictor of plants reactions to herbivory (Wise and Abrahamson 2007). The model takes into account whether the studied resource (focal resource) is limiting plant fitness, and whether the herbivory primarily affects this resource. In our case, the primary resource is the photosynthetic and/or reproductive plant tissue and the herbivores are affecting this resource by reducing it through defoliation or trampling. The model accurately predicts a higher tolerance of plants in the low stress environment (low herbivore density) which results in a higher number of flowers per plant in the low density compared to the moderate density horse grazed paddocks. However, in the cattle grazed treatments the photosynthetic and/or reproductive plant tissue seems not to be the primary resource, and therefore the removal does not lead to a reduced tolerance in moderate densities.

Livestock species

Livestock species (H2) had no significant effect on the damage per individual plant. A comparison of the impact of the different livestock species leads to opposite trends in moderate and low stocking densities. In low densities cattle and in moderate densities horses cause more damage and reduce the number of individuals per square metre stronger. Especially in the low density treatments *Aster* forms a larger part of the cattle diet compared to horses (chapter 2). This implies that cattle selectively forage on *Aster* and cause damage by defoliation. Indeed we found more damage by defoliation in the cattle-grazed treatments. In moderate densities, we found slightly less damage in cattle-grazed treatments compared to the horse grazed treatment of the same density. This might be explained by the increasing importance of random damage by trampling. Indeed, trampling damage occurred significantly more often in moderate density grazing. In a study on the trampling of artificial nests in the same study area horses were found to trample significantly more nests than cattle (Mandema et al. 2013). This result is in line with our findings as the selective damage by defoliation in low densities does not play a role in a study on artificial nests.

In contrast to the damage we found a significant effect of livestock species on the number of flowers per individual and per square metre. The higher number of flowers especially in the low density horse-grazed treatment is mainly explained by the observed lesser damage in this treatment. We conclude that the higher damage in the cattle grazed treatment was caused by the importance of damage by selective defoliation by cattle in low densities. In the moderate densities there was only a very small difference between the livestock species. Slightly more flowers per individual were produced in cattle-grazed treatments.

Salt-marsh zone/Distance to freshwater source

The results also show that the position of the plant influences its probability of being damaged (H3). We expected parts of the study area to experience different grazing pressures as animals concentrate around freshwater sources (*e.g.* Nash et al 1999). A study of the spatial distribution of the animals in the paddocks showed that compared to cattle, horses spent more time in the low marsh, and thus at a greater distance from the freshwater source. Additionally it was found that animals in moderate densities also spent more time in the lower marsh (Fig. 3.4) (chapter 2). The spatial distribution of the animals thus explains the higher amount of damage in the low marsh in horses compared to cattle and in moderate compared to low stocking densities. An experiment with extensive sheep grazing showed similar results with more damage in the low marsh in higher stocking densities (Kiehl et al. 1996).

Whether the salt marsh zone is a useful factor to represent the distance to the freshwater source is debatable. It should be remembered, that the gradient of decreasing grazing pressure with increasing distance to the freshwater source, which was also found in other studies (*e.g.* Nash et al 1999, Kiehl et al. 1996), is highly correlated with the most important abiotic factor for plants, the elevation gradient. This elevation gradient probably has an effect on *Aster* fitness and densities. As *Aster* is primarily a low-marsh plant, we would expect a reduced fitness of the plant in the high marsh. However, when comparing the number of flowers per individual in the ungrazed control treatments we find more flowers per individual in the high marsh (mean 127; SD 173.7) and fewer flowers per individual in the low marsh (49; SD 68.3). In the combined grazed treatments there is no, difference between the mean number of flowers per individual between marsh zones. In comparison to the ungrazed marsh we can, however, conclude that grazing reduced the number of flowers in the high marsh to a greater extent than in the low marsh as was expected based on the grazing-gradient hypothesis. The density of *Aster* was found to be higher in the low (mean 23 individuals/m^2; SD 6) compared to the high marsh (mean 11 individuals/m^2; SD 5) in the ungrazed treatment. It might be expected that the stochastic probability of being damaged is higher for plants in higher plant densities and thus in the low marsh. We found, however, the opposite with on average more damage in the high marsh (mean 78%; SD 28) than in the low marsh (mean 28%; SD 39). The mentioned differences between abiotic conditions and density between marsh zones could not explain the results in the two marsh zones and we therefore assume the zone to be a valid representative of the distance to the freshwater source and the grazing gradient.

Additionally, the number of flowers per individual is strongly related to the initial height of the plant in spring. Plants that were very small in spring are likely to have only a small number of flowers, whereas plants that were tall are able to produce a larger number of flowers. We found no interaction between the initial height and the livestock species or stocking density, which leads us to the conclusion that the animals do not differently affect certain plant sizes.

Effects of soil compaction

In this study we investigated the effect of direct biomass removal and trampling by herbivores. Trampling, however, can also have an indirect effect on plants via the compaction of soil which we did not include in this study. Grazing was found to decrease nitrogen mineralization, air filled pore space, and decomposer activity in comparison to a long term (37 year) ungrazed control in a salt marsh with clay soils (Schrama et al. 2013). The lack of oxygen in the soil might be a possible explanation why *Aster* as a low marsh plants is common in grazed high marsh areas (Bakker et al. 1985), where it is usually outcompeted by the tall grass *Elytrigia atherica* (Bakker et al. 2003). We are therefore concluding that *Aster* is generally well adapted to compacted soils and would expect soil oxygen content not to be a limiting resource in the sense of the limited resource model (Wise and Abrahamson 2007). Whether this is the case should also be tested in an experimental setup where the effects of defoliation and soil compaction are mimicked by *e.g.* clipping and manual compaction, and can thus be separated. This is not possible in an experiment with herbivores.

Effects on population dynamics

Although this study gives a good overview of the direct impact of different grazing treatments on the target species *Aster*, we are unable to draw any conclusions about how defoliation and lack of seeds influence long-term population dynamics. Already the number of individuals was affected by the treatments and we found differential effects of livestock species in different stocking densities. In low densities there were more individuals per square metre in horse grazed paddocks, while in moderate densities we found the opposite. In the future, the reduction of plant tissue in the study year is likely to prevent the plant from investing in storage organs. A study on the pseudo-annual herb *Trientalis europea* found that grazed individuals produced shorter stolons and smaller tubers (Piqueras 1999). This mechanism might lead to a reduced fitness in the next year (Piqueras 1999) as found for the perennial species *Sanicula europaea* L. (Gustafsson 2004). In contrast, Olejniczak (2011) found a higher root biomass in perennial plants were the apical buds were experimentally removed. A study on the perennial forb *Heteropappus altaicus* (Wu et al. 2010) found negative effects of clipping on the individual level (plant height, aboveground biomass, pollen production per floret), while the population level was effected positively (population density). The effect of grazing on the population dynamics of *Aster* is yet unclear, but a reduced survival and fitness by a reduction of storage organs and a reduction of flowers might over longer timescales lead to a strong reduction in densities of *Aster* in some treatments.

Implications for management

In the future management schemes, which try to accomplish the protection of single species, should take into account how the behaviour of different livestock species in varying densities can influence the target species. This study also shows that it is difficult to compare management schemes which only use the stocking density of grazing animals and not also the livestock species. The short-term ungrazed treatment seemed to be most beneficial for *Aster* in this study. The same recommendation is given by Kiehl et al. (1996). However, both studies only investigated population dynamics for one to four years. It is unlikely that an ungrazed treatment will be favourable for *Aster* on the long term. After longer time intervals the cessation of grazing in salt marshes generally leads to the spread of the competitive tall grass *Elytrigia atherica* (Bakker et al. 2003). Thus, it is very likely that a long-term ungrazed treatment will lead to the disappearance or strong reduction of *Aster*. An alternative might be rotational management schemes, where ungrazed years are followed by grazed years. In this way, the spread of species such as *Elytrigia atherica* is reduced, while target species like *Aster* are able to produce flowers and seeds in the ungrazed years. We would expect the results of this study to be applicable to other salt-marsh species which are selectively eaten by cattle such as *Triglochin maritimum* (chapter 2). In contrast, species such as *Cirsium* spec. which are avoided by cattle, but frequently included in the diet of horses, are likely to increase in abundance in cattle-, but not in horse-grazed treatments and in low rather than moderate densities.

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Chapter four

4

Effects of three years of experimental grazing on salt marsh vegetation - a progress report

Stefanie Nolte, Peter Esselink, Jan P. Bakker

Abstract

Artificially created mainland salt marshes are semi-natural grasslands which provide a habitat for many specialised plant and animal species and are therefore important for the conservation of biodiversity in north western Europe. In order to conserve plant-species richness in these areas, grazing with livestock in low stocking densities is frequently applied as a nature-management tool to prevent the spread of mono-specific late-successional stages. Although many studies dealt with the question which stocking density would be most beneficial for plant species richness, no consensus is reached. In addition to the effect of stocking density it is still unclear what effect different livestock species may have. Furthermore, alternative options such as grazing regimes in which fallow years are followed by years with livestock grazing need to be studied. To investigate the effect of different grazing treatments a grazing experiment was installed in a salt marsh in the area 'Noord-Friesland Buitendijks'. There the effect of two livestock species (horses and cattle) in two stocking densities (0.5 and 1.0 animal/ha) and a rotational treatment on plant species richness and abundance was investigated in permanent plots. The number of species per permanent plot was compared between treatments as a measure of plant-species richness. The effect of treatments on the species composition and species-composition change over time were investigated with multivariate analyses. Both the comparisons of plant-species richness and species composition did not differ significantly between treatments. Whether trends in the species composition change will lead to significant differences between treatments in the future should be further monitored to give recommendations for nature management.

Introduction

Salt marshes are important areas for the conservation of biodiversity in north Western Europe, as they harbour many specialised plant (Adam 2002) and animal species (Meyer et al. 1995, Olff et al. 1997). Salt marshes either established naturally, like many island marshes, or originate from man-made sedimentation fields (Bakker et al. 2002). In Europe, the latter are made of structures built to increase sedimentation and have a very long tradition of livestock grazing (Esselink et al. 2002). An extensive area of salt marshes is still used for agriculture today, but the area of abandoned salt marshes is increasing (Bakker et al. 1997). The main reasons for the abandonment of agricultural practices are firstly that grazing is not economically feasible anymore and secondly the establishment of nature conservation areas such as National Parks (Bakker et al. 2002). Especially in Germany, the installation of National Parks was followed by a stop of all human interference in 50% of these formerly intensively grazed areas to allow a natural succession to take place (Esselink et al. 2009). Yet, the natural succession of many salt marshes is known to lead to species-poor communities dominated by single plant species (Leendertse et al. 1997). Therefore, the installation of the National Parks in Germany in 1985 led to the question whether grazing should be continued in salt marshes in low stocking densities for nature conservation purposes to retard succession (Kiehl et al. 1996). Grazing is widely used as a tool in nature management of grasslands to increase plant species richness (Metera et al. 2010). The mechanisms by which grazing leads to an increased plant species richness are (1) promoting structural diversity through patch grazing (*e.g.* Rook et al. 2004, Bakker et al. 2003, Dumont et al. 2007a), (2) reducing light competition (*e.g.* Bakker et al. 2006) and (3) increasing colonization rate by the formation of gaps (*e.g.* Bakker et al. 2006). The effect of grazing on plant species richness is, however, not straightforward and depends on factors such as the productivity of the ecosystem (Olff and Ritchie 1998, Bakker et al. 2006). Moreover, comparisons are often made among grazed vs. ungrazed situations, without taking into account livestock species and stocking densities. The importance of stocking density has been investigated in both salt marshes (*e.g.* Andresen et al. 1990, Kiehl et al. 1996, Kleyer et al. 2003) and other grassland ecosystems (Metera et al. 2010). Low densities allow the livestock to be more selective and therefore create a mosaic of short and tall patches (Adler et al. 2001, Loucorgaray et al. 2004) thereby increasing the plant species richness (Olofsson et al. 2008). Differences between selectivity were also found between different livestock species (Scimone et al. 2007), thus possibly allowing differences in species richness. Hence, careful planning is needed to successfully use grazing as a management tool (Metera et al. 2010). Grazing experiments were installed to investigate the effects of sheep grazing with different stocking densities on plant species richness in salt marshes compared with cessation of grazing (Kiehl et al. 1996). Studies investigating the effect of cessation after nine, ten and eleven years found *Elytrigia atherica* to invade the high marsh which might lead to a future loss of species richness (Schröder et al. 2002, Gettner 2003, Kiehl et al. 2007). With respect to the effect of different stocking densities on species number Andresen et al. (1990) found species richness to be lower in high cattle stocking densities and recommend a density of 0.5 cattle/ha. Similar results were found in a study on the small island of Langeness, where the highest species richness was found in intermediate densities (0.6 cattle ha), while slightly lower numbers were found for both low densities (0.4 cattle/ha) and higher densities (1.3 cattle/ha) (Kleyer et al. 2003). In the low marsh of the grazing experiment at Hamburger Hallig, the strongest increase in species number was found in the moderate grazing density (0.75 sheep/ha) (Kiehl et al. 2007). In the high marsh, Kiehl et al. (2007) found species number to increase in all sheep stocking densities probably due to the seed input of grazing sensitive plants from adjacent ungrazed areas. In the same area, Rickert et al. (2012) found the highest plant species richness in low densities (1-2 sheep/ha) while an increasing density led to a decrease in species number. Therefore low grazing densities have been adopted as a strategy for nature management in salt marshes (Adam 2002), and are recommended by the Trilateral Monitoring Assessment Program (TMAP, Bakker et al. 2005). However, different studies recommend a variety of stocking densities (Andresen et al. 1990, Bakker et al. 2002, Kleyer et al. 2003). Additionally, the choice of livestock species for grazing management is often only based on fragmentary or anecdotal evidence (Rook et al. 2004), or a matter of tradition. Therefore the role different livestock species can play in salt-marsh management should be further investigated. To answer the question 'how to graze?' a grazing experiment is required which compares the effect of both different livestock species and stocking densities (Bakker et al. 2003).

Another possible option hardly taken into account in management schemes are rotational regimes, where years in which marshes are grazed by livestock are alternated with fallow years. This strategy might allow grazing sensitive target plants such as *Aster tripolium* to produce seeds in fallow years, while the expansion of competitive plants such as *Elytrigia atherica* is reduced in grazed years. To investigate the effects of different grazing treatments a grazing experiment was installed at the mainland coast of The Netherlands in 2010. The species composition in permanent plots was monitored to answer the following question with respect to the effects of a) different livestock species in two stocking densities and b) the effect of rotational grazing: 1) Do we find differences in plant species richness after three years of grazing?, 2) Do we find differences in species composition?, and 3) is there a temporal trend in the species composition change caused by different treatments?

Study area and methods

Study site

A large-scale grazing experiment comparing five different grazing treatments was established in 2010 (year 1) in a salt marsh in the study area 'Noord-Friesland Buitendijks' (NFB) situated at the mainland coast of the Netherlands (53°20'11", 5°43'40") (see also Mandema et al. 2013). The area is characterized by a distinct salt-marsh vegetation zonation caused by an elevation gradient from the low elevated and frequently flooded pioneer zone, over the low marsh to the higher elevated and seldom flooded high marsh. The pioneer zone is dominated by halophytic pioneer species such as *Salicornia europea* and *Suaeda maritima*. The low marsh is characterised by the grass *Puccinellia maritima*, which occurs together with herbaceous halophytes such as *Aster tripolium*, *Triglochin maritima* and *Plantago maritima*. In the high marsh we find the grasses *Festuca rubra* and the tall-growing *Elytrigia atherica*, which outcompetes most other plant species in ungrazed marshes as succession progresses. Additionally, brackish and glycophytic species which are able to tolerate infrequent inundations such as *Agrostis stolonifera* and *Potentilla anserina* are common in the high marsh zone. Large parts of the study area were recently acquired by the NGO 'It Fryske Gea' and are managed for nature conservation purposes. As is the case for most other mainland salt marshes in the Wadden Sea, NFB originates from man-made sedimentation fields (Esselink et al. 2009) and is therefore considered an artificial salt marsh with a regular pattern of drainage ditches. Maintenance of the smaller drainage ditches stopped in 2000 (van Duin et al. 2007) which led to their filling up with sediment.

The experiment consisted of three blocks called West, Mid and East, which were each subdivided into five paddocks of approximately 11ha (Fig. 4.1). Two blocks include mainly vegetation of the low and high marsh zone, while the third also includes a considerable area of pioneer zone. The following grazing treatments were applied: grazing with horses in two stocking densities (0.5 animals/ha, 1.0 animal/ha), grazing with cattle in two stocking densities (0.5 animals/ha, 1.0 animal/ha) and a rotational grazing regime. In the rotational regime a fallow year (year 1, year 3) was followed by a year of cattle grazing (1.0 animal/ha; year 2). The grazing treatments were randomly assigned to the paddocks, with the restriction that horse treatments were not placed next to each other to avoid the horses of two treatments to interact. Summer grazing lasted from the end of May until October. Previous to the grazing experiment the area was grazed intensively with horses or cattle in case of the blocks Mid and East, while the West block was ungrazed for at least 30 years. In 2009 (year 0), before experimental grazing started, grazing was installed in the West block to allow for better comparability of blocks. All paddocks included a freshwater source situated in the high marsh.

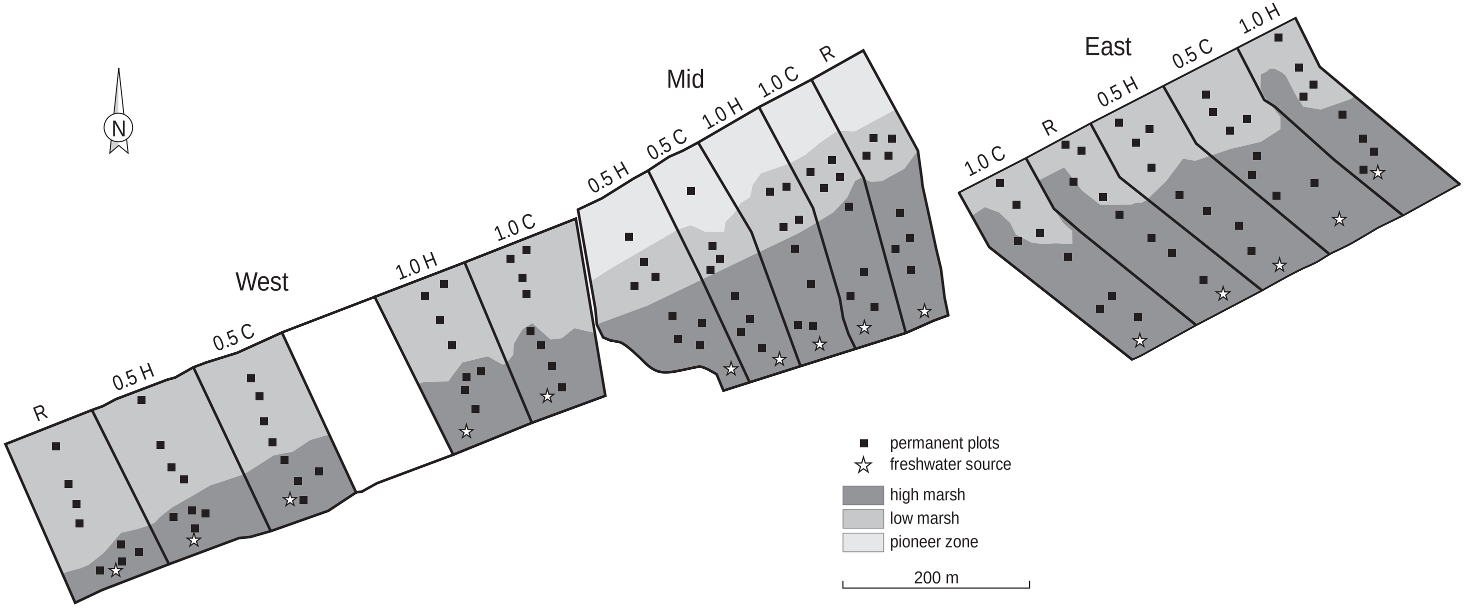

Figure 4.1 Overview blocks with treatments and permanent plots. The position of permanent plots (■) and freshwater sources (☆) are indicated by symbols. The different vegetation zones are represented by different greys. The livestock species is indicated by H = horse, C = cattle, while R = indicates the rotational treatments. Stocking densities are represented by numbers and represent animals/ha.

Permanent plots

In year 0, a total number of 120 permanent plots were installed in the experiment to study the vegetation composition change. We placed eight plots in each treatment with an equal number of plots in the high- and the low-marsh zone (Fig. 4.1). The position of plots was chosen within a homogeneous vegetation cover before the start of the experiment. Additionally, plots within the same block and marsh zone were positioned on a comparable elevation along the gradient. The average elevation of permanent plots above mean high tide (MHT) can be found in Table 4.1. The minimum distance between plots and to the fence was ten metres. All permanent plots were 4m × 4m. Plots were marked with inconspicuous metal pins to avoid disturbance by animals attracted to poles. These metal pins could be found with a metal detector. To simplify the detection of plots, but minimize the interference through animals, wooden poles were positioned at four metre distance from the plot. The vegetation composition (species number and species abundance) was recorded every year in late August or early September by estimating the cover percentage of each plant species according to the decimal scale (Londo 1976).

Statistical analyses

All statistical analyses were performed with respect to a) the differences between the four different grazing treatments (cattle 0.5/ha, cattle 1.0/ha, horses 0.5/ha, horses 1.0/ha) and b) the differences between rotational and continuous cattle grazing (1.0/ha).

The number of species per permanent plot is used as a measure for species richness, as all permanent plots have the same size and shape. We used a generalized estimation equation model (GEE) with a Poisson distribution (Liang and Zeger 1986, Zuur et al. 2009) to analyse the effect of a) the factors livestock species, stocking density and their interaction effect, and b) rotational vs. 1 cattle/ha treatment on the number of species per permanent plot in year 3. Because of the nested sampling

Table 4.1 Mean elevation of permanent plots within the three blocks and two marsh zones in the study area NFB.

Block	Marsh zone	mean elevation above MHT [cm]	SD
East	high	83	5.3
East	low	59	7.2
Mid	high	79	6.9
Mid	low	53	16.6
West	high	42	13.5
West	low	29	8.4

design a coding variable was used to identify all plots from the same zone within one block. The correlation structure exchangeable was used. Stepwise backward model selection was performed by dropping each variable in turn and comparing models using ANOVA (Zuur et al. 2009). The GEE models were analysed using the library 'geepack' (Højsgaard et al. 2006) for the statistical software R version 2.15.0 (R Development Core Team 2012).

The effect of a) livestock species and stocking density and b) rotational grazing vs. 1.0 cattle/ha on the species composition in permanent plots was analysed using redundancy analysis (RDA). The following analyses were performed using the statistical software CANOCO version 4.55. Species cover was log-transformed. The a) livestock species and stocking density and b) the rotational vs. continuous 1.0 cattle/ha treatment were used as explanatory variables. The block was used as a covariable to account for the nested sampling design. We also used elevation as a covariable, as the effect of elevation on species composition is not of interest in this study. Significance was tested based on Monte-Carlo permutation tests, with 499 permutations restricted by block.

To test whether a temporal trend in the species composition caused by different treatments can be detected a RDA analysis was performed using all data including the year 0 documenting the species composition before the start of the experiment. Species cover was log-transformed. The interaction effects of a) livestock species and stocking density with year and b) the rotational vs. continuous 1 cattle/ha treatment with year were used as explanatory variables. Year and the dummy variable plotID were used as covariables. Significance was tested based on Monte-Carlo permutation tests, with 499 permutations restricted by plotID.

Results

Number of species

Both livestock species and stocking density did not have a significant effect on the number of species per permanent plot (Fig. 4.2). The comparison of the rotational vs. continuous 1.0 cattle/ha treatment also did not show significant effect of treatment, although there seemed to be a trend of lower number of species per permanent plot in the rotational treatment (Fig. 4.2).

Species composition

Both livestock species and stocking density did not have a significant explanatory effect on plant species composition in permanent plots in year 3 in the RDA (Table 4.2). Both constrained axes explained a very small amount of variability in species data (0.9% and 0.3%). Although the effect was not significant, there seems to be a trend for some plant species to appear more often in cattle grazed treatment (Fig. 4.3;

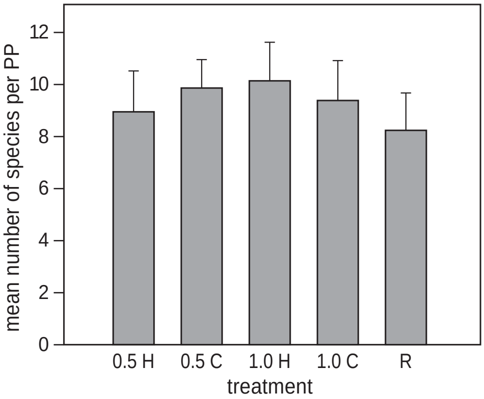

Figure 4.2 The mean number (n = 24) of species per permanent plot compared between the five different treatments. Error bars represent standard error.

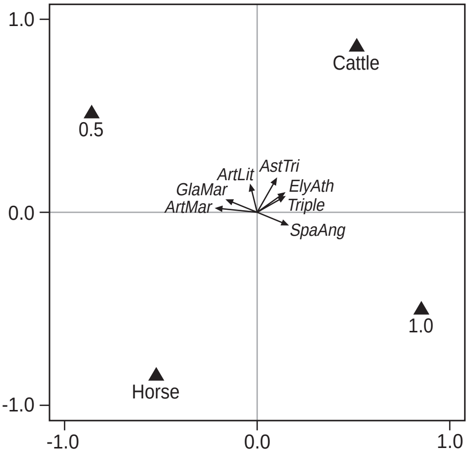

Figure 4.3 Biplot of the RDA analysis illustrating the non-significant effect of the environmental variables (triangle) livestock species and stocking density on species composition. Species with less than 2% species fit range were not depicted.

Table 4.2 Results of the RDA analyses investigating the effect of a) livestock species and stocking density, and b) rotational vs. continuous cattle grazing on the species composition in permanent plots in year 3 and the temporal trend in species composition change from year 0 to year 3.

	Eigenvalue 1st axis	Eigenvalue 2nd axis	p value
Composition year 3			
a) Livestock species & stocking density	0.009	0.003	0.506
b) Rotational vs. 1 cattle/ha	0.024	0.155	0.118
Temporal trend			
a) Livestock species & stocking density	0.002	0.001	0.301
b) Rotational vs. 1 cattle/ha	0.005	0.145	0.092

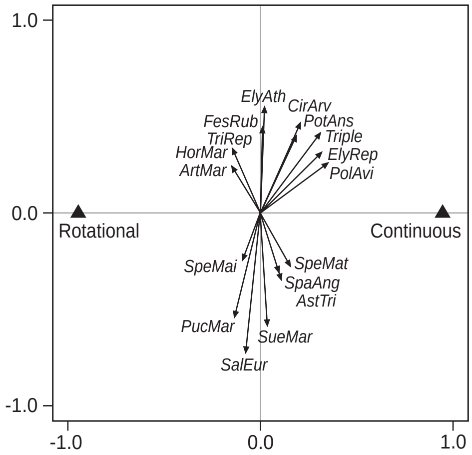

Figure 4.4 Biplot of the RDA analysis illustrating the non-significant effect of the environmental variables (triangle) rotational vs. continuous grazing on species composition. Species with less than 2% species fit range were not depicted.

Aster tripolium, *Elytrigia atherica*, *Tripleurospermum maritimum*). Low stocking densities seem to be favourable for *Glaux maritima* and *Artemisia maritima*.

In the analysis comparing the effect of rotational vs. continuous 1.0 cattle/ha treatment on species composition, only the first axis is constrained by the environmental factor treatment and explains 2.4% of variation in the data. The second axis is not constrained by any environmental factor and therefore explains considerably more variation (15.5%). Species composition in the two treatments was found not to differ significantly from a random composition. However, the biplot shows some trends for various plant species (Fig. 4.4). Among the high marsh species, *Hordeum marinum* and *Artemisia maritima* are slightly more common under the rotational grazing, while *Cirsium arvense*, *Potentilla anserina*, *Tripleurospermum maritimum*, and *Elytrigia repens* were more often found in the continuous 1.0 cattle/ha treatment. In the low marsh, *Spergularia maritima*, *Spartina anglica* and *Aster tripolium* are more common in the continuous 1.0 cattle/ha treatment, while *Puccinellia maritima* seems to benefit from rotational grazing.

Temporal trend

The livestock species and stocking density explained only 0.2% and 0.1% of the variation in the data of the temporal trend in species composition from year 0 to year 3 represented by the first and second axis in the RDA. The trend in species composition change was not found to be significantly different from a random species composition and therefore we have to accept the null-hypothesis that the temporal trend in species composition is independent of treatments (Fig. 4.5).

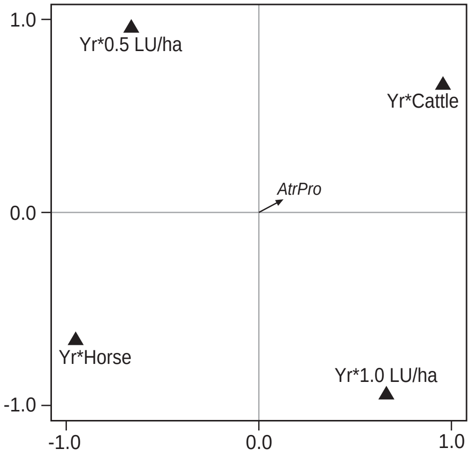

Figure 4.5 Biplot of the RDA analysis illustrating the non-significant temporal trend in species composition change constrained by the interaction effects of the environmental variables (triangle) livestock species and stocking density with the year on species composition. Species with less than 1% species fit range were not depicted.

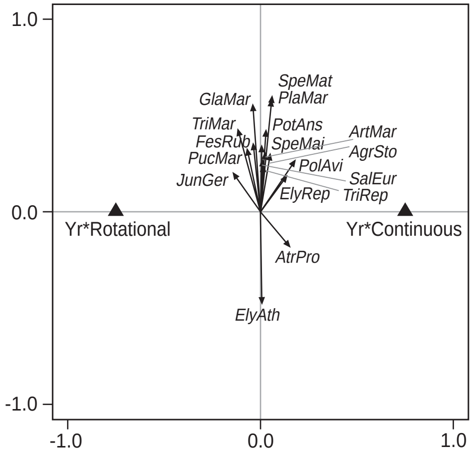

Figure 4.6 Biplot of the RDA analysis illustrating the non-significant temporal trend in species composition change constrained by the interaction effects of the environmental variables (triangle) rotational vs. continuous grazing with the year on species composition. Species with less than 1% species fit range were not depicted.

The rotational treatment had no significant effect on the temporal trend in the species composition change compared to the continuous 1.0 cattle/ha treatment (Fig. 4.6). Only 0.5% of the variation in the species composition was explained by the first constrained axis representing the treatments.

Discussion

In this study the plant species richness measured as number of species per permanent plot was influenced neither by the livestock species nor stocking density. The number of species seems to be slightly lower in the rotational compared to the continuous 1.0 cattle/ha treatment. Also, no significant effect of livestock species and density or rotational grazing could be detected with respect to species composition and temporal changes in species composition within three years. However, there are some trends which might lead to changes in the future.

The comparison of livestock species and stocking densities shows some interesting trends with respect to single plant species. The tall grass *Elytrigia atherica* seems to be more common in cattle compared to horse grazed treatments. This may be explained by behavioural differences between the two livestock species. Horses require a higher amount of forage per day compared to cattle (Gordon 1989, Duncan et al. 1990, Menard et al. 2002). Therefore preferred plant species are depleted earlier in horse-grazed treatments, and the animals may become less selective and include a higher amount of low-quality tall grass into their diet (Duncan et al. 1990, Dumont et al. 2012). Indeed, the diet of horses was found to contain on average more fibre compared to the cattle diet in the study area (chapter 2). The effect of different livestock species on *Elytrigia* is of special importance for nature conservation, because the spread of this species leads to species poor stands (Leendertse et al. 1997) and it is avoided by geese (Bos et al. 2005). Another species of high conservation interest is *Aster tripolium*, because it is the food plant for a high number of invertebrate species (Meyer et al. 1995). Based on its high abundance in the diet choice of cattle (chapter 2), we would have expected *Aster* to be more common in horse-grazed treatments. *Aster* was found to be less damaged by horses in the 0.5 animals/ha stocking density, while in higher densities the higher general forage intake and higher activity of horses caused more damage in horse-grazed treatments in the first study year (Nolte et al. 2013a). After three years it seems that *Aster* was more common in cattle-grazed treatments. Possibly the effect of higher forage intake and higher activity of horses accumulated over time and led to less favourable conditions for *Aster* also in the 0.5 horse/ha density treatment. The lower activity of cattle might also be the reason for the higher cover percentages of *Atriplex prostrata* and *Artemisia maritima*, which were both not common in the animal diet.

The rotational treatment in comparison to the continuous 1.0 cattle/ha treatment was found to have slightly lower number of species per plot. This indicates that the grazing intensity in the rotational treatment might not be high enough to create gaps for the establishment of new species and to supress tall growing competitive species. Especially on the high marsh the competition for light was found to be one of the major mechanisms leading to disappearance of low-statured species (Olff and Ritchie 1998). Indeed the canopy height in the rotational treatment is on average twice as high as in the 1.0 cattle treatment (1.0 cattle mean 13.4 cm, SE 1.7; Rotational mean in fallow year 26.6 cm, SE 1.7, Nolte et al. unpubl. data). However, *Elytrigia*, the major tall growing grass species, seems not to be effected by the two treatments (Fig. 4.4 and 4.6), possibly, because plots that were already covered by *Elytrigia* in year 0 with a high cover percentage, did not change in species composition but remained covered by *Elytrigia*. In case of an already high cover percentage the taller canopy of *Elytrigia* in the rotational treatments will probably also not lead to distinct changes in cover percentage. Therefore the spread of *Elytrigia* in the experiment should not only be monitored in permanent plots, but in vegetation maps documenting the area covered by the *Elytrigia* vegetation type (see Veeneklaas et al. 2013). It seems that *Hordeum marinum* is favoured by continuous 1.0 cattle/ha grazing, maybe because there are gaps in the canopy for the establishment of seedlings and because it is otherwise outcompeted by the tall grass *Elytrigia*. Many other species which generally occur in the highest part of the marsh were found slightly more often in the 1.0 cattle treatment. Among them are the glycophytic species *Cirsium* spec., *Potentilla anserina* and *Polygonum aviculare*, but also the salt-marsh plant *Tripleurospermum maritimum*. We also think that these are reduced in the rotational treatment because of competition for light with taller species such as *Elytrigia atherica* and *Elytrigia repens*.

Whether the trends we described in this study indeed will lead to stronger differences between the vegetation composition under different livestock species and densities should be further monitored. The study now included three years of experimental grazing, while Bakker et al. (1996) suggest that studies should last at least ten years. Additionally, permanent plots might not be the best strategy to study differences in grasslands with a relatively small species pool. The small species pool causes a great overlap in species composition even among the most extreme plots and therefore differences between plots might be too small to be detected using this technique. In some other salt marsh studies first differences in species number per unit area between grazed and ungrazed treatments became apparent after two years (Milotic et al. 2010), while other studies found no differences after five years (Kiehl et al. 1996). In the same area previously studied by Kiehl et al. (1996) the spread of *Elytrigia* only became apparent after eleven years (Gettner 2003). As the differences between grazed and ungrazed marshes are likely to emerge faster than those between different grazing treatments, the continuation of the experiment described in this study is crucial to draw any definite conclusions on the effects of grazing with different livestock species and stocking densities. Therefore we can only give limited recommendations for management. With respect to the dominance of *Elytrigia* it seems that horse grazing is a better tool to remove this tall growing low-quality grass. However, horse grazing was found to have other negative effects on the ecosystem especially in high stocking densities. Those negative effects are for example an increased trampling risk for nests (Mandema et al. 2013). Therefore we advise that horse grazing should only be applied if the target is to remove *Elytrigia* from an area that is already largely dominated by it. As a change of livestock species might be unpractical for management, we would advise a higher density of cattle than 1,0 animal/ha for the reduction of *Elytrigia*. If the abundance of *Elytrigia* is still small we would advise for cattle grazing in lower densities. With respect to stocking densities in general we can give no clear recommendation yet. However, the point needs to be stressed that, because of their higher forage intake, one livestock unit of horses is not comparable to one livestock unit of cattle. With respect to the rotational regime we cannot draw any clear conclusions yet. It seems that rotational grazing as applied in this study leads to an increased canopy height and a reduced number of species. This should, however, not be understood as a recommendation against rotational regimes. Instead it shows that the application of rotational regimes needs further studies to define stocking densities and grazing frequencies which lead to optimal results.

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Box 1

Box 1

The effect of grazing on plant species richness in salt marshes – A matter of scale

Stefanie Nolte, Peter Esselink, Jan P. Bakker

Introduction

Salt marshes are important ecosystems for the conservation of biodiversity in north western Europe, as they are inhabited by a large number of specialised plant, bird and invertebrate species restricted to these areas (Westhoff et al. 1993, Norris et al. 1997, Pétillon et al. 2005, Rickert et al. 2012). In these ecosystems grazing with livestock for agricultural purposes has a long tradition (Esselink et al. 2002). In the past century many salt-marsh areas were abandoned, because livestock grazing was not economically feasible or because of the creation of National Parks (Bakker et al. 2003). It was then found, that the cessation of grazing leads to the spread and dominance of single species, namely *Atriplex portulacoides* in the low-marsh and *Elytrigia atherica* in the high-marsh areas (Leendertse et al. 1997, Veeneklaas et al. 2013). This development led to a reduced number of species in ungrazed marshes. Therefore, the grazing of salt marshes with livestock became a common practice in nature management.

Most studies investigating the effect of grazing on species richness only measured the number of species in plots of a given size (*e.g.* Andresen 1990, Bos et al. 2002, Kleyer et al. 2003, Kiehl et al. 1996) and the effect of different spatial scales was seldom taken into account. Bakker et al. (2003) reported a lower number of plant species in an ungrazed marsh on all spatial scales. But is this true for different sites as well? For example, Stock and Kiehl (2000) hypothesized for mainland marshes, that a high species number can be preserved on a larger spatial scale in ungrazed conditions when drainage ditches are neglected, because this measure would lead to an increase in the spatial heterogeneity of environmental factors. In a grazing experiment on such a mainland marsh Rickert et al. (2012) found plant species richness to be highest in the lowest stocking density and to decrease with increasing stocking density, while plant species richness in the ungrazed treatment was still high after 20 years of abandonment in plots of 1×1 m. However, this is a small scale and with respect to the hypothesis of Stock and Kiehl (2000), that species diversity can be preserved on a larger spatial scale by neglecting the drainage ditches, the effect of grazing should be investigated on a variety of scales. The spatial scale of the investigated plots might also be the reason why grazing treatments with two livestock species and stocking densities led to clear differences in structural diversity (chapter 6), but not in plant species richness (chapter 4) between treatments in a grazing experiment in The Netherlands.

Therefore, we investigated Q1) the effect of spatial scale on plant species richness in different stocking densities in two long-term (25 years) grazing experiments (Sönke-Nissen-Koog and Friedrichskoog). Furthermore, we investigated in a grazing experiment in The Netherlands whether Q2) an effect of grazing treatments with two livestock species and stocking densities on the number of species might only be found on certain spatial scales. Additionally, we investigated Q3) whether the trend of lesser species per unit area based on the measurements of 4 m × 4 m plots in a rotational regime compared to continuous cattle grazing with 1 animal/ha could be further confirmed by investigating different spatial scales.

Study area and methods

We investigated the effect of grazing on plant species richness on different spatial scales in three different grazing experiments on mainland salt marshes in Germany and The Netherlands (Fig. B1.1). Two of these grazing experiments, the areas Friedrichskoog (FK) and Sönke-Nissen-Koog (SNK) were established 25 years ago (1988) and focus on the effects of different stocking densities of sheep. The third experiment, Noord-Friesland Buitendijks (NFB), was established in 2010 and compares two livestock species (horses and cattle) in two stocking densities (0.5 and 1.0 animal/ha) and a rotational treatment. In the rotational treatment fallow years alternate with years in which the stocking density of cattle is 1.0 animal/ha during summer.

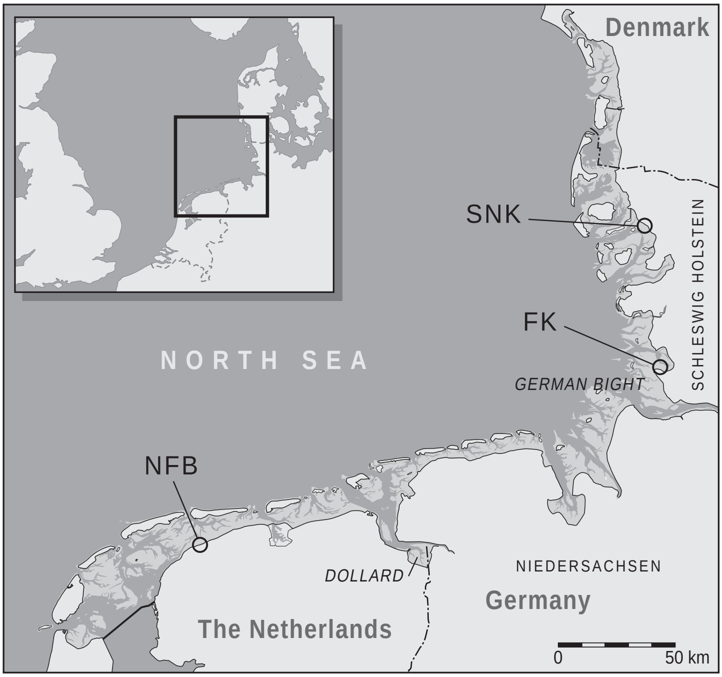

Figure B1.1 Location of the study sites Noord-Friesland Buitendijks (NFB), Friedrichskoog (FK) and Sönke-Nissen-Koog (SNK) along the mainland coast of the Wadden Sea.

Friedrichskoog (FK) and Sönke-Nissen-Koog (SNK)

The study sites FK (54°2'30", 8°54'30") and SNK (54°38'4", 8°50'2") are part of the Schleswig-Holstein Wadden Sea National Park, which was established in 1985. They originate from man-made sedimentation fields and are characterized by straight drainage ditches. Both marshes were grazed intensively (10 sheep/ha) prior to the start of the grazing experiments in 1988. The grazing experiments included five different treatments at both sites: 0, 1.5, 3, 4.5 and 10 sheep/ha (Kiehl et al. 1996, Berg et al. 1997). Some of these treatments were, however, abandoned and we therefore use the following treatments in this study; for the FK the treatments 0, 3, and 10 sheep/ha and for the SNK 0, 3, 4.5 and 10 sheep/ha were studied. The FK marsh is dominated by high-marsh vegetation (*Festuca rubra*) and the SNK marsh is dominated by low-marsh vegetation (*Puccinellia maritima*).

Noord-Friesland Buitendijks (NFB)

The salt-marsh area NFB is situated on the mainland coast of The Netherlands (53°20'11", 5°43'40") and originates from man-made sedimentation fields. Maintenance of drainage ditches stopped in the area in 2000 (Van Duin et al. 2007). Large parts of the area are owned by the NGO 'It Fryske Gea' and are managed for nature conservation. A large-scale grazing experiment consisting of three blocks was started in the area in 2010 (see chapter 4; Mandema et al. 2013). Prior to the experiment, two of the blocks were grazed intensively by cattle or horses while the third was ungrazed (Esselink et al. 2009). Grazing in the previously ungrazed block was started in 2009 (year 0), one year before the experiment, to approximate the situation in the previously grazed blocks. All blocks were subdivided into five paddocks of *ca.* 11 ha each. The following grazing treatments were applied: summer grazing with horses in two densities (0.5 horse/ha and 1.0 horse/ha), summer grazing with cattle in two densities (0.5 cattle/ha and 1.0 cattle/ha) and a rotational grazing regime. In the rotational regime a fallow year (year 1, year 3) was followed by a year of summer grazing with cattle (1.0 cattle/ha; year 2). To avoid interaction between horses of two paddocks, horse-grazed treatments were never placed in neighbouring paddocks. Apart from this restriction, treatments were randomly assigned to paddocks.

Sampling plots

The number of species was counted in different sized non-nested plots in each aforementioned treatment in September 2011 (year 2). Coordinates for plots were randomly chosen using vegetation maps of the areas and the software ArcGIS 10. At FK and SNK the size of plots was 0.04, 0.25, 1, 4, 16, 25, 100, and 400 m^2. Plots were placed in the vegetation type high marsh in case of FK and low marsh in case of SNK. All plots between the size of 0.04 and 4 m^2 had three replicates within one treatment. Because the experimental design differed between the two German sites and the Dutch site with respect to paddock area and block design we used plots of 0.04, 0.25, 1, 4, 16, 25, 100, 400, 1600, and 6400 m^2 at NFB. All different sized plots were repeated once per treatment per block. At NFB the position of plots was randomly chosen within the high-marsh vegetation.

Statistical analysis

We created species–area curves and investigated how species richness at different spatial scales was influenced by grazing treatments with an analysis of covariance (ANCOVA). Both area and species number were log-transformed before analysis and met the assumptions for ANCOVA. As counts are never negative, we did not add one to the number before transformation. Model selection was performed by stepwise backwards dropping of non-significant terms (Crawley 2007). All analyses were performed with the statistical software R 2.15.0 (R development core team 2012).

To investigate (Q1) the effect of stocking density on species number on different spatial scales we analysed the data of plots from FK and SNK. A linear model was fitted to the data with the dependent variable number of species (log-transformed) and with the independent variables area (log-transformed) and stocking density, as well as the interaction term. Additionally, multiple comparisons between treatments were performed using the package multcomp (Hothorn et al. 2008).

To determine (Q2) how different livestock species and stocking densities influence the number of species on different spatial scales we used the NFB data from the treatments 0.5 and 1.0 horse/ha and 0.5 and 1.0 cattle/ha and performed an ANCOVA. A linear model was fitted with the log-transformed number of species as dependent variable. The independent variables were area (log-transformed), livestock species, stocking density and the interaction effects. The rotational treatment was compared to the continuous 1.0 cattle/ha treatment (Q3) in a separate analysis. For this purpose a categorical variable called treatment was created indicating whether the plots were positioned in a rotational or continuous treatment. The linear model included the log-transformed number of species as the dependent, and the log transformed area and the categorical variable treatment as independent variables.

Results

Friedrichskoog (FK) and Sönke-Nissen-Koog (SNK)

At the site FK, both area (Df 1; F 15.5; $P < 0.001$) and stocking density (Df 1; F 22.1; $P < 0.001$) were found to have a significant effect on number of species (Fig. B1.2A). Multiple comparisons showed that the number of species in the ungrazed treatment was significantly lower than that in both the 3 sheep/ha (t 11.5; $P < 0.001$) and 10 sheep/ha (t 10.0; $P < 0.001$) treatments. The two grazed treatments did not differ significantly (t 1.4; $P = 0.346$). In contrast, at the SNK-site only area had a positive significant effect on number of species (Df 1; F 2.8; P < 0.001), whereas an effect of stocking density could not be detected (Fig. B1.2B).

Noord-Friesland Buitendijks (NFB)

The area had a strong positive effect (Df 1; F 102.5; P < 0.001) on number of species (Fig. B1.3A). No effect of livestock species or stocking density was found. The comparison of the rotational *vs.* the continuous 1.0 cattle/ha treatment showed a significant effect of both treatment (Df 1; F 4.9; P < 0.05) and area (Df 1; F 101.9; P < 0.001) on the number of species on different spatial scales (Fig. B1.3B).

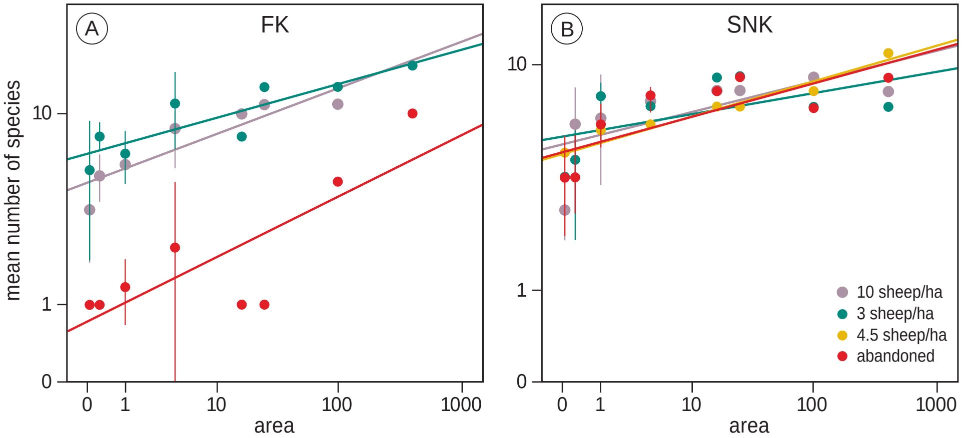

Figure B1.2 Comparison of species-area curves in different grazing regimes with sheep in (A) the Friedrichskoog salt marsh (A) and (B) Sönke-Nissen-Koog salt marsh.

Discussion

The area was found to have a strong positive effect on species number in all grazing treatments and therefore monitoring schemes in salt-marshes should carefully consider scale (Drakare et al. 2006). A clear effect of the cessation of grazing on different spatial scales was found at FK, but not at SNK. In both sites, we expected to find the plots to be dominated by single species which would lead to a reduced species number (Bakker et al. 2003). However, it seems that this is only true at FK, which is mainly covered by high-marsh vegetation. In the high marsh, it seems that *Elytrigia atherica* covered many plots with mono-specific stands as was described by Veeneklaas et al. (2013). In contrast, we selected low-marsh sites at SNK and did not find any effect of cessation of grazing here. Possibly a reduced drainage due to the neglect of the drainage ditches caused low redox potential and prevented the spread

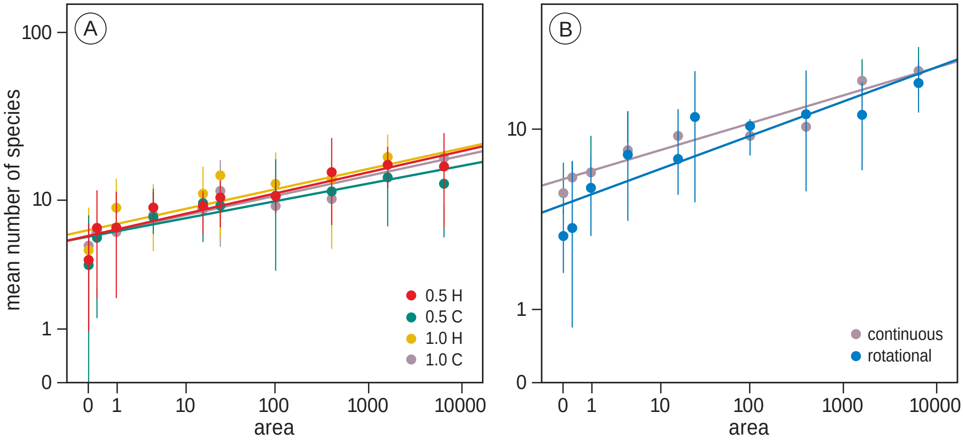

Figure B1.3 Species-area curves comparing the effect of different livestock species cattle and horses and stocking densities on species number on different spatial scales (A) and the effect of rotational vs. 1 cattle/ha treatments (B) in the study area Noord-Friesland Buitendijks (NFB).

of *Atriplex portulacoides* (Kiehl et al. 1996, Esselink et al. 2000, Davy et al. 2011). Yet, ditches in the research area were still deep (pers. obs.). Another explanation for the lack of effect of cessation of grazing could be the sampling design. Plots were selected to be in the low marsh based on a vegetation map. As the *Elytrigia atherica* vegetation type is not considered high marsh, plots were never in this zone and therefore grazed and ungrazed plots were very likely similar. A study on the moth communities in salt marshes conducted in an area close to the SNK salt-marsh site also found plant species number still to be relatively high in the ungrazed marsh (Rickert et al. 2012). However, Rickert et al. (2012) also restricted the position of plots to the low marsh vegetation zone which means no plots were placed in the *Elytrigia* vegetation type. The spread of *Elytrigia* was found to cause a decrease in plant species number. However, in this study all the plots were chosen not to be in the *Elytrigia* zone, and therefore the vegetation did not differ greatly between treatments. In contrast, a random choice of plots in the whole area without respect to the vegetation type would probably by chance also included plots in these areas. This procedure would likely have led to a reduced number of species in the ungrazed area.

We did not find any clear effect of stocking density on species number both at FK and the SNK. At the FK there is a trend for a lower species number in the high compared to moderate density in small areas. This might be caused by the formation of small patches which leads to an increased plant species richness at the small scale (*e.g.* Olofsson et al. 2008), while at a larger scale both treatments have a similar species number. This effect was less clear at the SNK maybe because of less strong differences in species composition between tall and short patches.

In the experiment comparing both different livestock species and stocking densities no significant differences could be found between treatments at different scales. This confirms the results of Nolte et al. (chapter 4) who found no significant difference in number of species between treatments at a 4 m×4 m scale. However, the experiment was running for only three years and differences might still appear in the future. Already differences between vegetation structure patchiness appeared among treatments (chapter 6). Cattle were found to create smaller patches in comparison to horses. Therefore, especially on the small scale, cattle grazing might lead to higher plant species richness. Yet, there are the first signs of the spread of the tall grass *Elytrigia* and the tall annual *Atriplex prostrata* in the cattle-grazed treatments, which were observed to form species-poor stands in an adjacent ungrazed marsh (pers. obs.). Therefore, a spread of these species might decrease the number of species in the cattle-grazed treatments. In contrast, a study comparing the effect of cattle, horses and mixed grazing in a coastal grassland in France found species number was highest in horse-grazed areas (Loucorgaray et al. 2004). Because clear results are not yet available, the monitoring of species number at different spatial scales should be repeated in future to draw conclusions on the effect of different livestock species and stocking densities and give recommendations for management.

Rotational vs. continuous cattle grazing

The trend of less species per unit area in the rotational grazing treatment detected by Nolte et al. (chapter 4) on the basis of 4 m×4 m plots can be indeed detected on smaller scales. The difference between treatments seems not to be strong on the same scale (log(16) $m^2 = 1.2$ m^2) in our measurements (Fig. B1.3B). On smaller scales there is, however, a clear and significant effect on species number. The lower number of species in the rotational treatments might be attributed to the increased light competition in the tall canopy. Low-statured species are outcompeted and disappear and the tall canopy reduces the number of possibilities for annual species to germinate and establish (Bakker et al. 2006).

We can summarize that the scale can have an important effect on the outcome of plant species richness monitoring and should therefore be considered carefully (Drakare et al. 2006). With respect to the spread of dominant tall species such as *Elytrigia atherica*, it is advisable to combine monitoring approaches on plots based to species mapping in transects (Esselink et al. 2000) and vegetation mapping investigating the spread of vegetation types in the study site (Veeneklaas et al. 2013). Without this approach, a spread of mono-dominant vegetation stands might be overlooked in studies based on permanent plots alone. The same is true for the experiment comparing different livestock species and stocking densities. Additionally we would advise to repeat the measurements in this experiment after a longer time to allow possible differences between grazing treatments to establish.

Acknowledgements

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Chapter five

5

Large grazers in various densities affect vegetation structure distinctively in two different grassland types

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Abstract

Large grazers influence the vegetation structure of grasslands by affecting canopy height. Higher grazer densities are likely to create larger patches of short canopy than lower densities. However, relatively little work has examined, how various grazer densities affect the mean canopy height and proportion of short and tall canopy in different types of grasslands over time. We analysed the effect of sheep grazing at four levels of stocking densities (1.5, 3, 4.5 and 10 sheep/ha) in low (*Puccinellia maritima* (Huds.) Parl.) and high (*Festuca rubra* L.) elevated salt marshes on the vegetation structure. Data were collected in a long-term experiment (1988-2001) along the mainland coast in Germany. The mean canopy height decreased, and the proportion of short canopy increased with increasing stocking density, but at a steeper rate in the low than in the high salt-marsh site. Since the animals used a freshwater source at one side of each *ca.* 10 ha paddock, the distance to the freshwater source also had a significant effect on canopy height. Canopy height increased at a steeper rate towards the salt-marsh edge in the low than in the high salt marsh. Therefore, how large grazers modify the structure of the vegetation depends to a large extent on both the density of grazers, the position of other resources such as access to drinking water, and the grassland type.

Introduction

Large herbivores induce structural and compositional variation on grassland plants (Milchunas et al. 1988, McNaughton et al. 1989, Collins et al. 1998, Olff and Ritchie 1998) with consequences for bird (Norris et al. 1997, Fuller and Gough 1999), and invertebrate (Morris 2000, Kruess and Tscharntke 2002) diversity. Intensive herbivore grazing in grasslands results in a homogeneous, short canopy of grass. In contrast, minimal or no herbivore grazing results in a homogeneous tall canopy of grass in different types of temperate grasslands (Bakker 1998). Intermediate grazer densities may result in a vegetation mosaic of short and tall canopy patches (Berg et al. 1997, de Knegt et al. 2008). These patches establish, because herbivores usually prefer high-quality forage consisting of protein-rich tillers and a high leaf:stem ratio. When the regrowth of grazed vegetation is of enhanced quality the grazers tend to revisit these areas and create and maintain short vegetation or grazing lawns (Ydenberg and Prins 1981, McNaughton 1984, Dumont et al. 2007a). Therefore, the average canopy height of grassland may depend on the density of grazing herbivores. Previous studies have shown that the average height of vegetation decreases with an increase in the density of herbivores in Europe (Hester et al. 1996, Berg et al. 1997, Pakeman et al. 2003, Isselstein et al. 2007, Celaya et al. 2010).

In addition to the overall grazer density, the canopy height is also influenced by the local grazing intensity. The local grazing intensity is determined by the spatial distribution of the animals which was found to be influenced by the position of management infrastructure. Previous observations have shown that the creation of artificial freshwater sources for livestock decreased the canopy height of sagebrush steppe in the US along a distance gradient up to 2 km (Adler and Hall 2005). Similarly, the creation of a stable for sheep negatively influenced the canopy height of heathlands in the Netherlands over a similar distance (Bakker 1998). The above examples imply that the impact of grazing near water would lead to a large proportion of low vegetation because of a high local grazing and trampling intensity. Hence, average vegetation height should consist of short vegetation close to freshwater sources alternating with areas of tall vegetation away from freshwater sources. However, the proportion of short canopy depends on the stocking density, and the locally produced plant biomass.

The effect of herbivore density as a key determinant of the impact of herbivores on the vegetation structure has not been addressed in large-scale experimental field studies. Fortunately, a long-term field experiment was established in 1988 along the mainland coast of Germany in a low-marsh site at Sönke-Nissen-Koog (54°38′N 8°50′E), and a high marsh at Friedrichskoog (54°02′N 8°54′E) (Kiehl et al. 1996). We used these experiments to test the hypotheses that canopy height (1) increases with increasing distance from a freshwater source, because grazing and trampling are more intense close to water. Additionally, we hypothesize canopy to (2) decrease with increasing stocking density, associated with higher grazing intensities. We also expect the proportion of short canopy (*i.e.* canopy height <10 cm) to (3) decrease with increasing distance from freshwater sources, because of intense grazing and trampling close to water, but (4) to increase with increasing stocking density, associated with higher grazing intensities.

Methods

Study sites

Salt-marsh ecosystems are characterized by the interaction of plants and sediment trapped during tidal inundation. The resulting vertical accretion causes succession from pioneer communities with *Salicornia* species, and *Spartina anglica* C.E.Hubb.,

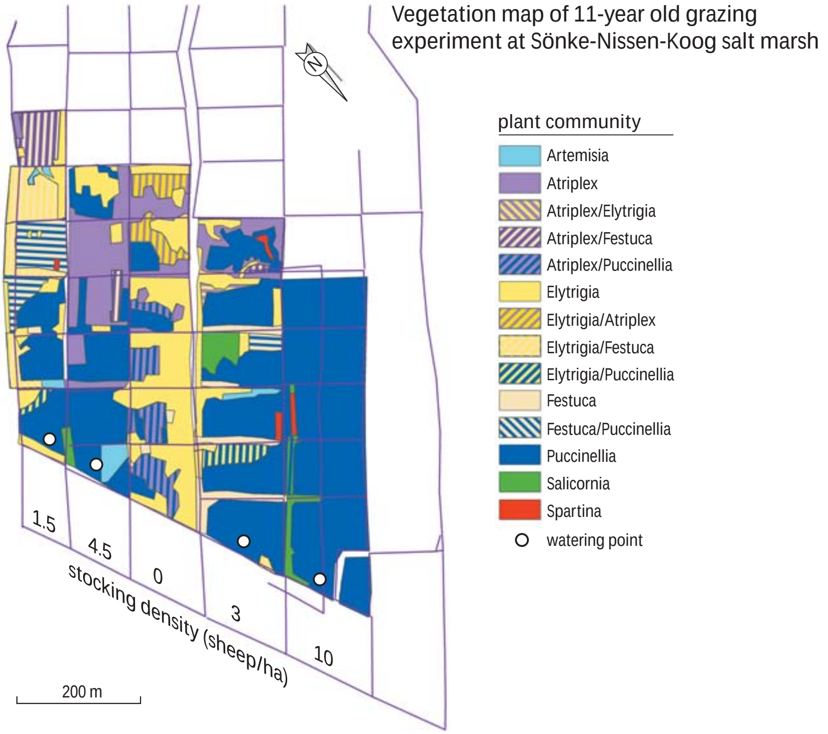

Figure 5.1 Vegetation map of 11-year old grazing experiment in the low salt marsh of Sönke-Nissen-Koog, with four stocking densities of sheep and the ungrazed control paddock. The paddocks are separated by a creek or a fence. Each paddock is subdivided in blocks separated by cross ditches. Sheep can not graze further towards the seaward edge of the salt marsh, as the very wet parts are excluded from grazing.

via low-salt marsh communities with the short-growing grass *Puccinellia maritima* (Huds.) Parl. to high salt-marsh communities with the short-growing grass *Festuca rubra* L., and later the tall grass *Elytrigia atherica* (Link) Kerguélen (Esselink et al. 2009). This successional sequence mirrors the spatial zonation along the elevation gradient from pioneer to low and high marsh in mainland salt marshes (de Leeuw et al. 1993). Hence, in these marshes, zonation reflects vegetation succession.

The study was conducted in September 2001 on two mainland salt marshes along the German Wadden Sea coast. These salt marshes were artificially developed from sedimentation works (Doody 2008). The sites experienced intensive sheep grazing (10 sheep/ha) until the end of 1987. In 1988 a grazing experiment was started. In both sites five adjacent experimental paddocks (each ca. 10 ha) were established: an ungrazed control field and four paddocks with stocking densities of 1.5, 3, 4.5 and 10 sheep/ha, respectively (Fig. 5.1 and Fig. 5.2). Paddocks were separated by a main

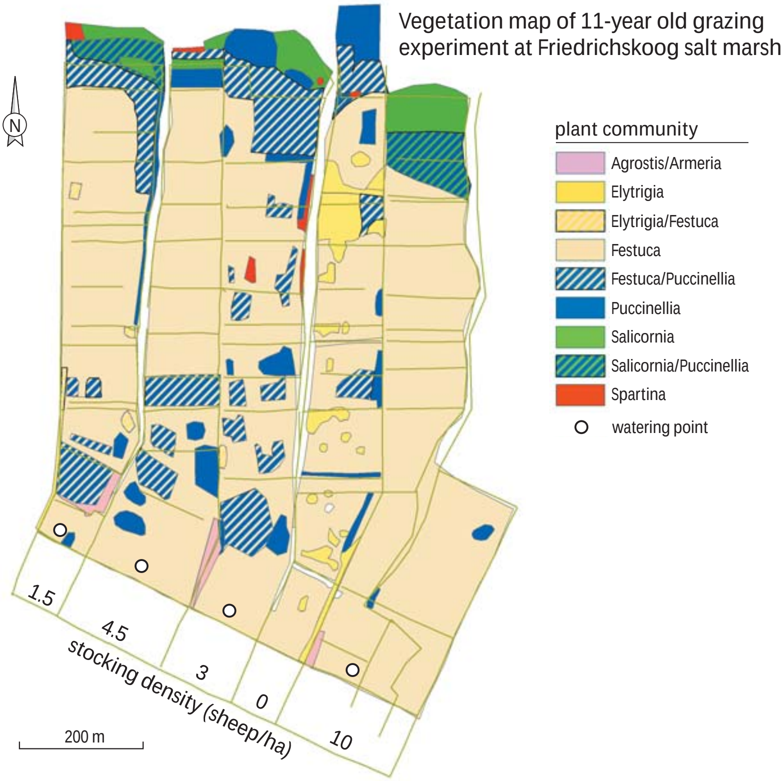

Figure 5.2 Vegetation map of 11-year old grazing experiment in the high salt marsh of Friedrichskoog with four stocking densities of sheep and the ungrazed control paddock. The paddocks are separated by a creek or a fence. Each paddock is subdivided in blocks separated by cross ditches. Sheep can graze until the seaward edge of the salt marsh.

creek or a fence. Each paddock was subdivided by cross ditches into blocks (Fig. 5.1 and Fig. 5.2). Fresh drinking water was only available close to the seawall. During the first years of the experiment short grasses were dominant at both sites. *P. maritima* dominated the low-marsh site at Sönke-Nissen-Koog, whereas *F. rubra* dominated the high marsh at Friedrichskoog (Kiehl et al. 1996).

The low marsh at Sönke-Nissen-Koog had an elevation of 0.2 – 0.3 m above mean high tide (MHT) at the start of the experiment in 2001. The net elevation increase (accretion) was 1-5 mm/yr during the late 1980s, but 11 mm/yr between 2001 and 2007 (Table 5.1). The soils had a relatively high clay content of 30% and above-ground peak biomass was 790 g dw/m^2. After 11 years (*i.e.* 1999), the short-grass community of *P. maritima* still dominated the intensively grazed paddock (10 sheep/ha) in the low marsh of Sönke-Nissen-Koog. Large parts of the ungrazed paddock, and smaller parts of the paddocks grazed with 1.5, 3 and 4.5 sheep/ha were covered by the tall-grass community of *E. atherica* (Fig. 5.1). The salt marsh at Sönke-Nissen-Koog is further referred to as 'low marsh'.

The high salt marsh near Friedrichskoog was situated at 0.5 – 0.6 m above MHT. Net elevation increase (accretion) amounted to 2-9 mm/yr during the late 1980s (pers. comm. K. Kiehl), and 6 mm/yr between 2001 and 2007 (Stock, unpubl.). The soils here were sandier compared to the low marsh with a clay content of 10% and above-ground peak biomass was 777 g dw/m^2 (Table 5.1). The vegetation in the heavily grazed paddock (10 sheep/ha) at the high marsh of Friedrichskoog was still dominated by the short *F. rubra* community after 11 years (*i.e.* 1999). The tall *E. atherica* community covered small areas in the ungrazed paddock (Fig. 5.2). The salt marsh at Friedrichskoog is further referred to as 'high marsh'. Nomenclature follows van der Meijden (2005).

Table 5.1 Characteristics of the low and the high salt-marsh sites in the ungrazed paddocks.

Site	Low salt marsh Sönke-Nissen-Koog	High salt marsh Friedrichskoog	Reference
Elevation (cm + MHT)	20-40	65-70	Kiehl et al. 1997
Inundations/year	80-200	40-50	Kiehl et al. 1997
Accretion rate (mm/yr)	1-5	2-9	Dierßen et al. 1994
Accretion rate (mm/yr)	11	6	Stock (unpubl. data 2001-2007)
Clay content (%)	30	10	Kiehl et al. 2001
Above-ground peak biomass (g dw/m^2)$^{*)}$	790	777	Dierßen et al. 1994; Kiehl et al. 1997

$^{*)}$4-year average from 2 – 6 years after start of grazing experiment

Vegetation measurements

Canopy height was measured every two metres along transects from the freshwater source near the seawall to the fence at the very wet parts of the low marsh (Fig. 5.1), and to the intertidal flats in the high marsh (Fig. 5.2) in the different grazing treatments within each site. The number and the length of the transects in the two marshes were chosen in accordance with the length and the width of the experimental paddocks. In the low salt marsh, we established five (3 sheep/ha) or six transects (1.5, 4, 10 sheep/ha and the ungrazed paddock). In the high salt marsh, measurements were carried out along four transects for each grazing treatment. Each transect had a length of about 1200 m (Fig. 5.1 and Fig. 5.2). Within each paddock, individual transects were at least 20 m apart. Canopy height was measured with a calibrated stick and a styrofoam disc (20 g, diameter 30 cm). The disc was dropped along this stick and the height of the canopy was recorded to the nearest cm. Measuring points that fell within the drainage ditches which regularly intersected the transects, were skipped.

Statistical analyses

CANOPY HEIGHT

We used a linear regression model to relate canopy height of every two metres to both stocking density and distance from the freshwater source in the low and high salt marsh. The model included linear and quadratic terms in stocking density and distance from freshwater source as continuous variables. We used dummy coding to be able to relate canopy height to possibly different interaction terms involving stocking density and distance to freshwater source for each of the two salt marshes. Since the models contained both linear and quadratic terms in stocking density and distance from freshwater source, we used sequential F tests (for Type1 hypotheses) to account for the dependence of the quadratic on the linear term. The models were fit using ordinary least squares. The ungrazed paddock in the low salt marsh contained dense stands of the tall-growing grass species *Elytrigia atherica* that were laying on the ground due to their heavy spikes. As a result, relatively low canopy heights that were not representative of the actual stem lengths were recorded 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 measurements from the ungrazed paddocks in all statistical analyses.

PROPORTION OF SHORT CANOPY

Canopy height measurements every two metres along each of the transects radiating from freshwater sources in each grazing treatment were assigned to either "short" (canopy height <10 cm) or "tall" (canopy height >10 cm) category. The proportion of short canopy vegetation was then calculated as the total number of times canopy height was <10 cm every 2 metres along each transect divided by the total number of transects in each grazing treatment or paddock to control for the variable number of transects in each treatment. To examine how this proportion varied with stocking density and distance to freshwater source, we regressed it against linear and quadratic terms in both predictors and their interactions using a generalized linear model with a binomial error distribution and a logit link function. The model incorporated site, (*i.e.* a categorical factor with two levels, viz. low and high salt marsh), and used dummy coding of the two sites to accommodate possibly site-specific distinctions in the interaction terms.

Results

Canopy height

When comparing the low and high marsh, the mean canopy height was found to be generally higher in the low than in the high salt marsh. In both the low and high salt marsh, the mean canopy height was similar for 3 sheep/ha, but was significantly higher at 1.5, 4.5 and 10 sheep/ha in the grazed paddocks of the low salt marsh compared to the high salt marsh (Fig. 5.3). In the ungrazed paddock of the low salt marsh, the canopy height was lower compared to the ungrazed paddock in the high salt marsh. This was largely due to the flattened stands of the tall-growing grass species *E. atherica.* In fact, in this paddock shoots actually grew to a length of up to

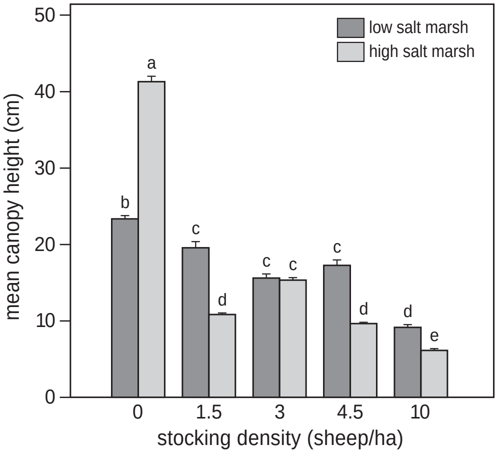

Figure 5.3 Mean canopy height with standard errors for four different stocking densities and the ungrazed control paddock in the low and the high salt marsh, 13 years after the start of the grazing experiment. Different letters indicate significant differences based on multiple pairwise comparisons of means adjusted for multiplicity with the Tukey-Kramer method. The level of significance is $P < 0.001$. The vegetation at the ungrazed low marsh was flattened, hence the vegetation on ungrazed low and high marsh were not taken into account in other analyses.

50 cm. We therefore decided to refrain from using the canopy height in the ungrazed paddocks of both sites in further analyses.

The results reveal where canopy height is highest in relation to stocking density and distance from the freshwater source and how strongly canopy height responds to these gradients, as indicated by the location of peak canopy height in the high and low salt marshes. Stocking density and distance to freshwater source interactively influence canopy height in both high and low salt marshes but this influence varies between the two types of salt marshes (Table 5.2).

Canopy height is higher and more sensitive to increasing stocking density in the low than the high salt marshes. More specifically, canopy height peaks at a low stocking density and decreases more steeply for each unit increase in stocking density in the low than the high salt marsh. Canopy height increased at a steeper rate for each unit increase in distance from freshwater source in the low than high salt marsh (Fig. 5.4). But in both the low and high salt marshes, stocking density exerted a relatively stronger influence on canopy height than distance to freshwater source did (Table 5.2).

In the high salt marsh, canopy height was lowest closest to freshwater source and increased with increasing distance away from the freshwater source and decreasing sheep stocking density. In contrast, canopy height was lowest at intermediate distances from water increasing steeply at further distances from water and decreasing stocking density in the low salt marsh.

Table 5.2 The coefficients (estimate) and their standard errors (SE) for the regression of canopy height on sheep stocking density and distance from the freshwater source in low and high salt-marsh sites 11 years after the start of the grazing experiment.

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

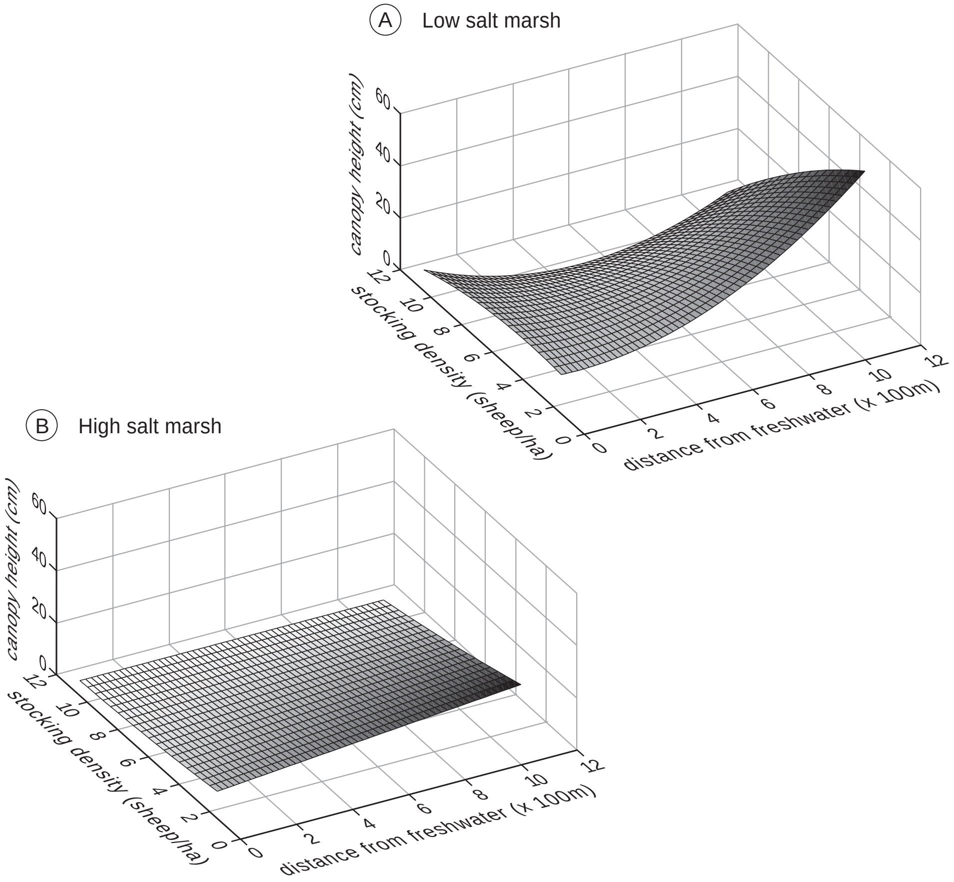

Figure 5.4 The expected mean canopy height (cm) for (A) low and (B) high salt marshes as functions of the distance from the nearest freshwater source and sheep stocking density based on predictions of the regression model.

Proportion of short canopy

Stocking density and distance from freshwater source both significantly influenced the proportion of short canopy (*i.e.* canopy height <10 cm) and the strength of this influence varied significantly between the two salt marshes (Table 5.3). The proportion of short canopy increased with decreasing distance from the freshwater source and increasing stocking density to a maximum closest to the freshwater source and in areas with the highest stocking density, as expected. This pattern was broadly similar between the two salt marshes but was more pronounced in the low than the high salt marsh. The proportion of short canopy was higher and less sensitive to increasing stocking density in the high than the low salt marsh. It also increased more steeply for each unit increase in stocking density in the low than the high salt marsh (Fig. 5.5), implying a stronger impact of grazing on vegetation in the low than the high salt marsh. These results suggest increasing stocking density depletes more forage close to freshwater source and the depletion is more marked in the low than high salt marsh.

Discussion

Our results support the hypotheses that canopy height increased with (1) increasing distance from the freshwater source and (2) decreasing stocking density. Our observations also confirmed the expected decrease in the proportion of short canopy with (3) increasing distance from the freshwater source and (4) decreasing stocking density. The significant interaction effect of grazer density and distance to the freshwater source on both canopy height and proportion of canopy height <10cm indicates that sheep in higher stocking densities removed more biomass and thus had to search for food further away from the freshwater source to meet their requirements. In a salt-marsh study, Andresen et al. (1990) found that the canopy height of the *Aster tripolium* L. layer was increasing with increasing distance to the dike, which these authors interpreted as an indication for a decrease in local grazing intensity.

Table 5.3 The estimated coefficients (estimate) and their associated standard errors (SE) for the regression of the proportion of canopy height measurements <10 cm on stocking density and distance from the nearest freshwater source and their interactions for the low and high salt marshes 11 years after the start of the grazing experiment.

Effect	Estimate	SE	Z	P>|T|
Low salt marsh				
Intercept	0.832	0.162	5.125	<0.0001
Distance from water	-0.371	0.081	-4.568	<0.0001
Stocking density	-0.722	0.061	-11.824	<0.0001
Distance from water × distance from water	0.003	0.017	0.167	0.868
Stocking density × stocking density	0.087	0.005	17.564	<0.0001
Stocking density × distance from water	-0.031	0.007	-4.398	<0.0001
High salt marsh				
Intercept	0.935	0.134	6.979	<0.0001
Distance from water	-0.439	0.042	-10.502	<0.0001
Stocking density	-0.22	0.048	-4.635	<0.0001
Distance from water × distance from water	0.036	0.005	7.809	<0.0001
Stocking density × stocking density	0.059	0.004	14.152	<0.0001
Stocking density × distance from water	-0.013	0.005	-2.664	0.008

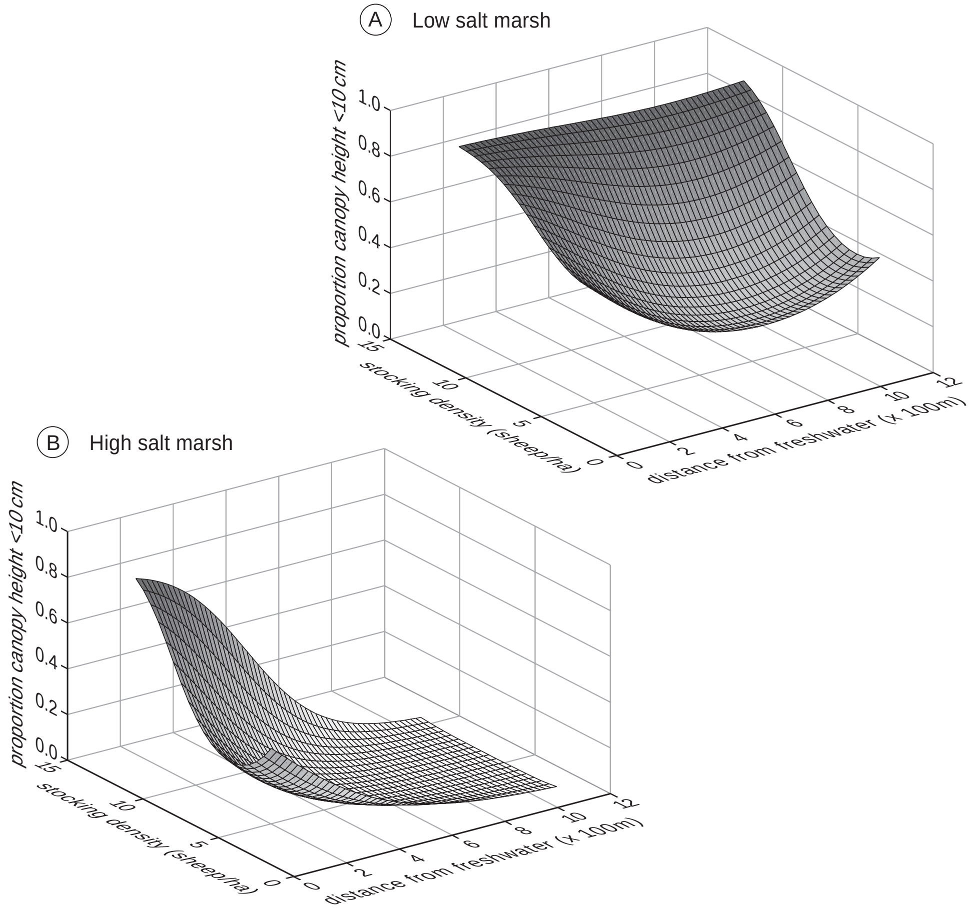

Figure 5.5 The expected proportion of canopy height <10 cm) for (A) low and (B) high salt marshes as functions of the distance from the nearest freshwater source and sheep stocking density from the quadratic regression model.

Additionally, they found the height of *A. tripolium* to decrease with increasing stocking density. The effects in the present study, however, were more pronounced in the low salt marsh than in the high salt marsh. This outcome is probably related to differences in site characteristics, especially the growth rate of the dominant plant species and the resultant forage availability for sheep.

Effect of differences in site productivity

Productivity of a system is important for the understanding of the effects of grazing (Bakker et al. 2006). Low productive areas are more susceptible to herbivory than high productive areas (Larson and Paine 2007). A three-year long comparative study on the effects of moderate and low cattle stocking densities revealed a higher spatial heterogeneity (assessed as the proportion of short and tall canopy) with moderate than with low stocking density in the United Kingdom (Scimone et al. 2007). The opposite pattern was observed in a similar comparative study in a German grassland (Scimone et al. 2007). These contradictory results may be explained by a difference in dominant species and hence to different productivity levels of the grasslands studied. Differences in productivity play an important role in the effects of grazers on the vegetation structure and should be accounted for before effects of other factors (such as different stocking densities) can be reliably revealed.

In our system, the nitrogen mineralization rate was found to be higher in the high marsh than in the low marsh (Kiehl et al. 2001). This suggests that the high marsh could have a higher productivity than the low marsh. A similar above-ground peak biomass was found in both salt-marsh sites, however (Table 5.1; Kiehl et al. 1997). Furthermore, we found a higher proportion of canopy height <10 cm at the high than at the low salt marsh. This seemingly discrepancy can only be understood when taking into account the growth rate of the dominant plant species in the high and the low marsh. Data on the relative growth rate (RGR) show 40 mg/g/day for *P. maritima* and 30 mg/g/day for *F. rubra* after 75 days growth under saline non-flooded conditions in the glasshouse (Rozema et al. 1985). Fast growing plants have a lower leaf dry-matter content (LDMC) (Weiher et al. 1999) than slower growing plants. The lower LDMC enhances decomposition and hence nutrient turnover (Quested et al. 2007). LDMC of P. maritma is 225 mg/g, that of *F. rubra* 300 mg/g according to the LEDA traitbase (Kleyer et al. 2008). We conclude that *P. maritima* is more productive than *F. rubra*. In a sandy salt marsh in The Netherlands, during summer, the annual above-ground net productivity of a community of *P. maritima* was twice as high as in the *F. rubra* communities (767 g dw/m^2 and 388 g dw/m^2; Looijen and Bakker 1987). Furthermore these authors measured a ratio of live:dead biomass in the *P. maritima* community of 2:4 compared to a ratio of only 1:5 in the *F. rubra* communities. Consequently, this implies that the low-salt marsh dominated by *P. maritima* is a relatively high productive marsh. In contrast, the high-salt marsh dominated by *F. rubra* is a relatively low productive marsh.

Our results suggest that the differences in canopy height between the low and high salt marshes associated with varying levels of stocking density correspond with the productivity measurements of the dominant grass species in both salt marshes. This is in line with a study by Mathisen et al. (2010), who carried out a four-year long experiment in which moose grazing was mimicked by year-round clipping of individual species in the field layer of a boreal forest. This resulted in a reduction of the canopy height with increased clipping or moose density along a productivity gradient. Mathisen et al. (2010) showed that the effect of moose browsing on canopy height was negative in low productive environments, but positive in more productive environments. Suominen et al. (2008) found in the same experiment that the impact of moose density affected spider richness positively at productive sites and negatively at unproductive sites. These results are in agreement with our findings with respect to effects of different stocking densities in ecosystems with different productivity.

Stocking density

The negative relationship between stocking density and canopy height accords with and reinforces similar findings of grazing experiments by Hester et al. (1996), Berg et al. (1997), Pakeman et al. (2003), Isselstein et al. (2007) and Celaya et al. (2010). However, these authors did not find a positive relation between herbivore density and the area of short canopy as we found in the present study. Scimone et al. (2007), however, compared the effects of moderate and low stocking densities in a three-year experiment with paddocks ranging from 0.4 to 3.6 ha in four European countries. Low stocking density implied stocking densities 30–40% lower than with moderate stocking density. They found that in two out of four study sites a higher proportion of short canopy was recorded with moderate than with low stocking densities. These two sites were moderately productive, whereas no differences were recorded in the two more productive sites. We also found that at all stocking densities, the proportion of short canopy was always greater at the relatively low productive high salt marsh with *F. rubra* than at the relatively high productive low salt marsh with *P. maritima*. But how does this match with the similar above-ground peak biomass at both sites? From the grazer point of view, the forage quality may play a role. On a sandy salt marsh in The Netherlands, cell-wall content ranged between 50-60%, and amounted to 65% during summer for *P. maritima* and *F. rubra*, respectively. Crude protein content ranged from 18 to 24% for *P. maritima* and amounted to only 15% for *F. rubra*, respectively (Bakker 1989). On a clay marsh in The Netherlands, crude-protein content was 20% for *P. maritima* and 15.5% for *F. rubra*, respectively (Nolte unpubl. data). The combination of higher productivity with fast regrowth of tillers and better forage quality of *P. maritima* than *F. rubra* makes that sheep will remove the same biomass from a smaller area (resulting in a low proportion of canopy height $<$10 cm, Fig. 5.5) in the low salt marsh than in the high salt marsh. This is in agreement with the notion that short canopy or grazing lawns are induced by herbivores when they select for good forage quality and maintain their own grazing lawns by returning to patches of short canopy harbouring protein-rich tillers and a high leaf:stem ratio (Ydenberg and Prins 1981, Mc Naughton 1984, Dumont et al. 2007b).

Distance to freshwater source

The expected effect of distance to the freshwater source on the canopy height could be found in our results, especially in lower stocking densities. Esselink et al. (2002) demonstrated that this pattern in canopy height reflected the spatial distribution of cattle in a similarly arranged mainland salt marsh. Patterns of shorter vegetation close to freshwater sources were also recorded by Brongers et al. (1990) in cattle-grazed salt marshes and Kiehl et al. (1996) in a sheep-grazed salt marsh. Adler and Hall (2005) modelled the effects of livestock freshwater sources on the height of the canopy with different numbers of animals. Their model predicts that an increase in the number of animals will increase the portion of the gradient affected by grazing, since animals will have to walk farther to meet their daily requirements.

Implications for management

Low canopy created by grazing reduces competition for light between plant species, and enhances both seedling recruitment and establishment of species, which in turn leads to an increase in local plant diversity (Collins and Barber 1986). After abandonment, a salt marsh that was initially intensively grazed, (first few years) produces many flowering plants and attracts many insects (Irmler and Heydemann 1986). However, after a longer period of abandonment (over 10 years) tall-growing plant species can take over. As a result, characteristic salt-marsh plant species (Bos et al. 2002), spring-staging migratory geese (Bos et al. 2005) and some invertebrates (Pétillon et al. 2007) decrease or eventually disappear. Other invertebrates (Pétillon et al. 2005) and breeding birds (Norris et al. 1997) prefer patches with taller canopy. Hence, salt marshes with both short and tall canopy may harbour higher biodiversity compared to intensively grazed or abandoned salt marshes.

Our results show the importance of plant species composition in predicting the impact of various densities of herbivores on the structure of grassland vegetation. In salt marshes dominated by *P. maritima*, a higher stocking density is needed than in marshes dominated by *F. rubra* to ensure the same proportion of short canopy. Furthermore, herbivore density and the position of other resources such as water are important in predicting and modifying biodiversity of grasslands. Hence, they play an important role in management options. Especially the proportion of short and taller canopy is important for species richness of plants, small vertebrates and invertebrates. The spatial arrangement of short and tall canopy with various stocking densities, as reported by Berg et al. (1997) and their consequences for diversity of plants and various groups of animals should be further studied.

Acknowledgements

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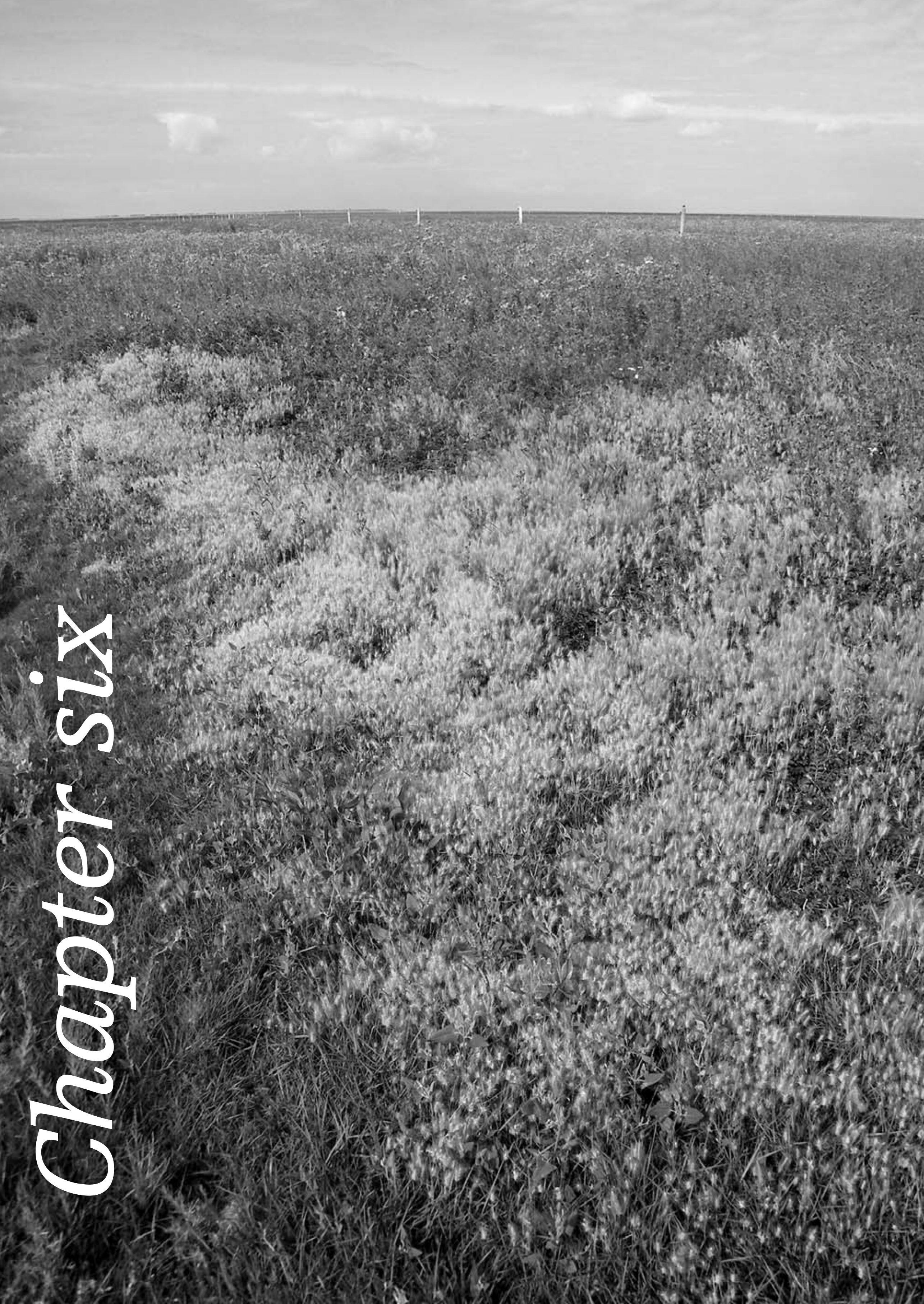
Chapter six



6

Herbivore species and density affect vegetation-structure patchiness in salt marshes

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Abstract

The importance of spatial patterns for ecosystem functioning and biodiversity has long been recognized in ecology. An important driver leading to spatial patterns in the vegetation structure is grazing by herbivores. How different herbivore species and their densities affect vegetation-structure patchiness is, however, poorly understood, and very few studies have simultaneously incorporated the underlying abiotic patterns. We investigated how different herbivore species and densities affect vegetation-structure patchiness. We conducted an experiment in a semi-natural grassland using horses and cattle in two densities each (0.5 animal/ha and 1.0 animal/ha). Transects of 25 m length were installed in the experiment and canopy height and soil elevation were measured every 25 cm to explore patterns in canopy height. Geostatistical variogram models were fitted to all transects using elevation as a covariable to correct for the underlying abiotic patterns. The range (as a measure of size of patches characterized by similar canopy height) and sill (as a measure for heterogeneity) of the variogram model were compared between horses and cattle and between two densities. Mean canopy height was lower in horse-grazed compared to cattle-grazed treatments and lower in higher herbivore densities. Patch size (range) (patches of similar canopy height) was significantly larger in horse-grazed treatments, and a trend of larger patch size was found for higher densities with both herbivore species. While herbivore species had no clear effect on heterogeneity, a trend of a higher heterogeneity (sill) was found in low densities. We found that the two herbivore species and densities have differential effects on canopy height, patch size and heterogeneity. Although some of these results were only found as trends, our study has important implications for conservation management of grazed salt marshes. To form heterogeneous small-scaled vegetation patterns we would generally recommend applying grazing with (1) cattle rather than horses, and (2) at low rather than high herbivore densities. We further discuss the relevance of our findings for other grazed ecosystems.

Introduction

The importance of spatial patterns in ecosystems has long been recognized in ecology (*e.g.* reviews by Rietkerk et al. 2004, Rossignol et al. 2011). Spatial patterns can be an important factor allowing species to coexist and thus may increase biodiversity (Olofsson et al. 2008). Moreover, they could be used to assess the stability of ecosystems *e.g.* in arid regions, because certain patch formations can indicate an imminent catastrophic shift (Rietkerk et al. 2004). In nature three general types of patterns can be detected (Fortin and Dale 2005): (1) trends or gradients, (2) patchiness and (3) randomness. Trends or gradients are generally found at large scales (kilometres), while randomness is mostly found at the smallest scales (centimetres). Patchiness is often detected at intermediate scales. A good example for patchy vegetation-structure is grazed grassland with typical and distinct co-occurring areas of short and tall canopy (*e.g.* Adler et al. 2001). While these patches clearly differ in canopy height, a random pattern is often found within these patches on smaller scales where short and tall canopy show no spatial autocorrelation. In these current times of on-going global change it becomes increasingly important to understand the mechanisms leading to spatial patterns to better assess ecosystem stability, and increase heterogeneity and biodiversity (Li 2000).

Spatial patterns emerge in different ecosystems and are induced by various mechanisms (Rietkerk et al. 2004). These mechanisms can be subdivided in plant-soil (*e.g.* Rietkerk et al. 2004) and plant-herbivore feedbacks (*e.g.* Adler et al. 2001). Plant-soil feedbacks are common in (semi)arid ecosystems (Rietkerk et al. 2004), where plant roots increase the water infiltration rate and reduce the evaporation of water from the soil by shading. Thus, once present, plants increase the local availability of water compared to the surrounding bare ground, which leads to a distinct spatial pattern of vegetated and bare patches. Plant-herbivore feedbacks, and resulting spatial patterns, have extensively been documented in grasslands, where herbivores stimulate the productivity of grass by grazing and keep re-visiting the previously grazed patches of short, high-quality grass, resulting in the so called ‘grazing lawns’ (*e.g.* McNaughton 1979, McNaughton 1984, Adler et al. 2001). In contrast to the selective feeding on high-quality grazing lawns, the avoidance of tall reproductive grass or plant species with defence mechanisms can be another cause for patch formation (Rossignol et al. 2011). The avoidance of such plant species which possess defence mechanisms can facilitate non-defended plants (*e.g.* Smit et al. 2010), and is known as associational defence (Hay 1986) or associational resistance (Smit and Ruifrok 2011). While plant-herbivore feedbacks have been studied in a wide range of grasslands, very few consider how underlying abiotic patterns might influence the outcome (but see Berg et al. 1997, Adler et al. 2001).

Information on the differential effects of different herbivore species on vegetation-structure patchiness is still scarce (*e.g.* Knapp et al. 1999, Metera et al. 2010, Dumont et al. 2012). The expected differences on the vegetation-structure patchiness might be caused by differences in selectivity and forage requirements among herbivore species. For example, generalists are expected to show random grazing patterns (Adler et al. 2001), but these random grazing patterns might not lead to the establishment of patchy vegetation-structure pattern. The selectiveness of herbivores is also directly linked to both nutrient (WallisDeVries et al. 1999) and total forage requirements (Duncan et al. 1990, Vulink and Drost 2001, Menard et al. 2002). For example, cattle as ruminants require less food per day, compared to horses as hind-gut fermenters (Duncan et al. 1990, Vulink and Drost 2001, Menard et al. 2002). Consequently, horses remove a higher amount of biomass per animal and are probably less selective. Therefore, horses compared to cattle are expected to produce a shorter canopy height and a less small-scaled vegetation pattern with a larger patch size of short canopy and lower heterogeneity.

Herbivore density greatly influences vegetation characteristics. An increase in herbivore density predictably causes a decrease in mean canopy height (Berg et al. 1997, Rossignol et al. 2011). The effect of different herbivore densities on patchiness is, however, more complex as herbivores are less selective in high densities (Augustine and McNaughton 1998). Berg et al. (1997) found that intermediate herbivore densities cause a pattern of short and tall patches with a high heterogeneity, while very high densities and the cessation of grazing caused a homogeneous short and tall canopy, respectively. Similar results were found in a model approach by de Knegt et al. (2008). A higher herbivore density leads to a higher removal of biomass (*e.g.* Berg et al. 1997, Kiehl et al. 2001, de Knegt et al. 2008). Therefore, higher herbivore densities are expected to generate a shorter mean canopy height. Furthermore, herbivores in higher densities probably become less selective and have to include unpreferred food items into their diet (Crawley 1983). This may lead to a less small-scaled pattern and we would, therefore, expect the patch to increase and the heterogeneity to decrease in higher densities.

The impact of grazing on grassland patchiness and biodiversity offers possibilities for nature management to apply grazing as a management tool (Metera et al. 2010). Whether grazing will indeed increase patchiness in grassland ecosystems (Adler and Lauenroth 2000), depends on factors such as underlying abiotic patterns (Adler et al. 2001), herbivore density (de Knegt et al. 2008) and selectivity of herbivores (Adler et al. 2001), which might differ between herbivore species. For example, grazing was found to either increase or decrease the vegetation heterogeneity in different communities within the same area in Spain (Alados et al. 2005). Therefore, the effect of grazing on different communities within a single area needs to be assessed carefully before application of grazing as a management tool. Grazing for nature conservation is nowadays often applied in salt marshes along the coast of the Wadden Sea (Esselink et al. 2009), because grazing at intermediate stocking densities positively influences the plant-species richness (*e.g.* Bakker et al. 1993, Bakker et al. 2003, Bos et al. 2002) and the abundance of birds such as migratory waterfowl (van der Graaf et al. 2002). Salt marshes were traditionally used for livestock grazing at high densities (Esselink et al. 2000). In the past century the value of salt marshes as an important habitat for plants and animals was recognized and protected areas were installed (Kiehl et. al 1996). Due to regular inundations of sea-water these marshes are dominated by salt-tolerant plant species while trees are absent. Plant-species composition shows a clear zonation from the most frequently flooded lowest areas (pioneer zone), over the intermediate zone (low marsh) to the seldom-flooded, higher-elevated high marsh zone (Adam 2002). Salt marshes along the Dutch Wadden sea mainland-coast can be classified as semi-natural grasslands as they developed from man-made sedimentation-field structures (Esselink et al. 1998). They are therefore characterised by a regular pattern of straight drainage ditches rather than natural creeks.

To investigate how different herbivore species and densities influence vegetation-structure patchiness we conducted an experiment in two dominant plant communities of a salt marsh (low and high salt-marsh zone) with a long grazing history. By including measurements of the soil elevation, we were able to exclude the effect of the underlying abiotic pattern on the vegetation and analyse the patterns induced by the animals. We expected to find differential impact of (a) livestock species and (b) herbivore density on the vegetation structure. More specifically, we expected: (1) the mean canopy height to be shorter, (2) the size of patches of short and tall canopy to be larger, and (3) the spatial heterogeneity to be lower in horse-grazed versus cattle-grazed grassland, and in grassland with higher herbivore densities.

Materials and methods

Study area and set-up

The study area ‘Noord-Friesland Buitendijks’ is a temperate salt marsh situated at the northern mainland coast of The Netherlands (53°20'11", 5°43'40", Fig. 6.1) and is part of the UNESCO world heritage site Wadden Sea. The average yearly mean temperature is 9.5°C and the average yearly precipitation is 820 mm (data Royal Netherlands Meteorological Institute). Local tidal amplitude is 2.1m.

The study area was intensively grazed by cattle or horses for the past 20 years before the establishment of the experiment (Esselink et al. 2009). The experimental setup consists of two blocks, which are approximately 1.4 km apart. In 2010 we installed four different grazing treatments within each block; each grazing treatment in a paddock of approximately 11 ha. Treatments include grazing with either horses or cattle in low (0.5 animal/ha) or high (1.0 animal/ha) densities (Fig. 6.1). Livestock was obtained from local farmers and grazing took place each year from May until October. Livestock had access to a freshwater source situated in the south of each paddock in the high marsh.

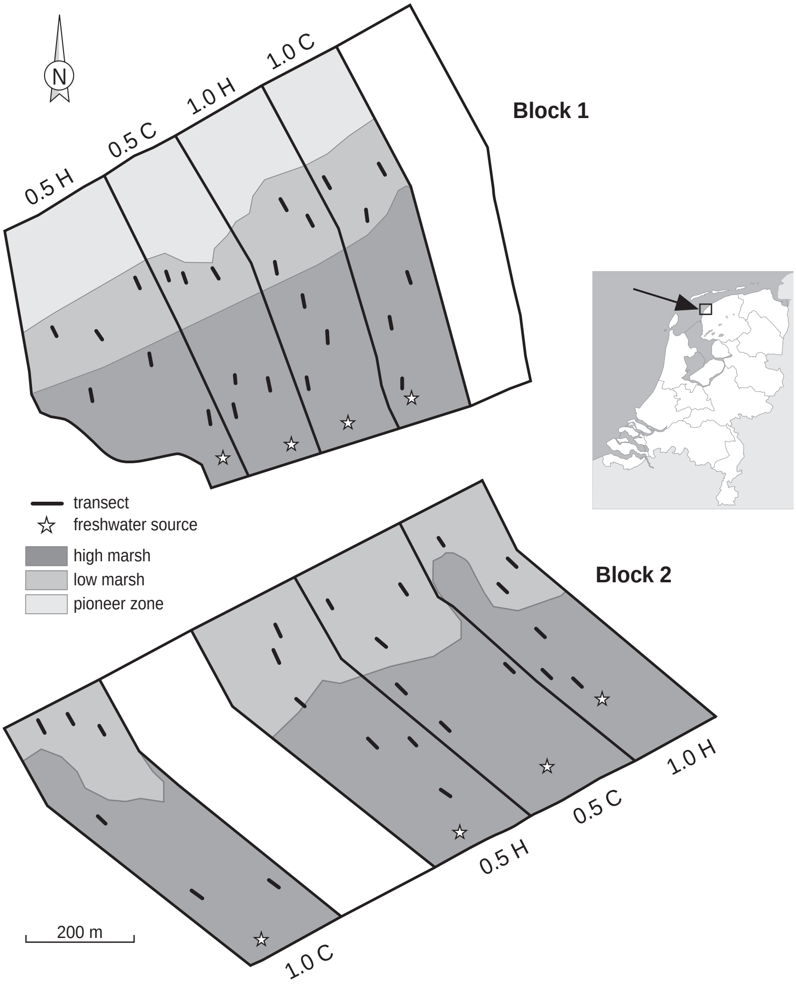

Figure 6.1 The position of the research area 'Noord-Friesland Buitendijks' at the coast of The Netherlands and a schematic overview of the experimental setup in block 1 and block 2. The experimental treatments are indicated by H = horses; C = cattle; 0.5 = 0.5 animal/ha and 1.0 = 1.0 animal/ha. The position of transects (short lines) and the freshwater source (☆) is shown within the different marsh zones. Marsh zones are indicated by different shades of grey. The additional paddock (white) is subject to a rotational grazing treatment and was not used in this study.

We installed 24 transects of 25 m per block, with six transects per treatment. The transect position (Fig. 6.1) was randomly chosen with the constraint that three transects per treatment were situated in the high marsh zone and the low marsh zone, respectively. No transects were installed in the pioneer zone, because it is scarcely used by livestock. All transects were orientated parallel to the drainage ditches to avoid vegetation-structure patchiness caused by these artificial structures. We measured the canopy height and elevation every 25 cm along each transect. The canopy height was measured to the nearest cm using a Styrofoam drop disc with a diameter of 25cm and a weight of 75g and a calibrated stick as a ruler (Stewart et al. 2001). The elevation was measured optically by means of a levelling instrument (Spectra Precision® Laser LL500 and Spectra Precision® Laser HR500 laser receiver by Trimble) relative to the Netherlands Ordnance Datum (NAP), and transformed to elevation above local mean high tide (MHT; 1.0 m +NAP). Measurements were performed in August 2011 when vegetation approximately reached its peak standing biomass.

Statistical analysis

CANOPY HEIGHT

Data exploration showed canopy height to have a normal distribution and homogeneity of variance. Block was found to have an effect on mean canopy height. We, therefore, modelled the mean canopy height applying a linear mixed effects model with block as a random factor (Zuur et al. 2009) using the R package 'nlme' (Pinheiro et al. 2013). The full model included canopy height as response variable, and herbivore species, herbivore density, marsh zone and all two-way interaction effects as explanatory variables. Stepwise backward model selection was performed by dropping each term from the model and performing comparisons with the full model using ANOVA (Zuur et al. 2009). To perform multiple comparisons of the mean canopy height between treatments we used the 'glht' (generalized linear hypothesis testing) command from the R package 'multcomp' for mixed effects models (Hothorn et al. 2008). All statistical analyses were performed using the software R version 2.15.0.

VARIOGRAM MODELS

To quantify the patch size and heterogeneity of the vegetation structure in the transects we used geostatistical variogram models (*e.g.* Palmer 1988, Dale et al. 2002, Murwira and Skidmore 2005, de Knegt et al. 2008). A variogram model is a function of the spatial autocorrelation of two points on a transect against the distance between these points (lag) (Eq. 1; Diggle and Ribeiro jr. 2007):

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_{i+h})]^2 \qquad \text{(Eq. 1)}$$

where $\gamma(h)$ is the variance at lag h, N(h) the number of observations for lag h, $z(x_i)$ the value of the regionalized variable at location x_i, and $z(x_i+h)$ the value of the regionalized variable at lag h from x_i (Murwira and Skidmore 2005, de Knegt et al. 2008). We used the R package 'automap' (Hiemstra et al. 2009) to fit a variogram model to the data for each transect. Among exponential, spherical or Gaussian models the best fitting model was chosen on the basis of the residual sum of squares (Webster and Oliver 2007). The bin size for the fitting process was chosen to be 25

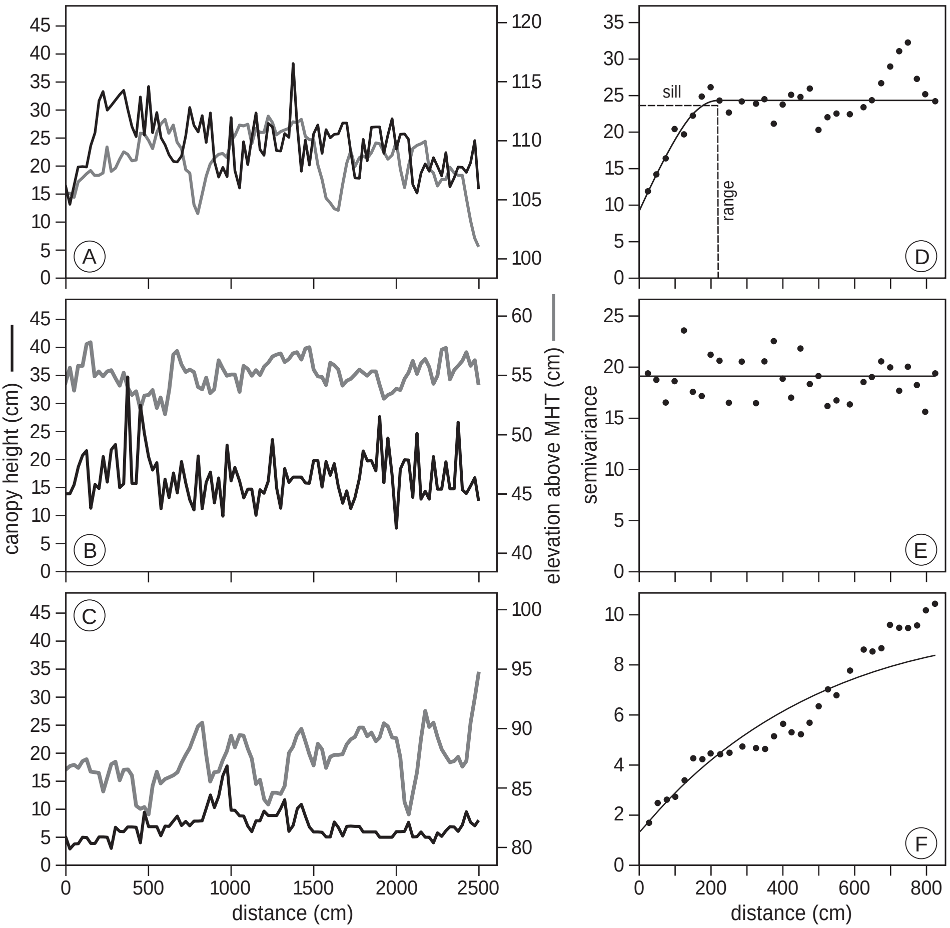

Figure 6.2 Examples for the three different types of pattern (patchy A, random B, gradient C). The values of canopy height and elevation are plotted along transects in panels (A-C). The resulting variogram for each transect is shown in panel D-F. In panel D the range with its inferred patch size and sill are indicated by dashed lines within the graph.

cm, which is the diameter of the drop disc and the smallest possible distance between two points (lag h) in transects (Diggle and Ribeiro jr. 2007). The elevation of the points along the transects was used as an explanatory variable to account for the trend in canopy height caused by the influence of elevation (Diggle and Ribeiro jr. 2007). In this way the effect of underlying abiotic patterns on vegetation-structure patchiness was excluded and the vegetation-structure patterns observed could be solely attributed to the effect of herbivore grazing. We extracted the two structural parameters range and sill from the fitted variogram model (Fig. 6.2D) and used them as a measure for patch size and heterogeneity, respectively (Murwira and Skidmore 2005, de Knegt et al. 2008). In case of complete spatial independence in the data, *i.e.*

where the variogram model showed a horizontal line (Fig. 6.2E; Palmer 1988), we chose the Nugget-model (Augustine and Frank 2001). Transects where the variogram model did not show a clear sill (Fig. 6.2F), *e.g.* because of a strong underlying gradient in the data, were excluded from further analysis. In total, five out of all 48 transects had to be excluded.

Patch size (range) and heterogeneity (sill)

The range and sill as measures of the patch size and heterogeneity of the vegetation structure were both found to follow a gamma distribution and matched the assumption of homogeneity of variance. In both cases, block did not have an effect and was thus not used as a random factor. In order to analyse the effect of the treatments on range and sill, we applied generalized linear models (GLM) with the 'glm' function of the R base package with a gamma family and the inverse link-function (Zuur et al. 2009). We included the range and sill as response variables, and the herbivore species, herbivore density, and salt-marsh zone, as well as all two-way interaction functions, as explanatory variables in the full model. The salt-marsh zone was included to investigate whether the effects of the treatments differ in two zones within the same paddock. Backward stepwise model selection was performed using the 'drop1' command based on χ^2-test (Zuur et al. 2009).

Results

Canopy height

The mean canopy height in transects varied between 4.7 cm and 24.2 cm. The final model indicates a significant effect of herbivore species ($DF = 1$, $F = 12.471$ $P < 0.001$) and herbivore density ($DF = 1$, $F = 26.751$, $P < 0.001$) on mean canopy height. A lower mean canopy height was found in horse-grazed (mean 11.7 cm, SE 0.9) compared to cattle-grazed treatments (mean 15.0 cm, SE 0.9) and in higher (mean 10.9 cm, SE 0.8) compared to lower herbivore densities (mean 15.8 cm, SE 0.8; Fig. 6.3).

Patch size (range)

The patch size (range) of similar canopy height in all transects was between 0 cm in case of random patterns (no spatial autocorrelation) and 684 cm, with a mean of 141.6 cm. The model showed a significant effect of herbivore species on the range (Fig. 6.4; $t = -2.256$; $P < 0.05$), with a higher range in horse-grazed (mean 186.9 cm, SE 44.4) compared to cattle-grazed treatments (98.4 cm; SE 12.2) (Fig. 6.4). Density or zone had no significant effect on the range, but there was a trend for a higher range in high (mean 166.8 cm; SE 40.7) compared to low herbivore densities (mean 117.7 cm; SE 23.6) and in the low marsh (mean 162.3 cm; SE 41.3) compared to the high marsh (mean 121.9 cm; SE 23.1).

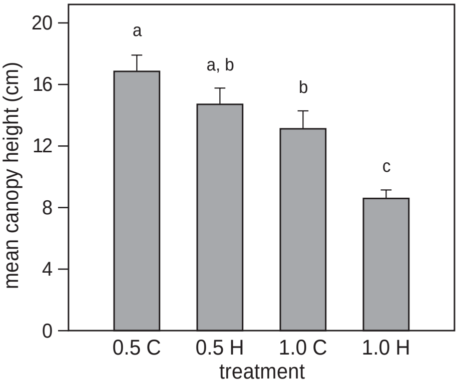

Figure 6.3 The mean canopy height for transects in different treatments. Error bars indicate standard error and letters indicate significant differences between treatments.

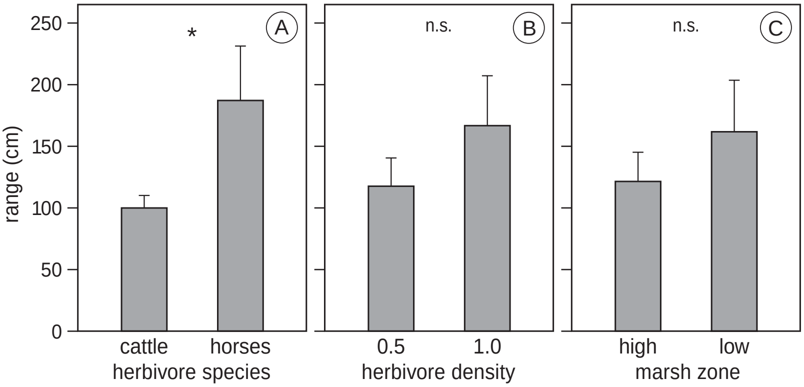

Figure 6.4 The mean range (patch size) in transects comparing (A) herbivore species, (B) herbivore densities and (C) the different marsh zones. Error bars indicate the standard error. Significance is indicated by (*) and non-significance is indicated by (n.s.).

Heterogeneity (sill)

The heterogeneity (sill) of the vegetation structure lay between 1.1 and 35.3 with a mean value of 11.2. The values were significantly higher for the high marsh than for the low marsh ($t = 2.189$; $P < 0.05$) (Fig. 6.5). We did not find a significant effect of herbivore species or herbivore density on the sill in the model. There seemed to be a higher sill in low (mean 13.0; SE 1.8) compared to high herbivore densities (mean 9.4; SE 1.4), but this difference was not significant.

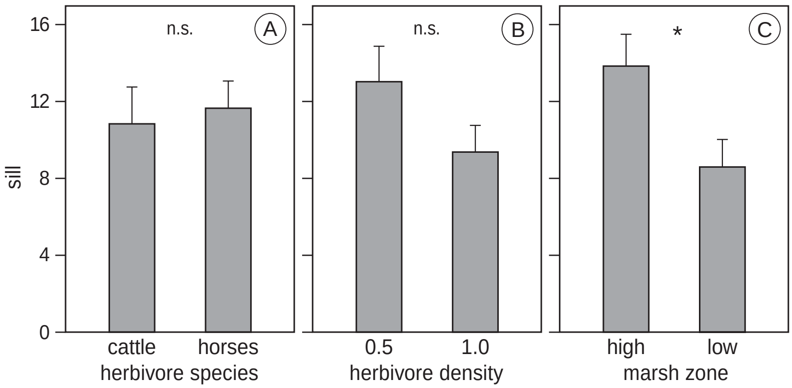

Figure 6.5 The mean sill (heterogeneity) in transects comparing (A) herbivore species, (B) herbivore densities and (C) the different marsh zones. Error bars indicate the standard error. Significance is indicated by (*) and non-significance is indicated by (n.s.).

Discussion

In this study we assessed the effect of herbivores on the patchiness and heterogeneity of vegetation structure. We accounted for the effect of the underlying abiotic patterns by using the elevation as an explanatory variable in the variogram model. Underlying abiotic patterns were thus not influencing the resulting variogram parameters, which were therefore only affected by the treatments. We found clear differences in the effect of both herbivore species and herbivore densities on mean canopy height. We also found clear effects of herbivore species on patch size (range), while effects on vegetation-structure heterogeneity were less clear but revealing some trends. We here discuss the underlying reasons for our findings and the relevance for conservation and restoration management for salt marshes and for grazed ecosystems in general.

Canopy height

We found that horses generated on average a shorter canopy than cattle (Hypothesis 1a). This result is likely caused by differences in physiology and anatomy between these herbivore species. Horses have a higher forage intake per day compared to cattle (Duncan et al. 1990, chapter 2) and their higher removal of biomass generates a shorter canopy. A higher amount of trampling might also add to a stronger reduction of biomass in horse-grazed treatments, as these animals were also found to cover longer distances per day (chapter 2). Furthermore, the mouth anatomy differs between the herbivore species. Horses use their pair of incisors to cut grass, and are thus able to create much shorter swards compared to cattle, which rip off parts of the vegetation with their tongue (Gordon 1989). Moreover, mean canopy height was lower under higher herbivore densities, because more biomass is removed by a higher number of animals as previously found by other studies (Hypothesis 1b) (Berg et al. 1997, Rossignol et al. 2011). Our results show that measures such as livestock units (LU) per surface area are not directly comparable between herbivore species, as these have different forage requirements and therefore create a different grazing intensity. Thus, the impact of herbivore density is species dependent, and herbivore density and species should therefore be chosen carefully for conservation management.

Patch size (range) and heterogeneity (sill)

The hypothesis that horses generate larger patches of similar canopy height compared to cattle (Hypothesis 2a) was supported by the results of the experiment. The larger patches were probably caused by the aforementioned higher removal of biomass and differences in mouth anatomy between cattle and horses. While horses produce a very short sward, cattle rip off parts of the vegetation with their tongue (Gordon 1989, Dumont et al. 2012). These behavioural differences may well explain the more small-scaled pattern indicated by a significantly smaller range in the cattle-grazed treatments and large patches of very short canopy in the horse-grazed treatments. The expected effect of herbivore density on patch size (Hypothesis 2b) and heterogeneity (Hypothesis 3b) was in both cases only found as a trend. There was no evidence supporting the hypothesis of higher heterogeneity in cattle compared to horse-grazed treatments (Hypothesis 3a). One of the reasons for the non-significant trends is probably the relative short duration of the experiment. In contrast to our two year study, Olofsson et al. (2008) found an effect of the exclusion of rabbit on species-distribution patterns after five years, while Alados et al. (2005) found differences in species-distribution patterns between grazed and ungrazed sites that were abandoned for even 10 or 30 years. Additionally, the differences in the vegetation between grazed and ungrazed treatments in these studies are likely to emerge faster than the differences between grazing treatments studied here. However, we would expect changes in the vegetation-structure patterns to emerge faster than the aforementioned species-distribution pattern (Alados et al. 2005, Olofsson et al. 2008), because the turnover of species will take some years while the effect of grazing on vegetation structure is more direct. Prolonged following of the development of vegetation structure would allow verification of the here described trends.

Another possible reason for the contrasts between treatments to be smaller than expected are the relatively small differences in palatability between the plant species involved. If differences in quality between species are low, the extra effort of searching will not increase the gain and we would expect to find random grazing pattern (Arnold 1987, Adler et al. 2001). Yet, even in a study where both short and tall patches were dominated by a single plant species, Berg et al. (1997) detected micropatterns at the scale <1m formed by grazing. They found that sheep were grazing on tall patches in May to improve their intake rate when tiller density was low, while in September, when tiller density was high, sheep selected short patches because of their slightly higher quality. The reason for patch formation found by Berg et al. (1997) in a system dominated by a single plant species might be explained by the higher selectiveness of sheep compared to cattle (Jensen 1985). A study of animal behaviour in the same experiment as the present study revealed small differences in the diet choice of herbivore species (chapter 2). In line with other studies (*e.g.* Gordon 1989) horses were found to include a higher concentration of neutral detergent fibre (NDF) in their diet compared to cattle, but no differences could be detected between herbivore densities (chapter 2). Thus, it should be further investigated how under the described treatments patchiness is created in systems with small and large quality differences between plant species.

Furthermore, our study shows that grazing intensities might differ generally between herbivore species and locally between different parts of the study area. Thus far, these factors are seldom included in studies on the effect of herbivores on vegetation patchiness (Adler et al. 2001). As already mentioned horses require more forage per day compared to cattle (Duncan et al. 1990) and therefore the grazing intensity (amount of biomass removed) is generally higher in horse- compared to cattle-grazed treatments of the same herbivore density. This finding was supported by focal observation of herbivores in our study area (chapter 2). Grazing intensities can also differ locally within a single treatment because of the spatial distribution of the animals (Adler et al. 2001). The spatial distribution of both wild and domestic herbivores is often influenced by factors such as the accessibility of fresh water (Adler et al. 2001). Grazing intensity in salt marshes was found to decrease with increasing distance from the freshwater source with sheep (Kiehl et al. 1996) and cattle (Esselink et al. 2002). Indeed such grazing gradients influenced by the distance to the freshwater source were also detected for our study area, more in cattle than in horse-grazed treatments (chapter 2). For this reason, grazing pressure can be considered higher close to the freshwater source in the high-marsh zone. These differences in local grazing intensity might also be the reason for the significant influence of marsh zone on heterogeneity. The very low local grazing intensity in the low marsh might have led to an homogeneous vegetation, while the grazing activities in the high marsh might have increased the heterogeneity. Other studies also found the effect of grazing on vegetation heterogeneity to differ between parts of the same study area (Alados et al. 2005), but do not mention spatial distribution of the animals. The spatial distribution of animals in our study results in a whole spectrum of different local grazing intensities, not only between treatments, but within a single treatment. This gradient of local grazing intensity leads to the large variation of the range and sill within one treatment and marsh zone. This large variation increases the standard error and might be the reason for the differences to be non-significant with the sample number in this study.

The recommended choice of grazing management largely depends on the nature management target (Bakker et al. 2003). Our study shows that herbivore density affects mean canopy height, and hence needs to be carefully chosen (Knapp et al. 1999, Metera et al. 2010). Moreover, herbivore species affect especially patch size of the vegetation. In general, for increased vegetation-structure patchiness in salt marshes, we would recommend the use of cattle rather than horses and low rather than high herbivore densities. The choice of herbivore density and species is likely to be of great importance for other grasslands too. In agricultural systems, this choice can create valuable refuges for endangered plant and animal species. This is especially important in regions where the human population is growing and the available area for nature is declining. In African savannahs for example, pastoral land adjoining protected areas is seasonally used by wild herbivores and creating protected areas which mimic moderate pastoral use is advised (Bhola et al. 2012). In other grassland areas, such as North-American prairies, where the native large herbivores such as Bison are no longer present, domesticated cattle might have a different effect on the ecosystem (Knapp et al. 1999). For grasslands in general, vegetation-structure patchiness is important because a high structural diversity increases the species richness of plant and animal species (Olofsson et al. 2008). Therefore the potential differential impact of various herbivore species and densities, as investigated in this study, should be considered before an adequate nature management can be chosen.

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Chapter seven

7

Measuring sedimentation in tidal marshes: a review on methods and their applicability in bio-geomorphological studies

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Abstract

It is increasingly recognised that interactions between geomorphological and biotic processes control the functioning of many ecosystem types as described *e.g.* by the ecological theory of ecosystem engineering. Consequently, the need for specific bio-geomorphological research methods is growing recently. Much research on bio-geomorphological processes is done in coastal marshes. These areas provide clear examples of ecosystem engineering as well as other bio-geomorphological processes: Marsh vegetation slows down tidal currents and hence stimulates the process of sedimentation, while vice versa, the sedimentation controls ecological processes like vegetation succession. This review is meant to give insights in the various available methods to measure sedimentation, with special attention to their suitability to quantify bio-geomorphological interactions. The choice of method used to measure sedimentation is important to obtain the correct parameters to understand the biogeomorphology of tidal salt marshes. This review, therefore, aims to be a tool for decision making regarding the processes to be measured and the methods to be used. We, subdivide the methods into those measuring suspended sediment concentration (A), sediment deposition (B), accretion (C) and surface-elevation change (D). With this review, we would like to further encourage interdisciplinary studies in the fields of ecology and geomorphology.

Introduction

The ability of plants or animals to directly or indirectly alter their own physical environment was already recognized by Darwin in the 19th century in his studies on earthworms (see Butler and Sawyer 2012). More recently, this phenomenon has been extensively described within the context of the ecological theory of ecosystem engineering (Jones et al. 1994), highlighting that certain organisms can modify their physical environment, and that these habitat modifications can have a feedback effect on the performance of the organism. For example, sea grasses or salt-marsh vegetation directly trap fine sediments by slowing down water currents (*e.g.* Bouma et al. 2005), while beavers indirectly influence their environment by building dams (*e.g.* Wright et al. 2002). In both these examples of ecosystem engineering, the habitat modification has a positive feedback effect on the organism. More recently, geomorphologists also highlighted the role of mutual feedbacks between organisms and their geomorphological environment in the evolution of landforms and landscapes, and this has increased the number of recent studies in the field of biogeomorphology (Darby 2010, Murray et al. 2008, Reinhardt et al. 2010, Corenblit et al. 2011) or zoogeomorphology (Viles et al. 2008, Statzner 2012). However, there are still many questions unanswered about the connection between the physical environment, and the ecology and evolution of species as summarised by Corenblit et al. (2011). Additionally, the idea to include ecosystem engineers in practical solutions for ecosystem restoration and the provision of ecosystem services has been proposed (Byers et al. 2006). However, objective monitoring and assessment of such solutions are still limited and further studies are needed on the application of ecosystem engineers (Borsje et al. 2011).

Studies connecting geomorphological and ecological processes are often performed by researchers with either an ecological or a geomorphological background. However, this interdisciplinary field requires geomorphologists to understand ecology (Corenblit et al. 2011) and *vice versa*. Ecologists need to gain knowledge of geomorphology to measure, for example, the effect of ecological processes on sedimentation in tidal areas. However, sharing of knowledge on methods and techniques rarely occurs between the disciplines (Reinhardt et al. 2010). We aim to amend this state of affairs with this review.

Tidal Marshes

The main focus of this review lies on coastal salt marshes, which can be found throughout the world along coasts that experience low wave action and sufficient fine sediment supply (Bakker et al. 1993). Sedimentation processes in intertidal areas and their link to ecological processes have lately been the object of many studies (*e.g.* Borsje et al. 2011, Eklöf et al. 2011, Mermillod-Blondin 2011). One important question in coastal ecology is how coastal marshes will cope with climatic changes, such as enhanced sea-level rise (SLR) (*e.g.* Temmerman et al. 2004a, Kirwan et al. 2010). A key mechanism that governs the ability of salt-marsh ecosystems to maintain elevation with rising sea level (*e.g.* Kirwan et al. 2010) and their long-term evolution (*e.g.* Olff et al. 1997) is sedimentation. Sedimentation in marshes is enhanced by the presence of vegetation (Bakker et al. 1993), which may slow down currents (Bouma et al. 2005, Möller 2006, Temmerman et al. 2012) (Fig. 7.1), diminish the impact of storm surges (Costanza et al. 2008, Wamsley et al. 2010), and counteract coastal erosion (Gedan et al. 2011). Vegetation succession is mainly driven by the elevation of the marsh and nutrient input through sediment (Olff et al. 1997, Reed 1989), which increases with increased sedimentation, leading to a positive feedback loop. This vegetation-sedimentation feedback enabled salt-marshes in the past to cope with SLR.

Vegetation-sedimentation feedbacks, however, are only one of many potentially important interactions. The main external controls of sedimentation are sea level (hydroperiod) and sediment supply, which is strongly related to the suspended sediment concentration (SSC) (Fig. 7.1), but the internal interactions between physical and biological features of coastal zones are also of great importance. Surface roots and algae may positively influence sedimentation (McKee et al. 2007). Additionally, the accumulation of biomass can play an influential role in accretion processes (Culberson 2004). On the other hand, bioturbation is often found to have a negative effect on salt marshes by causing erosion (*e.g.* Davidson and de Rivera 2010). However, the possible positive effects such as sediment mixing (Hippensteel 2005) and soil aeration (Daleo et al. 2007) should not be overlooked. There is even evidence that burrowing crabs caused both erosion and accumulation of sediments in their burrows within the same marsh, but in different zones (Escapa et al. 2008). Finally, human impacts such as ditching or management practices (*e.g.* livestock grazing) can alter processes related to hydrodynamics, vegetation composition, sedimentation and erosion. Wide regions of the European Wadden Sea coast, for example, have been traditionally grazed by livestock since 600 BC (Esselink et al. 2000), but the impact of these animals on sedimentation processes and compaction is rarely studied. All these different geomorphological and ecological dynamics have been separately investigated in a large number of studies using a variety of methods to measure different processes. Integrating the knowledge gained from these studies will help us understand the complex interplay between biotic and abiotic factors and sedimentation, which is important for protecting these ecosystems (Corenblit et al. 2011).

Aim of the review

The increasing research focus on ecosystem engineering and bio-geomorphological interactions in tidal marshes has motivated the writing of this overview. It is meant to enable researchers to choose an appropriate method for investigating the interactions between sedimentation and ecological processes. This review gives an inventory of the available methods to quantify sedimentation, vertical accretion and erosion processes in coastal marshes for researchers from different fields. Table 7.1 lists the characteristics of these methods, including important references. In order to further improve the quality of such measurements, we discuss the possibilities offered by and limitations of these various methods and suggest possible combinations of different methods. All methods have specific advantages as well as disadvantages. Often, such disadvantages result from the method influencing or disturbing some part of the sedimentation processes, or interfering with exactly the ecological process that is of interest in bio-geomorphological studies. Thus, depending on the aim of a study, a method should be chosen that measures the correct aspect of sedimentation, and which interferes least with the processes of interest. If, for example, the effect of vegetation structure on accretion rate is under investigation, a method that leaves the vegetation intact should be chosen.

Definition of terms

In this review, a wide variety of methods is analyzed. These methods are divided into four categories according to the process they are addressing (Fig. 7.1): the measurement of suspended sediment concentration (A in Fig. 7.1), sediment deposition (B), vertical accretion (C) and surface-elevation change (D). Below, the meaning of these four processes is first defined.

The terminology used in this paper is adapted from Cahoon et al. (1995) and van Wijnen and Bakker (2001) but we supplement it with the term, suspended sediment concentration (SSC) (A in Fig. 7.1). SSC (in g/l) is used to describe the dry mass of sediment that is suspended in a defined volume of water. This refers to water running in creeks or flooding the marsh surface. The process of sediment particles settling out of the water column onto the marsh surface is called sediment deposition (B in Fig. 7.1) or simply sedimentation (in g/m^2, *i.e.* dry mass of sediment deposited/surface area of the marsh surface). In contrast to sediment deposition, we define accretion (C in Fig. 7.1) as the vertical increase in surface elevation (in mm) relative to a specific layer of the soil. This vertical accretion combines deposition (B) and erosion of sediments, as well as the accumulation of dead biomass, such as roots. If the surface of the marsh is measured with respect to a fixed benchmark, we refer to surface-elevation change (D in Fig. 7.1) (in mm). In the literature, rates of accretion (C) and surface-elevation change (D) are often expressed per time unit (mostly per year), and referred to as accretion rate (mm/year) and rate of surface-elevation change (mm/year). The distinction between accretion and surface-elevation change is not always clear in literature. However, in this paper, we use the term surface-elevation change (D) only if the measurements are compared to a fixed bench mark of known elevation with respect to an ordnance datum. Both accretion and surface-elevation change include a certain amount of subsidence, which is sometimes also called settlement (Kaye and Barghoorn 1964) or autocompaction (Cahoon et al. 1995,

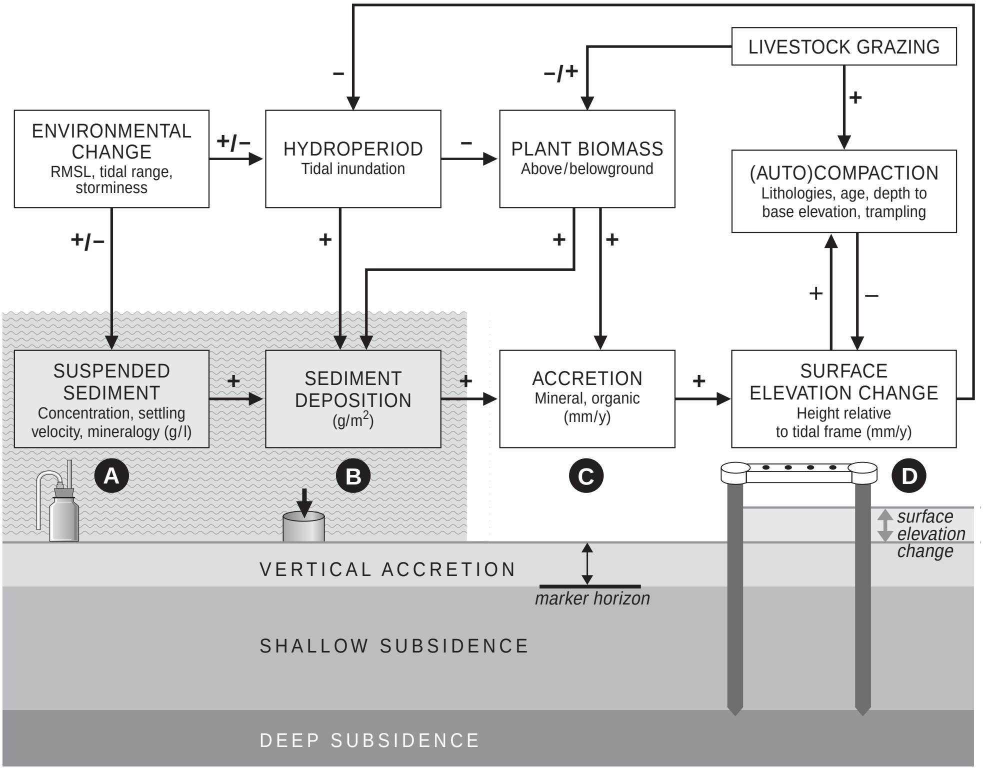

Figure 7.1 Factors affecting sedimentation processes in coastal marshes after Allen (2000) and Cahoon (2002a). The letters A, B, C, and D indicate the subsections of this review.

Bartholdy et al. 2010). Subsidence can be classified into shallow and deep subsidence (Cahoon et al. 1995). Shallow subsidence is the decrease of the marsh surface elevation due to sediment compaction in the top layer of the soil, *e.g.* by shrinkage of silt, clay or peat deposits due to drying, and decomposition of subsurface organic material. Deep subsidence also includes every form of subsidence that the instrument itself is subject to, such as tectonic and isostatic processes. Therefore, methods that measure vertical accretion (C) generally include the effects of only shallow subsidence, whereas measurements of surface-elevation change (D) include both shallow and deep subsidence in this review. In the case of vertical accretion measurements, the depth of the boundary between shallow and deep subsidence depends on the specific methodology. Thus, the precise definition of the distinction between shallow and deep subsidence varies between methods.

We divide the methods summarised in this review according to the process they are addressing, following the highlighted sections in Fig. 7.1. The distinction between methods which measure accretion (C) and surface-elevation change (D) is sometimes difficult. In this review, we thus add a chapter in which we summarise a hybrid method which can measure both processes (section 6). The methods in each chapter are then further sorted by the timescale they encompass (temporal resolution) (Fig. 7.2, Table 7.1).

The accuracy of a method is defined here as how close the measured value is to the real value, in contrast to the precision. The precision is defined as how similar results are to each other if the same measurement is performed repeatedly, preferably at the same time and position. Being able to identify the exact same location for repeated measures of accretion, for example, plays an important role in the method's precision. Both the accuracy and precision of each method is given in Table 7.1. A relative estimation of both accuracy and precision was made if no value was available from the literature.

Time

In this review, the term, temporal resolution, is defined as the possible time period covered by the method, which ranges between shortest and longest possible application time (Fig. 7.2). The user should be aware that seasonal effects can influence the measured outcome when choosing a method and measuring period. For example, a higher flooding frequency during the winter season can affect the sediment deposition rate (Temmerman et al. 2005) or the seasonal process of shrinking and swelling of sediments can affect the measured accretion rate (Cahoon et al. 1995). Furthermore, it is important to make the distinction between pre- and post-event methods

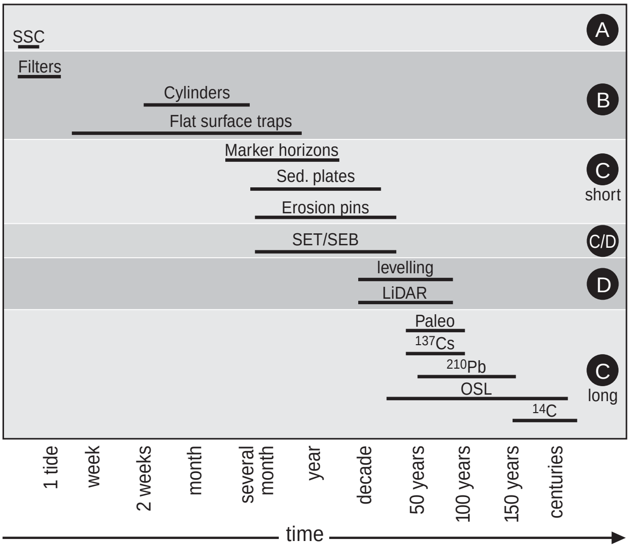

Figure 7.2 Overview of methods described in this review divided according to the measured processes and their timescales.

Table 7.1 The methods with references to the section and paragraph in this review, the unit in which they measure sediment(ation), an important reference, time resolution, pre- or post event, level of cost, level of labour intensity, estimated accuracy, estimated precision, disadvantages, and advantages

Chapter	Paragraph	Unit	Reference	Time Resolution	Pre/ Post event	Cost	Labour	Estimated Accuracy	Estimated Precision	Advantages	Disadvantages
2.A SSC	2.2 Bottle method	g/m^3	Temmerman et al. 2003a	1 tide- several weeks	Pre	Low	Medium	Low, increased with volume	Low (weather)	Important as model parameter	No information on accretion
	2.3 OBS/SAS	g/m^3	Thomas and Ridd 2004	Weeks – months	Pre	High	Low	Depends on equipment and calibration	High (instrument can stay on same location)	Semi continuous data	Cleaning of surface to get accurate measurements
	2.4 LISST/ ADCP	g/m^3	Fugate and Friedrichs 2002	Weeks – months	Pre	High	Low	Depends on equipment and calibration	High (instrument can stay on same location)	Semi continuous data	Cleaning of surface to get accurate measurements
3.B Sediment deposition	3.2 Filters	g/m^2	Reed 1989; Culberson et al. 2004	1 tide	Pre	Low	Medium	Tend to under-estimate because of wash-out of sediment	High; same location Low; seasonal changes	Repeatability; easy to measure organic matter	Disturbance by livestock
	3.3 Open cylinders	g/m^2	Hargrave and Burns 1979, Bloesch and Burns 1980	Weeks – months	Pre	Low	Medium	Tend to overestimate	High; same location Low; seasonal changes	Collection of sediment	Edge disturbing waterflow
	3.4 Flat surface traps	g/m^2	Steiger et al. 2003, Pasternack and Brush 1998	2 weeks – 1 year	Pre	Low	Medium	Tend to under-estimate because of wash-out of sediment	High; same location Low; seasonal changes	No edge disturbing water flow	Removal of vegetation

Table 7.1 Continued

Chapter	Paragraph	Unit	Reference	Time Resolution	Pre/ Post event	Cost	Labour	Estimated	Estimated Accuracy	Advantages Precision	Disadvantages
4.C Accretion (Short term)	4.2 Marker Horizons	cm/yr	Steiger et al. 2003, van Wijnen and Bakker 2001	Months – years	Pre	Low	Low	~5.0-10.0 mm (soil corer)	High; same location but tend to disappear over time	No influence on hydraulics, sampling success assessed directly	Autocompaction, bioturbation, redistribution of material, loss of material by sampling
	4.3 Sedimentation plates	cm/yr	Watson 2008, French and Burningham 2003	Months – 20 years	Pre	Medium	Medium	~1.5 mm (high)	High; same location	Not destroyed by sampling, can show shallow compaction	Disturbance of hydraulics and roots, uncertainty of plates staying level, burrowing
	4.5 'Erosion' pins	cm/yr	Saynor et al. 1994	Months – decades	Pre	Low	Medium	~1 cm; BUT disturbance by pin itself increases error	High; same location	Easy to handle	Over/under-estimation due to turbulences. Possibly unstable
5.C Accretion (Long term)	5.2 Paleo-environmental	cm/yr	Lefsky et al. 2002	Decades (50yrs)	Post	Medium	Medium	Intermediate	Low (cannot take the same core twice)	Data on vegetation included	Historical maps/ photographs necessary
	5.3 Caesium (Cs)	cm/yr	Callaway et al. 1996, DeLaune et al. 1978, Milan et al. 1995	Decades (50yrs)	Post	High	High	Intermediate; 137Cs moves through soil, average over many years	Low (cannot take the same core twice)	Can be combined with ^{210}Pb	Bioturbation, leaching, uncertainty of local peaks
	5.4 Lead (Pb)	cm/yr	Appleby 1978, Walling and He 1999	Decades (100–150yrs)	Post	High	High	Intermediate; includes calculations with error propagation	Low (cannot take the same core twice)	Can be combined with ^{137}Cs	Bioturbation, leaching

Table 7.1 Continued

Chapter	Paragraph	Unit	Reference	Time Resolution	Pre/ Post event	Cost	Labour	Estimated	Estimated Accuracy	Advantages Precision	Disadvantages
5.C Accretion (Long term)	5.5 OSL	cm/yr	Ollerhead et al. 1994, Madsen and Murray 2009	Decades – centuries	Post	High	High	Intermediate	Low (cannot take the same core twice)	Long time period	Inadequate sensitivity of the detector, thermal transfer, incomplete resetting of the material, handling of samples in red-light conditions
	5.6 Radiocarbon	cm/yr	Bowman 1990	Decades– centuries	Post	High	Medium	Low	Low	Longest time period	Large error in age calculation
6.C/D Hybrid methods	6.2 SET	cm/yr	Cahoon et al. 2000, 2002a, 2002b	Months – decades	Pre	Low	Medium	1.5 mm (high)	High (same location)	Very precise	Set-up bit more complicated than SEB
	6.2 SEB	cm/yr	van Wijnen and Bakker 2001	Months – decades	Pre	Low	Medium	1.5 mm (high)	High (same location)	Very precise, easy in minerogenic marshes	Disturbance at installation
7.D Surface Elevation Change	7.2 levelling	cm/yr	NN.	Decades	Pre	Low	Medium	0.5-1 cm (high)	Difficult to measure exact same location	Many measurements in short timespan	Difficult to cover large areas
	7.3 Airborne LIDAR	cm/yr	Nilsson et al. 1996, Lefsky et al. 2002	Decades	Pre	High	Medium	10-15 cm (low)	Difficult to match with references in field	Covers large areas	Need to correct for vegetation cover
	7.3 Ground based LiDAR	cm/yr	Huang and Bradford 1990, Nagihara et al. 2004	Decades	Pre	High	Medium	High	High, detailed 3D map	Detailed 3D map	Many scans to get accurate map

to measure accretion (C). Pre-event methods, on the one hand, need to be installed in the field before the event of interest takes place and are thus often only useful for relatively short-term investigations. Post-event methods, on the other hand, make use of already existing marker horizons (such as ^{137}Cs) and thus enable researchers to make assessments over longer time periods.

Space

The spatial resolution is the surface area covered by the method. In most cases, the spatial resolution is rather low and only includes the direct vicinity of the measurement (*e.g.* the surface of a sediment trap [cm^2]). Methods which combine low cost and low labour usually make it possible to perform a high number of measurements at different locations, thus enabling measurement of spatial variations in sedimentation processes. Only a very few methods, such as remote sensing, are able to cover larger areas *per se*.

Physical disturbances

Furthermore, methods should be chosen with respect to their resilience to disturbance. For example, poles and other structures are known to be disturbed by drift-ice. Other well-known causes for disturbance are the grazing activity of wild or domestic animals, such as grazing geese, sheep or cattle (Dijkema et al. 2005), or bioturbation by a wide number of animals such as crabs (Davidson and de Rivera 2010), small Crustaceans (Schrama et al. 2012), lugworms (van Wesenbeeck et al. 2007), water voles (Kuijper and Bakker 2012), and geese grubbing for belowground parts of the vegetation (Esselink et al. 1997). With respect to grazing, the exclusion of animals (*e.g.* by fences) is an option in only some cases to protect equipment from damage. Grazing animals are an important part of the ecosystem and if they are excluded, their effect on sedimentation (*e.g.* through grazing, causing reduction of vegetation structure and perhaps less sediment trapping) is not measured. This means that by locally excluding animals, the accretion rate may be altered and thus measurements inside exclosures would not represent the situation outside exclosures (Esselink et al. 2010). With respect to bioturbation, both natural and artificial marker horizons can be destroyed or mixed by this process. Bioturbation was found to have a high impact in North-American marshes (*e.g.* Talley et al 2001), but negligible effects in some, but not all (Wolters et al. 2005), European marshes (de Groot et al. 2011a).

Minerogenic vs. organogenic marshes

Finally, we find some differences in the applicability of methods to minerogenic vs. organogenic marshes. Minerogenic marshes are characterized by a dominance of mineral sediment input that is supplied from suspension in the inundating water. A local organic component of sediment comes from the vegetation on the marsh platform but to a lesser extent. When sea level is stable or falls, in response to century- or millennium-scale fluctuations in sea level, the organic sediment component becomes more dominant and minerogenic marshes may transform into organogenic ones (Allen 2000). At present, very few organogenic peat marshes occur in Europe, except in the Baltic Sea region (Dijkema 1987, 1990). In contrast, the East coast of North America features large areas of coastal peat marshes (Niering 1997). The rate of subsidence is normally higher in organogenic marshes as organogenic sediments are compacted or decomposed to a greater extent than minerogenic sediments. This review focuses on methods suitable for minerogenic marshes, although several may also be applied to organogenic marshes.

Suspended Sediment Content (SSC) (A)

Introduction

The SSC in water inundating coastal marshes determines the amount of sediment that can potentially be deposited on a marsh. The measurement of SSC alone in a marsh system, however, does not hold any information about the actual deposition rate, as the suspended sediment can be part of either erosion or deposition processes. The SSC often varies both at large scales (*e.g.* between marshes) and within a single marsh (Reed 1989, Allen and Duffy 1998, Allen 2000, Temmerman et al. 2003b). Measured in g/l or kg/m^3, low SSC values are an indication that the marsh is not likely to accrete over the long term through mineral sediment deposition, although organogenic accretion may be dominant. Including grain size analysis may yield more information on settling velocity and, consequently, sediment deposition rate.

There are two major reasons to measure SSC mentioned in literature. Firstly, it is measured to determine sediment fluxes and budget (Dankers et al. 1984, Asjes and Dankers 1994). Secondly, it is used as a parameter to improve sedimentation models (Temmerman et al. 2003b, 2005, French 2006, Kirwan et al. 2010). When used to calculate sediment fluxes and budgets, SSC measurements are taken at the beginning and end of tidal cycles, often at the mouth of a creek (*e.g.* Dankers et al. 1984, Asjes and Dankers 1994, van Duin et al. 1997, Temmerman et al. 2003b). Temporal variations in SSC may be associated with tidal range, inundation height, turbulence and (seasonal) weather conditions, such as storm events (*e.g.* Osborne and Greenwood 1992, Asjes and Dankers 1994, Allen 2000, Voulgaris and Meyers 2004, Temmerman et al. 2004a). The difference in SSC between the in- and outgoing water is assumed to have been deposited on the marsh surface (Dankers et al. 1984, Reed 1988, Brown et al. 2009). However, measuring at the creek does not give any information about sediment input via inundation from the marsh edge (Leonard and Luther 1995, van Proosdij et al. 2006), or the spatial distribution of the sediment over the marsh. When SSC is used as a parameter in models, it can be measured at one location (as an indication of available sediment), multiple locations (for use in spatial models; Temmerman et al. 2005), or at different heights in the water column (to monitor decrease of SSC during tides; Schuerch et al. 2012a).

Taking SSC into account can enhance our knowledge about the ability of ecosystem engineers to affect their environment and *vice versa*. For example, increased SSC levels in the Wadden Sea are thought to have contributed to the disappearance of sea grasses, thus inhibiting their re-establishment (van der Heide et al. 2007, Eriksson et al. 2010).

Bottle Method and Automated Sampling

SSC can be measured by taking water samples with bottles manually (Wattayakorn et al. 1990), with semi-automated samplers such as siphon samplers (Gregory and Walling 1971, Grazcyk et al. 2000) (Fig. 7.3A), or with fully automated samplers (Temmerman et al. 2003a). The collected water samples are usually filtered, dried and weighed (Dankers et al. 1984, Temmerman et al. 2003b), which requires substantial additional work in the laboratory. These methods are widely used on salt marshes (Gregory and Walling 1971).

Manual sampling with bottles (*i.e.* scooping up sea water) is generally associated with a higher uncertainty, because of the possibility of locally disturbing the sediment layer during the sampling process. This can be slightly improved by taking larger sampling volumes.

Using a siphon sampler is a cheap method for measuring SSC. A semi-automated method, it requires emptying of the bottles after every inundation event. Siphon samplers allow for the measurement of SSC at various depths and times during the flooding phase of inundation (Fig. 7.3A) (Reed et al. 1999, Grazcyk et al. 2000). This provides valuable information for model parameter estimation because SSC is not homogeneously distributed throughout the creek (French et al. 1995, Grazcyk et al. 2000, Temmerman et al. 2005). However, a siphon sampler cannot collect water samples during ebb tide and the sampler itself may substantially disturb the local hydro- and morphodynamics.

Automated samplers are able to take several samples during a tide. They are more expensive to implement than the other two methods, but they do not need to be emptied every tide (Temmerman et al. 2005), and it is possible to sample during ebb tide. Like the other methods, it is likely to disturb the local hydrodynamics.

Optical Back Scatter/ Sediment Accumulation Sensor

Optical Back Scatter (OBS) sensors and/or turbidity sensors also measure SSC (French 2000, Ridd et al. 2001, Thomas and Ridd 2004, Downing 2006). They were initially developed for near-shore use (Downing et al. 1981), but are now also used in tidal creeks and on marsh surfaces (Leonard and Luther 1995, Leonard et al. 1995, Davidson-Arnott et al. 2002). Usually, OBS-sensors are used to continuously measure

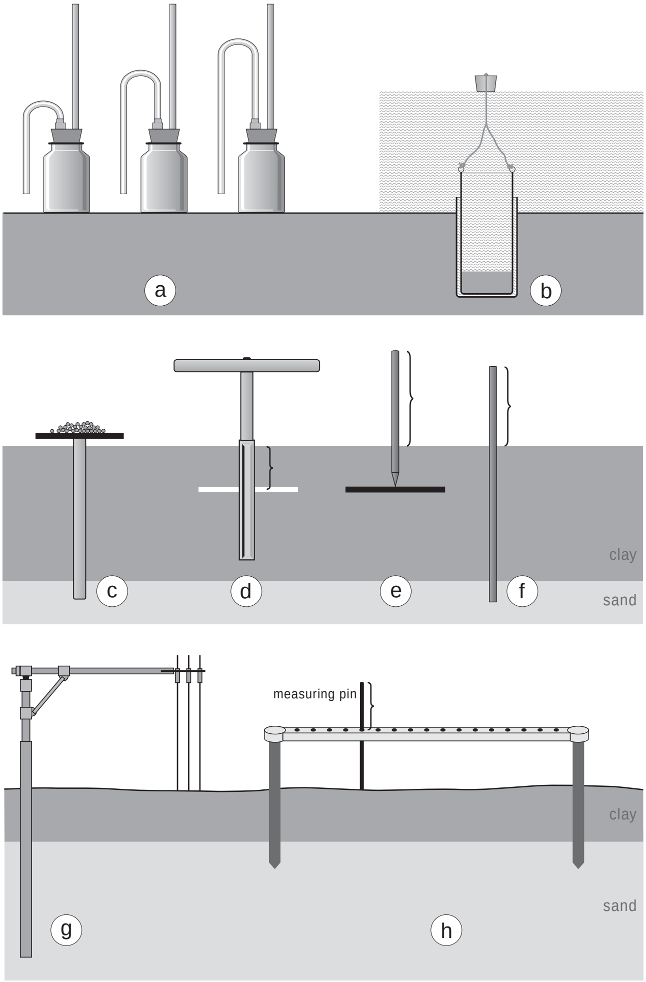

Figure 7.3 Schematic illustration of equipment for a) bottles, b) open cylinder, c) flat surface trap, d) marker horizon, e) sedimentation plate, f) 'erosion' pin, g) SET, and h) SEB.

SSC for up to several months. These continuous measurements allow for detailed information to be collected on SSC changes during tide inundations at one specific location. For information about the instrument mechanisms see www.campbellsci.ca/Download/LitNote_obsbasics.pdf.

Due to site-specific differences regarding particle properties (such as flocculation and reflectivity), the accuracy of the measurements depends on the proper calibration of the sensor signal against the SSC (Downing and Beach 1989, Kineke and Sternberg 1992, Bunt et al. 1999). When OBS is used on the marsh surface, vegetation has to be removed in order to not disturb the optical signal of the instrument.

The OBS-sensor is the precursor of the Sediment Accumulation Sensor (SAS) (Thomas et al. 2002, Thomas and Ridd 2004), which works in the same way. The initial equipment costs for such OBS or SAS sensors are high. However, these sensors are able to run autonomously for several months, depending on data logger frequency and battery life.

LISST and ADCP

Other automated methods for SSC measurements in fluvial environments include Laser In Situ Scattering and Transmissometry (LISST) (Agrawal and Pottsmith 1994, 2000, Fugate and Friedrichs 2002), Acoustic Doppler Current Profiler (ADCP) (Kaneko and Koterayama 1988, Kaneko et al. 1990) and the Acoustic Doppler Velocimeter (ADV). In contrast to OBS-sensors, for which calibration is often difficult, LISST was developed for off-shore studies to provide more accurate measurements (Fugate and Friedrichs 2002). Whereas OBS and LISST use light reflection on suspended sediment particles, ADCP and ADV are based on sound reflection (Kaneko and Koterayama 1988, Fugate and Friedrichs 2002). All of these methods need to be calibrated against SSC measured from water samples (Gartner and Cheng 2001). Although these methods have not yet been applied to tidal marshes, they are feasible candidates for use in tidal marsh research. Fugate and Friedrichs (2002) give a detailed review on OBS, LISST and ADV.

Sediment deposition (B)

Introduction

In contrast to SSC, which only measures potential sedimentation, the methods reviewed in this section measure actual sedimentation of particles in g/m^2 or g/m^2/time. The downward flux of sediment is not only important for studying sedimentation processes on marshes and their reaction to SLR, but can also help to understand the dispersal and deposition of other materials in tidal marshes, such as seeds (Wolters et al. 2004), nutrients (Zhang and Mitsch 2007), silica (Struyf et al. 2007), and organic matter (Costantini et al. 2009). A wide variety of devices, mostly referred to as sediment traps, are used. These traps range from simple plywood boards or tiles (Steiger et al. 2003) to automated sampling devices (Zuniga et al. 2008). The trapped sediment is collected and dried to quantify its weight (Grant et al. 1997, Braskerud 2001). One of the advantages of sediment traps is that the trapped sediment can be used for further analyses such as grain size and chemical or mineralogical characteristics. Especially important to bio-geomorphological studies, sediment traps allow determination of the nutrient content of deposited sediments, and subsequently, relationships with ecological processes such as vegetation productivity. By enabling evaluation of the restoration site's functioning with respect to deposition of sediment and sufficient seed dispersal, sediment traps are very useful in monitoring marsh restoration projects (Wolters et al. 2004) and determining whether goals such as vegetation composition will be met. One problem with these methods is that they do not take into account particles deposited on the vegetation, which may settle on the ground at a later time.

Filters

In this method, filter papers or membranes of a known weight are placed on the sediment surface. The sediment from the inundating water accumulates on the filter during one or a few tides, after which the filter is removed. The accumulated sediment is measured by drying and weighing the collected filters (*e.g.* Reed 1989, Temmerman et al. 2003a, Culberson et al. 2004). Plastic discs or Petri-dishes are usually used underneath the filter to prevent soil particles from adhering to the underside of the filter (Culberson et al. 2004).

Advantages of this method include low cost and easy repeatability (Table 7.1). In addition, the organic matter in the deposited material can be easily determined through combustion of the (ash-free paper) filters in 550°C after drying and weighing them (Reed 1989, Culberson et al. 2004). It is advisable to pre-weigh the dried filters before placing them in the field, in order to correct for any measuring errors that may occur through the drying process, particularly if deposition rates are very low.

Open cylinders

Cylindrical sediment traps consist of containers buried in the ground with the opening level to the soil surface. The variety of constructions ranges from bottles (Deicke et al. 2007), various plastic materials such as PVC pipes (Grant et al. 1997) to glass jars (Jordan and Valiela 1983). Differences also exist between simple cylinders (Grant et al. 1997) and conical traps with a funnel-shaped opening (Bloesch and Burns 1980). A slightly more complicated design was used by Braskerud (2001) (Fig. 7.3B).

A sediment trap design that combines elements of flat devices and cylindrical traps is described by Temmerman et al. (2003b, 2005): a very flat cylindrical trap with a rim of only a few mm high. The traps are attached to the soil surface using steel claws or a plastic rod running through the middle of the trap (Temmerman et al. 2003b). A buoyant cover, which is lifted by the tide, protects the deposited material from splashing by rain during low tide.

An important consideration when choosing a trap design is the aspect ratio (height/diameter), which strongly influences the turbulence around and within the trap (Hargrave and Burns 1979, Bale 1998). Both trap diameter and aspect ratio should be scaled according to the expected flow conditions and sediment load (Baker et al. 1988). For an extensive discussion on the practical aspects of trap design, consult Bloesch and Burns (1980), Hakanson et al. (1989), and Hargrave and Burns (1979).

Even though cylindrical traps are considered to be the best tool to measure downward settling fluxes within reasonable error limits (Bloesch and Burns 1980) by some authors, they can overestimate sediment flux compared to flat surface traps (section 3.4) (Kozerski and Leuschner 1999). In cylinders, deposition takes place in the absence of significant turbulences and in decreased flow velocities caused by bottom shear, which allows sediment particles to settle faster in the cylinder than they would outside. Depending on trap construction, the method is relatively cheap, but retrieving the traps and drying the samples is labour intensive (Table 7.1).

Flat surface traps

Flat sediment traps are positioned directly on the soil surface. Simple versions consist of flat plates (Pinay et al. 1995), plywood boards (Mansikkaniemi 1985), clay roof tiles (Brunet et al. 1994) or plastic discs with a roughened upper surface to prevent sediment wash-off (Kleiss 1996). Total deposition rates on surfaces of different roughness were not found to be significantly different by Steiger et al. (2003). Nevertheless, some studies used Astroturf mats (Goodson et al. 2003, Steiger et al. 2003, Deicke et al. 2007) to mimic the effect of vegetation. A slightly more complicated method is described by Pasternack and Brush (1989), who anchored the trap in the soil with an aluminium rod (Fig. 7.3C). An alternative design of a flat sediment trap is discussed by Kozerski and Leuschner (1999). They introduce another more complex device with a lid construction, which also serves as an alternative to cylindrical sediment traps.

Flat traps are sensitive to sediment being washed away by rain or tides, but the major technical problem is sediment loss during retrieval (Gardner 1980, Kozerski and Leuschner 1999). A further drawback is that the surface of the trap is generally smoother and less adhesive than the marsh surface, affecting the sedimentation and resuspension process. On the other hand, a big advantage of these traps is that they have no edge to disturb the water flow in contrast to cylindrical traps (Table 7.1).

Accretion (Short term) (C)

Introduction

Many studies investigating whether coastal marshes are able to cope with SLR have measured accretion. Therefore, a wide variety of methods exists for measuring accretion rates in mm/yr. We discuss them in the following two sections and classify them according to their timescale, which range from months to decades (short term, this section) or decades to centuries (long term, next section) (Fig. 7.2).

In contrast to earlier described methods, accretion measurements include erosion as well as sedimentation processes of both mineral and organic material. The accumulation of dead plant material, such as roots, can contribute substantially to the yearly elevational rise in marshes. In addition, the fraction of organic material in the soil influences characteristics such as soil moisture content, which is an important factor for plants. The process of accretion also buries seeds. Therefore, studies addressing the availability of seeds as a food source for animals or for the formation of a seed bank might benefit from assessing accretion rates. Additionally, erosion processes are more likely to occur in sparsely vegetated parts of the marsh, such as the pioneer zone. Thus, measuring (short-term) accretion could be used to assess the vegetation-sedimentation interactions constraining establishment of pioneer marsh vegetation.

Marker horizons

A marker horizon serves as a reference layer within the soil, against which accumulation of mineral and organic sediment can be measured using a soil corer (Cahoon and Turner 1989, Cahoon et al. 1995, van Wijnen and Bakker 2001, Krauss et al. 2010) (Fig. 7.3D). This measurement is taken with a soil corer and often repeated at regular time intervals, such as every year. A marker horizon generally consists of degradable material, as opposed to plates (section 4.3). Some coastal marshes have a natural marker horizon formed by an underlying sand or gravel layer. In such cases, the base elevation of the sandy (or gravel) surface can be used as reference framework if the time of marsh initiation is known (Olff et al. 1997, van Wijnen and Bakker 1999, de Groot et al. 2011b).

Artificial marker horizons have been constructed from different materials, which are applied to the soil surface, such as red sand (Nielsen 1935), aluminium glitter (Stumpf 1983), red tennis-court gravel (van Wijnen and Bakker 2001), white clay (Baumann et al. 1984), stable rare-earth elements (REE) (Knaus and Vangent 1989), sand (Stoddart et al. 1989, French and Spencer 1993, Nielsen and Nielsen 2002) and feldspar (Cahoon et al. 1995, Krauss et al. 2010). Material effectiveness depends on flooding frequency, wave activity and the retrieval time frame of the marker. Applying the marker material after clipping the vegetation is advisable in cases of dense vegetation (van Wijnen and Bakker 2001). However, this procedure might change flow conditions and subsequent accumulation of organic material in the first year. For less dense vegetation types such as *Phragmites* sp. or *Scirpus* sp., it is possible to place the marker horizon on the soil surface in between plant stems in order to minimise disturbance of the vegetation canopy (*e.g.* Temmerman et al. 2004b). Thus, if the research aim is to investigate the effects of vegetation canopy structure on accretion, the marker horizon technique may be a suitable method. However, the level of vegetation disturbance accrued during placement of the horizon depends on the specific vegetation type, and the vegetation canopy may need some time to recover after the placement. The marker horizon area should be marked by sticks, or belowground metal pins or plates that can be found with a metal detector. A new marker layer can be added to the surface every couple of years to minimize the effects of autocompaction on measurements. This should be done, however, in adjacent plots or by using different colours for each horizon to avoid confusing the separate markers. If autocompaction is the focus of the study, stacked layers of markers could be used to assess autocompaction rates.

Several problems hindering accurate recovery are associated with using marker horizons, such as bioturbation (Krauss et al. 2010), redistribution of the marker layer by severe floods (Steiger et al. 2003), and mixing with darker organic or inorganic material (Cahoon and Turner 1989). Furthermore, the necessary coring at repeated intervals removes marker material, resulting in sampling inaccuracy after several years (Stoddart et al. 1989). Lowering the frequency of coring is not a good option, because of the aforementioned autocompaction. Therefore, the size, intended lifetime of the marker, and the number of cores taken per measurement should be considered together. The costs depend mainly on the choice of material, but are generally low to medium (Cahoon and Turner 1989). In addition, sampling effort is not very high and sampling success can be assessed directly in the field (Cahoon and Turner 1989).

Sedimentation plates

In the sedimentation plate method, the marker horizon consists of a firm plate made of metal (Watson 2008, Stokes et al. 2010) or plastic (*e.g.* nylon or Perspex (French and Burningham 2003)) (Fig. 7.3E). The plate is buried in the soil just below the rooting zone under a carefully extracted block of marsh turf, which is then placed back on top of the sedimentation plate (French and Burningham 2003). Thus, vegetation disturbance is kept to a minimum. An alternative method (preferable for organogenic marshes) is to dig a hole and carefully push the plate horizontally into the sediment from the side. Small holes drilled into the plate reduce the influence of the plate on drainage conditions and plant rooting. The plates should be placed in a perfectly horizontal position to allow for reliable repeated measurements. After burial, the plates need to settle for at least one month before the first measurement can be taken (Stokes et al. 2010). To measure sediment accretion, a thin metal pin is pushed into the sediment until it hits the plate, and its length above the sediment is determined. As with marker horizons, metal plates can be found back by using a metal detector or marking them with sticks. For plastic plates, it is advisable to use metal pins to mark the position of the plate.

The costs for this method strongly depend on plate material but are estimated to be intermediate. The amount of labour involved is also intermediate and comparable to that involved with marker horizons. Errors may occur when plates fail to stay level or are disturbed by burrowing animals such as water voles.

‘Erosion’ pin

The ‘erosion’ pin method is usually used in dynamic areas such as dunes and beaches (Saynor et al. 1994, Edeso et al. 1999, Saynor and Erskine 2006, Hancock et al. 2010, Veihe et al. 2011), but can also be applied to salt marshes. With this method, accretion is measured similarly to the Sedimentation Erosion Table (SET) technique (Cahoon and Lynch 1997, section 6.2). In this method, pins of stainless steel or glass fibre are driven into the ground, leaving a small part aboveground (Stokes et al. 2010, Hancock et al. 2010). The length of the pin above the soil is measured repeatedly (Fig. 7.3F). Thus, the exact location can be re-assessed. However, a major problem of this method is that the pin itself can be unstable. Furthermore, the pin changes flow velocity and turbulence (Veihe et al. 2011), which may lead to scouring of sediment directly around the pin and therefore to an overestimation of erosion. The measurement error associated with this method was found to be about 1 mm (Edeso et al. 1999, Hancock et al. 2010). Method durability varies from months to years (Sirvent et al. 1997, Hancock et al. 2010).

Accretion (Long-term) (C)

Introduction

The methods in this section address the measurement of accretion rates over timescales ranging from decades to centuries (Fig. 7.2) and are used to answer questions on how environmental changes (natural and induced by humans) influence sedimentation processes over the long term. Using these methods, it is possible to increase knowledge on how systems might react to similar changes in the future when combined with, for example, aerial photographs, vegetation maps, and historical records of land-use change. For example, the influence of storm surges on sedimentation rates can be assessed after the events took place (post-event method) using a combination of the ^{137}Cs- and ^{210}Pb-dating method (Bellucci et al. 2007, Schuerch et al. 2012b). As the frequency of storms is predicted to increase, this connection will be very important in determining whether marshes can survive SLR. Other very important factors influencing marsh accretion over the long-term include various human activities. For example, dredging leads to changes in sedimentation rates on salt marshes along the river Schelde (Dyer et al. 2002). Another factor likely to affect accretion rates is grazing by livestock, which is a very common practice both for agricultural and nature conservation purposes in Europe, as the animals modify the vegetation structure and may add to compaction by trampling.

In contrast to the measurement techniques discussed in the previous section, most of the long-term accretion methods can only be employed if erosion during the investigated time span is assumed to be negligible. This is because measurements are made post-event and rely on the accurate estimation of the time period during which a reference layer has been buried. This limitation usually restricts the application of these methods to parts of the marsh that were already present during the time period of interest. Additionally, most methods mentioned in this section can be disturbed by bioturbation as they all depend on the availability of marker horizons or on clear sedimentation layers.

Paleo-environmental Method

The paleo-environmental method links historical vegetation data to natural marker horizons consisting of vegetation remains. This technique can be applied to study marsh accretion rates over timescales up to millennia (*e.g.* Brush 1989, Neumann et al. 2007, Tanaka et al. 2011) but it is also suitable for shorter time scales such as decades (Temmerman et al. 2003b). Over long timescales, ecosystems generally show a change in plant communities due to succession or land-use change. When conditions are favourable, plant remains such as pollen, roots, or peat are preserved in the soil. The method consists of taking soil cores, slicing them into layers and identifying the vegetation remains in each layer. The depth of transition layers between plant communities is then related to the date of these changes obtained from historical information (Temmerman et al. 2003b) or dating techniques (Orson et al. 1998, Dobrowolski et al. 2012). Such historical information may include aerial photographs or vegetation maps that document when these transitions between successional stages or land uses took place.

Firstly, this method requires historical data on plant communities and/or land use and, secondly, the right circumstances (*e.g.* anoxia), for preservation of recognizable plant remains. Furthermore, the number and clarity of successional changes define the time resolution of this method because only a change in species composition results in a datable marker horizon. Note that this method cannot untangle accretion from autocompaction processes but is relatively cheap if labour intensive.

Caesium dating (^{137}Cs)

This method takes advantage of existing marker horizons formed from ^{137}Cs, which is an anthropogenic radionuclide. ^{137}Cs is deposited onto the soil surface after being released to the atmosphere as a product of nuclear accidents. Peaks in the historical release of ^{137}Cs into the atmosphere lead to peaks in ^{137}Cs activity concentrations in the soil profiles of sedimentary environments with relatively constant accretion rates, such as tidal marshes. Nuclear incidents contributing significantly to caesium deposition vary between regions. In Northern Europe, caesium deposition is dominated by atomic bomb tests conducted in the early 1960s and the Chernobyl accident in 1986, leading to two distinct ^{137}Cs horizons (Fig. 7.4) (Bellucci et al. 2007). Some authors have also found a minor peak at 1974-1977 in cores from the North and Baltic Sea, originating from an incidental release at the Sellafield nuclear reprocessing site (Kunzendorf 1998, Andersen et al. 2000). Chinese and French nuclear bomb tests conducted in 1973 created a significant peak in China (Wang et al. 2008). In America, the deepest occurrence of ^{137}Cs in the soil is assigned to the beginning of atomic bomb testing in 1954 and the highest activity to the peak of these tests in

1963 (DeLaune et al. 2003). The Fukushima accident of 2011 may form a new horizon in Asian marshes.

Samples are taken by pushing a tube or cylinder into the soil (Callaway et al. 1996). During and after this procedure, it is important to measure the difference between the rim of the tube and the soil surface inside and outside the tube to quantify the compaction that occurred during the sampling process (Milan et al. 1995, Callaway et al. 1996). Additionally, the length of the core should also be measured before and after extrusion (Callaway et al. 1996), or the core tube (*e.g.* a PVC tube) should be cut open along its entire length when retrieving the sample from the core tube. The soil core is then cut into slices of 1 cm or greater, and dried (Callaway et al. 1996). The levels of ^{137}Cs are measured by gamma spectrometry and have a detection limit of 0.2 Bq kg^{-1} (Zwolsman et al. 1993, Turner et al. 2001, Bellucci et al. 2007).

The activity of ^{137}Cs in the soil has been shown to increase with smaller grain sizes and higher organic matter content (Kirchner and Ehlers 1998). In case of larger variations in these factors, normalizing this effect should be considered. Therefore, grain size and the organic carbon content should be measured in the same soil cores used to sample caesium.

Interpretation of the ^{137}Cs profile is not always straight forward. For example, the Chernobyl accident is sometimes difficult to distinguish due to regional differences in the fallout, which result from precipitation patterns and additional minor peaks such as Sellafield (Nikulina 2008). Therefore, additional validation of the age with an independent method is advisable, such as ^{210}Pb (discussed below), historic aerial photographs (Schuerch et al. 2012b), and/or the paleo-environmental method (section 5.2). Dating of the layer based on the ^{137}Cs peak may further be complicated

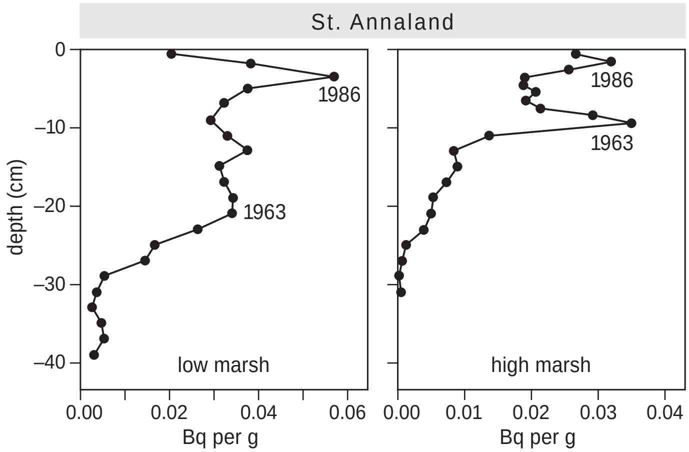

Figure 7.4 ^{137}Cs profiles of cores from St. Annaland Marsh, Netherlands (Callaway et al. 1996).

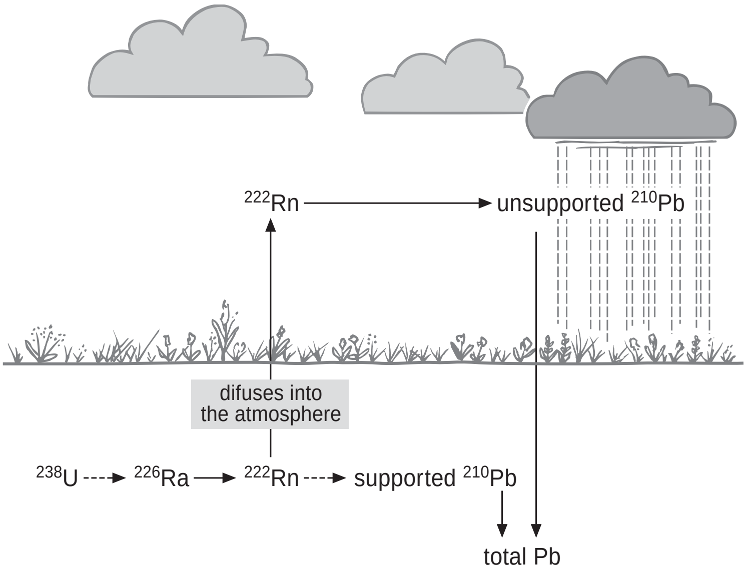

Figure 7.5 Formation and pathways of ^{210}Pb until deposition onto the soil surface (Walling and He 1999).

by bioturbation and the downward migration of ^{137}Cs (Milan et al. 1995). Finally, ^{137}Cs has a half-life time of 30.5 years so that layers become more difficult to clearly distinguish over time.

Lead dating (^{210}Pb)

The radionuclide, ^{210}Pb, is a product of the natural decay series of ^{238}U, which consists of a chain of isotopes including ^{226}Ra (Walling and He 1999). The ^{210}Pb found in the soil can result from two origins (Fig. 7.5). Firstly, 'supported ^{210}Pb' is continually produced locally from the decay of ^{238}U via the long-lived radioisotope ^{226}Ra and the short-lived ^{222}Rn within the soil, which is in equilibrium with ^{226}Ra. Secondly, 'unsupported or excess ^{210}Pb' is deposited from the atmosphere, because parts of the highly mobile ^{222}Rn escape into the atmosphere, where it further decays to ^{210}Pb. Therefore, the unsupported ^{210}Pb also contributes to the total ^{210}Pb inventory in the soil. Thus, unsupported ^{210}Pb is calculated by subtracting the supported ^{210}Pb from the total ^{210}Pb (Fig. 7.5) (Walling and He 1999), which in turn is measured in combination with ^{226}Ra, for dating purposes. Due to its radioactive decay (half-life time of 22.3 years) the unsupported ^{210}Pb activity concentration in each layer in the soil declines exponentially with its age (Fig. 7.5) (Appleby and Oldfield 1978, Gelen et al. 2003). This exponential decline can be used to calculate the age of the sediment at different depths from which the sedimentation rate is derived.

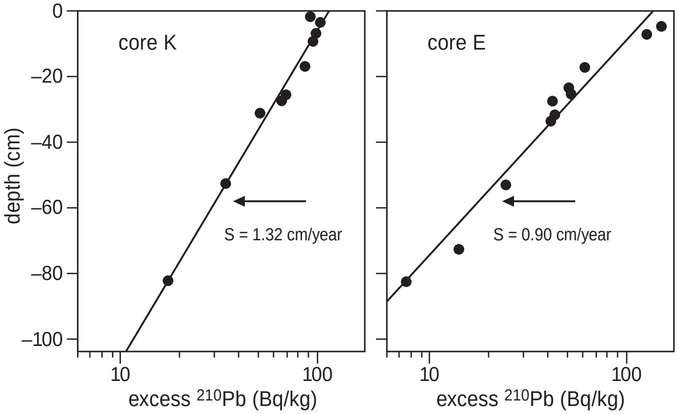

Figure 7.6 Relation between depth and ^{210}Pb, which is used to calculate accretion rates (slope) (Zwolsman et al. 1993).

Sampling and sample processing require the same steps as described for ^{137}Cs measurements. In fact, ^{210}Pb and ^{226}Ra are usually measured simultaneously with ^{137}Cs from the same sample. There are several approaches to measure the activity of ^{210}Pb. The most widely-used method is to directly determine the activity of ^{210}Pb via counting gamma-emissions using a gamma-ray spectrometer (often a Germanium detector) (He and Walling 1996, Walling and He 1999, Nie et al. 2001, Wang et al. 2008). Before measuring, samples should be hermetically sealed and stored for 20-30 days to allow equilibrium to establish between ^{226}Ra, ^{222}Rn and shorter-lived ^{222}Rn daughters (He and Walling 1996, Gelen et al. 2003, Wang et al. 2008). Indirect methods consist of measuring alpha-emissions of ^{201}Po (Frignani and Lagone 1991, Zwolsman et al. 1993, Bellucci et al. 2007) or ^{210}Bi (Tsai and Chung 1989, Applequist 1975, Chung and Chang 1995) instead of ^{210}Pb itself.

After measuring ^{210}Pb activity, an appropriate model should be applied to calculate the date of sedimentation of the respective layer and the related accretion rates. These models are based on different assumptions in connection with ^{210}Pb and its deposition. The Constant Initial Concentration model (CIC) is based on the assumption that accumulation rates of both unsupported ^{210}Pb and suspended sediment are constant over time at the sampling location (Appleby and Oldfield 1978, Andersen et al. 2000, Gelen et al. 2003). From this assumption, it follows that the activity of unsupported ^{210}Pb decreases exponentially with depth in accordance with its half-life time of 22.3 years (Fig. 7.6) (Roman et al. 1997, Andersen et al. 2000, Gelen et al. 2003). Thus, the constant accretion rate can be determined from the slope of the least-square regression of the exponential decrease of unsupported ^{210}Pb with depth (Fig. 7.6) (Robbins and Edgington 1975, Goldberg et al. 1977, Zwolsman et al. 1993).

In contrast to the CIC model, the 'Constant flux' or 'Constant rate of supply' model (CRS) assumes that the influx of the isotope ^{210}Pb has been constant over time, but accretion rate has not (Bellucci et al. 2007). The CRS model allows for calculation of sediment age in soil profiles even when there is evidence of rapidly changing accretion rates (Pennington et al. 1976, Appleby and Oldfield 1978). Other studies have tried to improve this approach by calculating age/depth profiles and accretion rates, but these are not yet widely used (He and Walling 1996, Nie et al. 2001). Several studies have compared the validity of these models (Appleby and Oldfield 1978, Gelen et al. 2003, Wang et al. 2008).

Overall, the ^{210}Pb method is widely applied in marine and coastal research. Disadvantages of the method include the possibilities of physical disturbance of the sediments (*e.g.* erosive events or periods), bioturbation, leaching, and the uncertainties surrounding model selection.

Optically stimulated luminescence dating (OSL)

In the time since Huntley et al. (1985) used the OSL method to date sediments, studies have shown that younger (<60 yr) sediments can also be successfully dated with this method (Ollerhead et al. 1994, Madsen et al. 2005). A review of these studies is given in Madsen and Murray (2009). This method uses the phenomenon that natural radiation within the soil affects the crystalline structure of some minerals, such as quartz and feldspar. Energy from natural radiation is stored in imperfections of the mineral structure (Aitken 1985, Madsen and Murray 2009), and can be released through emission of photons, using heat (thermo luminescence) or light (optically stimulated luminescence) as a stimulus (Murray and Wintle 2000, 2003, Madsen and Murray 2009). The amount of stored energy is used to determine when sediments were last exposed to light, *i.e.* the moment that they were buried under younger sediment deposits. Consequently, it is important that samples are kept in the dark (Reimann et al. 2010) and handled under subdued red light conditions (Pietsch 2009). In addition, specific detectors (including gamma-ray detectors) are necessary to measure total energy absorbed per unit mass (the dose) and the rate of energy absorption (dose rate) in order to calculate burial time. Further detailed information about the principles of OSL can be found in Aitken (1985), Duller (2004), Lian and Roberts (2006), and Duller and Wintle (2012).

In their review, Madsen and Murray (2009) examine the validity of OSL results by assessing several coastal and marine studies (including one salt marsh) where OSL results were compared to an independent method (*e.g.* ^{210}Pb method). No evidence for systematic over- or under-estimation was found, so that the OSL method can be characterised as reliable. An excellent agreement between OSL and ^{210}Pb methods was for example found in the younger part of a core (<60 yr) in fine-grained intertidal sediments in the Danish Wadden Sea (Fig. 7.7) (Madsen et al. 2005).

For further information about technical problems associated with the OSL method, see Madsen and Murray (2009). Drawbacks of the method include very

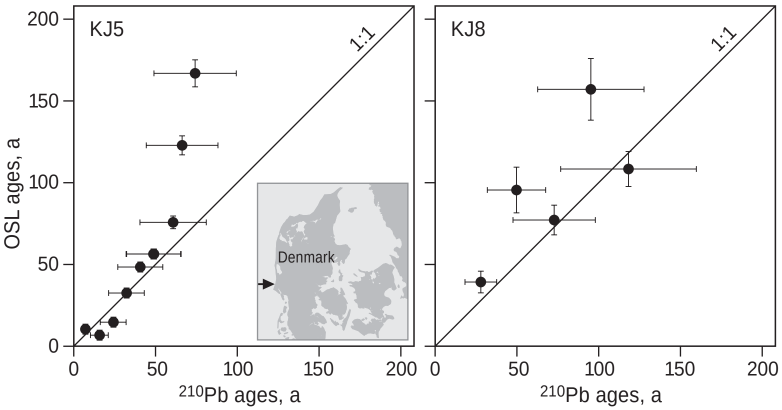

Figure 7.7 Comparisons between ages determined using OSL and ^{210}Pb in two sediment cores recovered from the intertidal zone in the northernmost part of the Wadden Sea (Madsen et al. 2009).

time-consuming laboratory work and the need for specialized equipment, making this method relatively expensive. Additionally, this method is sensitive to bioturbation. During bioturbation, stored energy contained within exposed sediments is completely re-set before soil is reincorporated in the soil column (Madsen et al. 2011) so that accretion rates suddenly seem to increase in upper layers of the soil core. Madsen et al. (2011) identified this sudden increase in calculated accretion rate as the border of bioturbation in the soil and consequently used it as a way to assess bioturbation rates.

Radiocarbon dating (^{14}C)

The method using ^{14}C to date organic material is well known in archaeology. It is sometimes used to determine changes in sea-level by dating basal salt-marsh peats (*e.g.* Gonzales and Törnqvist 2009, Yu et al. 2012). It is also possible to determine long-term sedimentation rates from freshwater (Toledo and Bush 2008) or marine ecosystems (Shaw and Ceman 1999, Watson 2004, Parker et al. 2008, Sabatier et al. 2012) using ^{14}C dating.

During photosynthesis, plants fix atmospheric CO_2 thus incorporating the ratio of $^{14}C/^{12}C$ isotopes found in the atmosphere at that time. The ^{14}C isotope in organic material decays at a specific rate (half-life of 5,730±40 years), which makes it possible to calculate the age of a sample. The amount of ^{14}C in the atmosphere was not always constant therefore ages must be calibrated to calendar years (Blaauw 2010).

Possible materials suitable for ^{14}C analyses include carbonate shell samples (Sabatier et al. 2012) or fossil plant remains (Shaw and Ceman 1999, Watson 2004), such as basal peats (Gonzales and Törnqvist 2009, Yu et al. 2012). For a summary of soil dating using radiocarbon analysis, see Scharpenseel and Schiffmann (1977). In the past, ^{14}C-measurements used to be performed by counting the radioactive decay of single carbon atoms by gas proportional counting or liquid scintillation counting. Nowadays, most samples are analysed using accelerator mass spectronomy (AMS) (*e.g.* Watson 2004), which allows direct counting of the ^{14}C-atoms instead of indirect assessment from radioactive decay. Details of the method can be found in Bowman (1990) and Goslar and Czernik (2000).

Sedimentation rates estimated from ^{14}C are rough measurements, as they sometimes encompass a small number of measuring point suspended over a long timescale (*ca.* 300–62.000 years). For example, approximately 2800 years are represented by five measuring points in a study of how human activity, such as deforestation, influenced sedimentation rates in the UK (Parker et al. 2008). Additionally, disturbance can lead to the contamination of samples with younger material, which in turn leads to misinterpretation of sample age. Nevertheless, this method can still provide valuable insights into changes in sedimentation rates over very long timescales (Bowman 1990).

Hybrid methods (C/D)

Introduction

Hybrid methods can be used to measure either accretion (C) or surface-elevation change (D), depending on how they are applied. Technically, these methods measure accretion (C) but can be used for surface-elevation change (D) when they are measured in relation to a recent fixed ordnance datum, thus incorporating deep subsidence processes.

Surface Elevation Table (SET) and Sedimentation Erosion Bar (SEB)

The Surface Elevation Table (SET) was developed from the Sedimentation Erosion Table (Schoot and De Jong 1988), which was introduced by Boumans and Day (1993) (Fig. 7.3G). The SET was first applied in the Mississippi river delta by Cahoon et al. (2000). In order to enable SET measurements, a benchmark pole is inserted into the ground until it reaches a stable horizon, such as a sand layer. During actual measurements, the benchmark is used to attach a portable metal arm, with a horizontal metal plate at the end containing nine holes (Cahoon et al. 2002b)(http://www.pwrc.usgs.gov/set/). Metal pins are carefully put through the holes until they touch the soil surface. The length of the pin above the plate is measured to determine the relative surface-elevation change (Boumans and Day 1993, Cahoon et al. 2000). In order to stabilise the benchmark, the Rod SET (RSET) was introduced (Cahoon et al. 2002a).

The Sedimentation Erosion Bar (SEB, Fig. 7.3H) is further based on the principles of the SET (van Duin et al. 1997, van Wijnen and Bakker 2001, van Duin et al. 2006) but the equipment setup is slightly modified. The setup consists of two horizontally aligned poles, and during measurements, a 2 m-long bar with 17 holes is placed on the poles. Some studies use three poles in a triangle formation to increase the amount of measuring points per station (Van Wijnen and Bakker 2001). There are several minor variations in the construction of the SEB (Daborn et al. 1991, Perillo et al. 2003). In comparison to the SET, this method is less costly and usually applied in Northern Europe on minerogenic salt marshes with low tidal ranges, fine grained sediment, and low accretion rates. In contrast to organogenic marshes, deep compaction is negligible in these marshes.

Both methods are able to measure the exact same points repeatedly, thus increasing the accuracy of the time series to about 1.5 mm vertically (van Duin et al. 1997, Cahoon et al. 2002b). Installation of the benchmarks is labour intensive, and additionally in areas with high accretion rates, the poles need to be replaced often to prevent burial by fresh sediment. However, the actual measurement process is relatively fast. Installation of SET/SEB can disturb local sediments, which may decrease accuracy at the start of the experiment. For SET, these disturbances can be minimised by using a walkway during both installation and measurements (Cahoon et al. 2002a, b). During SEB installation, however, disturbances will be more difficult to minimise because the measurement points are relatively closer to the poles than for SET.

The SET/SEB-methods were initially designed to measure net surface-elevation change (Cahoon et al. 2000, 2002a, b). However, using SET/SEB to measure surface-elevation change requires that the poles are regularly recalibrated with respect to ordnance datum, or that subsidence of the poles can be ruled out. When poles are not connected to an ordnance datum, the method then simply measures accretion rate.

Surface-elevation change (D)

Introduction

Surface-elevation change is often measured in studies on the influence of SLR on coastal zones. Additionally, it is an important factor used to explain changes in characteristics of coastal marsh ecosystems that depend on inundation frequency, such as vegetation composition. The basic principle of the method is to measure surface elevation with respect to ordnance datum repeatedly, in order to calculate surface-elevation change. Surface-elevation change is measured in mm/yr, like accretion rate, but includes the effect of both shallow and deep subsidence and should always be related to a given ordnance datum. This section only includes methods for which these requirements are met.

Levelling

Levelling is a method used to calculate the elevation change of an area by repeatedly measuring the elevation of the same points (Olff et al. 1997, Esselink et al. 1998, de Groot et al. 2011a). This is done using conventional topographical surveying equipment, such as laser level (*e.g.* Parkhurst 1928) and total station theodolite (Keim et al. 1999, Lavine et al. 2003). Other techniques include Real Time Kinematic (RTK) and Differential GPS (DGPS), which makes use of satellite GPS signals. Although the latter two techniques are often used in land surveys, their vertical resolution is not always accurate enough for tidal marshes. For example, the vertical accuracy of both RTK and DGPS (several cm) is much less than that of the total station (5 mm).

Relative elevation measurements need to be linked to a fixed benchmark, which is calibrated to an ordnance datum, in order to calculate accurate values of absolute elevation (Keim et al. 1999). Accuracy of the measurements can be estimated by the closure error, *i.e.* the difference in measured elevation between the same point at the beginning and end of the survey. This error can depend on instrument quality, and weather conditions affecting sight and instrument stability (*e.g.* wind). The level of labour necessary for this method depends on the type of instrument used and proximity to a benchmark. Furthermore, in the case of repeated measurements, the precision of the method is low.

LiDAR

LiDAR (Light Detection And Ranging) is a remote sensing method based on laser scanning to measure the distance between objects. In this section, we discuss airborne LiDAR and ground-based LiDAR. Ground-based LiDAR consists of 3D laser scanners that emit optical arrays to capture the topography of an area (Huang and Bradford 1990, Fan 1998, Nagihara et al. 2004). Trees and other objects can sometimes obstruct the view of the lasers. To counteract this, multiple scans of an area are commonly used (Nagihara et al 2004). In general, the merging of multiple scans results in an integrated, detailed and very accurate 3D-map of an area with a resolution of several mm (Nagihara et al. 2004).

Airborne LiDAR is applied from an airplane or helicopter (Nilsson 1996). An advantage of LiDAR is the large geographical area that can be covered in just one flight. Also, the possibility to assess biodiversity in the air (Turner et al. 2003) may be the main reason to use this method in some studies. However, the presence of vegetation affects the quality of the results. Techniques for correcting for the presence of vegetation have improved over the years, and include using a collinear green wavelength (Nilsson 1996, Lefsky et al. 2002), adding markers (Nilsson 1996), and measuring canopy height in the field. The vertical accuracy is in the order of *ca.* 10–15 cm (Glenn et al. 2006, 2011), which renders this method less suitable for measuring short-term elevation changes. Frequently, salt-marsh researchers may have access to airborne LiDAR data, which were collected by management authorities (*e.g.* http://www.csc.noaa.gov/digitalcoast/data/click/index.html). In such cases, it is important to check horizontal and vertical resolution, as these may vary considerably between surveys. Additionally, even though the spatial resolution may be high, the temporal resolution is often not accurate enough for biogeomorphological research (Reinhardt et al. 2010).

Discussion

Aim

The wide range of methods available to measure sedimentation processes in interdisciplinary biogeomorphological research of tidal marshes has been summarised in this review. The discussion provides guidelines to help choose the method that is best suited for a specific research question. These guidelines are intended to improve biogeomorphological research on, for example, ecosystem engineers and their application to restoration of ecosystems and their services (Byers et al. 2006).

First of all, the process under consideration has to be identified, which then significantly constrains the number of suitable methods. Secondly, temporal and/or spatial scales need to be determined. Thirdly, more practical considerations for the choice of method are considered: minerogenic vs. organogenic marsh, types of external disturbance expected *i.e.* livestock, drift-ice or even tourists. A combination of different methods may also help to unravel the interplay between different abiotic and biotic influences on sedimentation processes. Unravelling such interactions is the aim of many bio-geomorphological research studies. We will give several examples of how a combination of methods may improve the knowledge and understanding of coastal ecosystems.

Processes

The first step in choosing an appropriate method, for investigating a specific research question about sedimentation processes, is defining the most relevant process. Does the study focus on SSC (A), sediment deposition (B), accretion (C) or surface-elevation change (D) (Fig. 7.1)? The distinction between accretion and elevation change can be subtle but important to make. Accretion, on the one hand, can be measured as the additional accreted sediment on top of a marker horizon (mm/yr). This may include, for example, accumulation of organic material, but excludes the influence of deep subsidence or autocompaction underneath the marker horizon (Fig. 7.1). Thus, if the future trajectory of marsh development is to be predicted, it is especially important to distinguish accretion (C) from surface-elevation change (D) in marshes that are strongly influenced by deep subsidence. If measurements of accretion alone are used, the net change of elevation may be strongly overestimated.

A combination of at least some of the different processes described here should be included if data are collected as input for dynamic models predicting future marsh development. Predictions of these models may also be more robust if they are based on data that were collected by using a combination of different methods. For example, basing dynamic models of coastal sedimentation on physical descriptions of suspended sediment settling and including SSC as a parameter may yield better results than more empirically-based models (Kirwan et al. 2010, Fagherazzi et al. 2012).

Time

The temporal scale is very important in biogeomorphology. For example, an ecosystem engineer's impact may be greatly affected by the scale of its activity over time (Jones et al. 1994). Therefore, depending on the ecosystem engineer, the appropriate time period to be considered can differ significantly, thus affecting the choice of an appropriate method. This choice may further depend on the time that is available for measurements, thus determining whether it is better to use a pre- or post-event method. Pre-event methods may enable the immediate understanding of patterns over short (ecological) time scales (*i.e.* individual tides to a few years), such as seasonal availability of SSC (*e.g.* Asjes and Dankers 1994). In contrast, post-event methods are useful in investigating prolonged temporal patterns of sediment deposition relative to ambient conditions, such as the influence of storm frequencies on accretion rates (Schuerch et al. 2012b, Bellucci et al. 2007).

Many long-term techniques are post-event and make use of existing markers in the soil. Temporal resolution for these post-event methods often depends on the deposition rate in the study area. The longest time periods are covered by the ^{14}C-method (300–60.000 yr; Bird et al. 1999, Turney et al. 2001, 2006) and the OSL-method (up to 100.000 yr; Huntley et al. 1985). Caution is needed when interpreting the results obtained using long-term methods since processes, such as autocompaction (Bartholdy et al. 2010), may considerably influence the measurements. In general, deeper sediments are more compacted. Therefore, accretion rates measured in the first years of measurement may be systematically higher than those of later years (Cahoon et al. 1995). As a result, the estimated average accretion rate becomes smaller with increasing depth of a marker in the soil profile (Fig. 7.8). Recently, methods have been developed to correct for compaction (Williams 2003, Bartholdy et al. 2010). These corrections can help to evaluate the efficacy of marker horizons. Nevertheless, soil properties that influence compaction can be affected by many factors, such as vegetation type, bioturbators (Schrama et al. 2012) and trampling by livestock.

Using post- and pre-event methods in combination (*e.g.* ^{137}Cs and SET/SEB) can help to resolve how sedimentation processes have changed over time. This was demonstrated by a 15-year study on the Peazemerlannen in The Netherlands, where an underestimation of yearly accretion was identified in the first two years (van Duin et al. 2007). The underestimation was linked to lack of sediment import by winter storms during these first two years (Bakker et al. 2002) (Fig. 7.9).

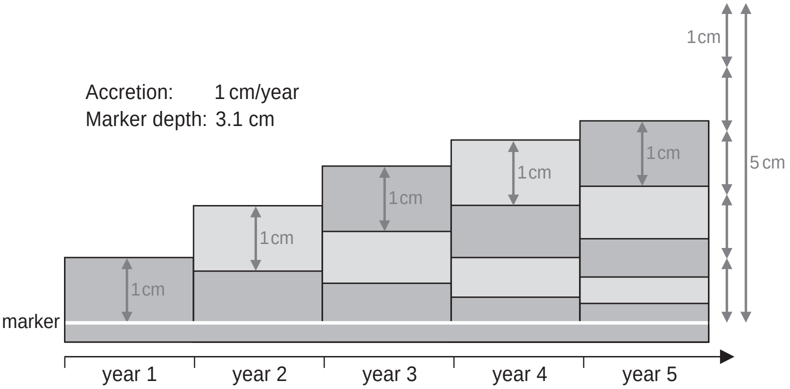

Figure 7.8 Schematic illustration of the effects of autocompaction. The actual accretion rate is 1 cm y^{-1}. If measured 5 years after application, the marker horizons is found at a depth of 3.1 cm, because of the autocompaction of deeper layers. This would result in a calculated accretion rate of 0.6 cm y^{-1} and leads to an underestimation of yearly accretion rate.

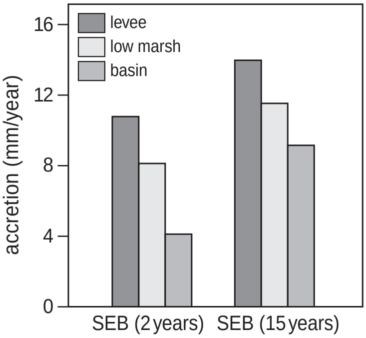

Figure 7.9 Comparison of accretion rate measurements using SEB measurements for 2 years and 15 years. Measurements were done on levees, in the low marsh, and in basins at the Peazemerlannen salt marsh, The Netherlands. The two year measurements represent a period without major winter storms, which leads to an underestimation if general conclusions are drawn over short timescales.

Space

Ecosystem engineers can have localized impacts, such as mussel beds stabilizing sediment (Eriksson et al. 2010), but their engineering can also affect large areas, such as the disappearance of sea grass is thought to have affected the turbidity of the entire Dutch Wadden Sea (van Katwijk et al. 2010, Eklöf et al. 2011). Furthermore, landscape features, such as proximity to tidal channels, influence the bio-geomorphological development of an area over the long term (French et al. 1995, Temmerman et al. 2003b). Therefore, the spatial resolution of a method is important to many research questions. Many of the described methods do not have large spatial resolutions *per se*, or do not have the necessary vertical accuracy needed for some questions. The spatial resolution of most methods can be increased by spreading the stations over a larger area instead of placing them in clusters (de Groot et al. 2011a). Increasing the accuracy, however, is somewhat more difficult. For example, airborne LiDAR covers large spatial scales, but is not very accurate (*ca.* 10–15 cm). Airborne LiDAR, therefore, is mostly suitable for creating digital elevation maps or digital terrain models, which can be used for various (spatial) analyses (Petzold et al. 1999, Keim et al. 1999).

Geostatistical models can be applied for spatial interpolation of point measurements when combining methods. In many cases, one method may be difficult or expensive to measure (*e.g.* OBS-sensor), but the measurements maybe correlated with a second, simpler method (*e.g.* sediment trap) or a method with a large spatial resolution (*e.g.* LiDAR). Using the spatial correlation between OBS and sediment traps, for example, may increase the spatial coverage value of the OBS-sensor (Diggle and Ribeiro Jr. 2007).

Minerogenic vs. organogenic tidal marshes

The differences between minerogenic and organogenic marshes are important when choosing and applying methods to measure sedimentation processes. On minerogenic marshes, mineral sediments are generally the most important contributor to marsh accretion (Allen 1990, 2000). On organogenic marshes, however, organic deposition, originating from dead plant material such as roots (Niering 1997), is the most important contributor.

The significance of different processes (Fig. 7.1) may be different in these two types of marches. In organogenic marshes, applying SSC (A) and sediment deposition (B) methods may not be relevant, because of the low mineral input. Combining accretion (C) and surface-elevation change (D) methods to quantify shallow subsidence rates may be especially useful in these organogenic marshes. Shallow subsidence may be more important in organogenic than minerogenic marshes, since organic particles are decomposed and compacted to a higher degree than mineral particles. To address this problem, some studies use a combination of marker horizons and SET (Cahoon et al. 2000, Day et al. 2011). Additionally, due to the differences between organogenic- and minerogenic marshes, method adaptations are sometimes advisable. For example, it is not possible to bury a sedimentation plate in an organogenic marsh by extracting a piece of marsh turf, because organogenic marsh soil is less stable. Also due to the relative instability of organic soil, Cahoon et al. (2002a, b) used wooden walkways to prevent disturbances during measurements.

Physical disturbance

When measuring sediment processes, we encounter two different types of disturbance. Firstly, the process of interest itself can be disturbed by the equipment or the act of measuring. Secondly, the accuracy of the measurements can be negatively affected by external physical disturbances of the equipment (*e.g.* livestock or drift-ice).

The shape of the device used to measure sediment deposition can often affect wind and wave activity, especially near the end of tidal submersion. For example, the shape of the sediment trap can have a very large influence on water flow velocity and direction, which can lead to an overestimation of settled sediment (Hargrave and Burns 1979, Bale 1998). To avoid this problem, a flat device may be a better option. However, many flat devices increase the probability of losing sediment during recovery (Gardner 1980, Kozerski and Leuschner 1999). Another example of disturbance exerted by measuring equipment is the possible influence of sedimentation plates on soil hydrological processes and on the production of roots. When these processes are relevant to the aims of the study, using an SEB/SET might be a better option.

It is advisable to consider the possible effects of equipment disturbance in the research area before installation. Many instruments are easily disturbed or destroyed by extreme events such as severe floods (marker horizons may then be eroded just after installation), drift ice (poles of SEB) or mowing. Poles are also known to attract both wild- and domestic animals (Dijkema 2005), as well as people. This activity may influence the measurements through trampling effects, for example, which was shown in the Peazemerlannen, The Netherlands. Here, the underestimation of accretion increased by 20% due to livestock grazing (unpublished data). Therefore, the use of inconspicuous methods, such as sedimentation plates, may be preferable in such areas. Furthermore, bioturbation can disturb both natural and artificial marker horizons, as well as the layering of sediments, leading to errors in accretion measurements. If the only bioturbators are small animals, such as the Crustacean, *Orchestia gammarellus* (Schrama et al. 2012), common sedimentation plates may be a good alternative to artificial marker horizons. If the burrowing animals are bigger, such as the water vole (Kuijper and Bakker 2012), they may also disturb the plates and it is advisable to use hybrid methods.

Biogeomorphology on tidal marshes

The increased interest of ecologists in the interplay between biotic and abiotic factors has illuminated other aspects of geomorphological methods. In ecological and geomorphological studies, it is often realized that the biota are influenced by the geomorphology and *vice versa*. These interactions may be easy to recognize over short time scales, such as how plants trap sediments and then are affected by nutrients from these sediments. On longer time scales that also encompass evolutionary processes, the influence of the biology on the development of geomorphology is less recognised and/or less understood than the influence of geomorphology on biology

(Corenblit et al. 2011). Research on short-term interactions can nevertheless enhance the understanding of long-term interactions.

The methods discussed in this review focus on geomorphological processes. However, the methods can also be used to assess biological processes on tidal marshes. For example, the dispersal of seeds and other propagules can be studied with sediment traps, as these seeds are caught together with the sediment. However, these traps are not always appropriate when studying the effect of ecosystem engineers, such as *Spartina anglica*, as they may underestimate the sediment deposited on the plant and the protection *S. anglica* confers on deposited sediments against resuspension. Additionally, sediment deposition measurements do not measure the accumulation of dead biomass. To study these kinds of vegetation-sedimentation interactions, buried plates or SET/SEB may be better options as they disturb the interactions between vegetation and sediment less.

Another interesting but largely unstudied factor is livestock grazing, especially in European marshes. Grazing may have a major effect on vegetation-sedimentation dynamics on tidal marshes. On the one hand, grazing livestock may influence accretion rates directly through compaction of the soil. On the other hand, there are various indirect ways in which livestock may affect sedimentation processes. For example, livestock are known to reduce vegetation density in marshes (*e.g.* Berg et al. 1997), which may in turn alter flow conditions of inundating water and lead to differences in sediment deposition rates and patterns. Additionally, grazing may increase the accumulation of biomass in the soil, as plants which experience grazing are known to produce more roots (Esselink et al. 1998). However, soil conditions maybe become more anoxic for decomposers through compaction and thus grazing may actually reduce the decomposition of biomass (Schrama in prep.). In this way, grazing may stimulate organogenic accretion in marshes but this negative effect might be counterbalanced to a certain extent by the positive effect of bioturbation (Schrama et al. 2012). To assess the impact of grazing on marshes, it is thus important to unravel the potentially confounding factors associated with 1) changes in vegetation structure, by measuring sedimentation in grazed and ungrazed vegetation, from those associated with 2) changes resulting from compaction by trampling, by monitoring accretion and shallow subsidence in grazed and ungrazed marshes. It is not advisable to use methods that influence vegetation structure to assess influence on sedimentation processes. To install sediment traps, for example, it is necessary to clip the local vegetation to obtain a bare surface and thus sediment traps are not useful to study the effect of vegetation structure. To do this, we advise the use of SEB in combination with marker horizons, for example, or plates in grazed and ungrazed areas to assess both accretion and shallow compaction. By additionally taking soil samples close to the plot, it is also possible to gain extra information on differences between grazed and ungrazed marshes in soil texture, porosity, and organic matter content.

These examples show how the interplay between abiotic and biotic components of marshes, such as seen in ecosystem engineers, can be studied using a variety of methods to measure sedimentation processes or by applying combinations of these methods. However, ecosystem engineers and bio-geomorphological interactions are present in many other ecosystems. For example, sea grasses in the Wadden Sea have been shown to maintain their own preferred environment of fine sediments on intertidal flats (Van Katwijk et al. 2010, Eklöf et al. 2011). Similarly in a lagoon in South-Africa, organic matter content of the sediment was highly influenced by the interaction between reefs, crabs and hydrodynamics (Bruschetti et al. 2011). These are just two examples, and much is still unknown about how these ecosystems function. In the future, more research is needed to understand sedimentation processes and the abiotic and biotic factors influencing them, especially in these times of global change when these ecosystems are threatened by SLR. The guidelines for application, for the methods presented in this review, are probably also valid for research in other ecosystem types with vegetation-sedimentation interactions, such as river floodplains, dunes, and aquatic systems. Insight into these vegetation-sedimentation interactions will hopefully enable researchers to find solutions to protect ecosystems by recruiting the ability of ecosystem engineers to modify their own environment.

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Chapter eight

8

Does livestock grazing affect salt marsh resilience to sea-level rise in the Wadden Sea?

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Abstract

Sea-level rise (SLR) can be a major threat to coastal ecosystems, such as salt marshes. The resilience of salt marshes to SLR is largely determined by their ability to respond with increased accretion rates. In European salt marshes, livestock grazing is common practice, but its effect on marsh accretion has hardly been studied. Grazing by livestock might influence accretion rates directly, by increasing soil compaction through trampling, and indirectly, by reducing aboveground biomass and thus decreasing sediment deposition rates. We therefore expect accretion to be lower in grazed compared to ungrazed salt marshes. In four study sites along the mainland coast of the Wadden Sea, accretion rates, sediment deposition rates and soil compaction of grazed and ungrazed marshes were analysed by using the ^{137}Cs radionuclide dating method. At each study site, landward and seaward locations were differentiated. Accretion rates were on average 11.6 mm yr^{-1} during recent decades and thus higher than current and projected rates of SLR. Neither accretion (medians: grazed 8.2 and ungrazed 8.7 mm yr^{-1}) nor sediment deposition rates (medians: grazed 6.6 and ungrazed 8.9 kg m^{-2} yr^{-1}) were significantly different between grazing treatments. Contrasting results in different marshes led to non-significance of the results, and it can, consequently, be assumed that other factors might influence whether grazing has an effect on accretion and sediment deposition rates. Both rates were higher on the seaward than on the landward location (medians accretion: seaward 10.3 and landward 7.5 mm yr^{-1}; medians sediment deposition: seaward 8.4 and landward 4.8 kg m^{-2} yr^{-1}). Soil compaction was clearly affected by grazing with significantly higher dry bulk density on grazed compared to ungrazed parts (medians 0.65 and 0.52 g cm^{-3}, respectively). We conclude that the effect of grazing on marsh growth does not follow a direct causal chain, but possibly has a great importance when interacting with other biotic and abiotic processes on the marsh.

Introduction

Many coasts of the world show an enhanced rate of sea-level rise (SLR) over the last century, and studies predict it to accelerate even faster in the future (IPCC 2007, Vermeer and Rahmstorf 2009). Global SLR was 3.1 mm yr^{-1} between 1993 and 2003 (IPCC 2007). For the Wadden Sea, a long-term SLR of 1–2 mm yr^{-1} was reported for the last 50 to 100 years while mean high tide (MHT) even increased by 2–2.5 mm yr^{-1} (Oost et al. 2009, citing several authors). However, these rates might be lower if datasets were corrected for the lunar nodal cycle as calculated for the short-term local SLR of the years 1995–2010 (0.7 mm yr^{-1} and 2.3 mm yr^{-1}, with and without correction for the lunar nodal cycle, respectively; Baart et al. 2012). As a consequence of SLR, 5–20% of all coastal wetlands could be lost until 2080 (Nicholls 2004). Among these coastal ecosystems are mangroves (*e.g.* Krauss et al. 2010), tidal freshwater forests (*e.g.* Craft 2012) and salt marshes (*e.g.* Morris et al. 2002), for example. Salt marshes provide many ecosystem services (Short et al. 2000), such as improving coastal protection by attenuating wave energy (Möller 2006), carbon sequestration (Callaway et al. 2012), and they harbour a unique flora and fauna (Schmidt et al. 2012).

The resilience of salt marshes to SLR is largely determined by their ability to compensate higher water levels by increased accretion rates: Only if accretion rates are sufficiently high, a salt marsh will be able to keep pace with relative SLR. Salt-marsh accretion is defined as the increase in surface elevation relative to a marker horizon or a local measuring device (Cahoon et al. 1995, van Wijnen and Bakker 2001). The accreted material on top of the marker horizon is subject to shallow subsidence caused, for instance, by autocompaction (Bartholdy et al. 2010). Even if many studies have already investigated accretion rates in salt marshes (e. g. Cahoon and Turner 1989, Bellucci et al. 2007, Baustian et al. 2012) and a number of models exists to predict the future development of salt marshes (*e.g.* Allen 1990, Temmerman et al. 2003, Bartholdy et al. 2004, Schuerch et al. 2013), the question if accretion rates in salt marshes will suffice to outpace SLR is still a point of discussion (*e.g.* Suchrow et al. 2012).

In general, important factors influencing accretion rates in tidal marshes are distance to the sediment source such as creeks or the marsh edge (*e.g.* Esselink et al. 1998, Reed et al. 1999, Bartholdy et al. 2004), elevation affecting flooding frequency and duration (*e.g.* Richard 1978, Stoddart et al. 1989, Temmerman et al. 2003a), and suspended sediment concentration (SSC) of the inundating water (Kirwan et al. 2010). An important mechanism for the spatial variability of sediment deposition rates is the reduction of the flow velocity above the vegetated marsh surface (Temmerman et al. 2012), which can lead to increased sediment deposition at sites with higher biomass (Morris et al. 2002) and/or in the vicinity of tidal creeks or the marsh edge (Christiansen et al. 2000, Temmerman et al. 2004a, van Proosdij et al. 2006).

Whether and how grazing management affects accretion rates on these marshes is scarcely studied (*e.g.* by Andresen et al. 1990, Neuhaus et al. 1999, Stock 2011, Suchrow et al. 2012). Mainland salt marshes at the Wadden Sea coast represent 10% of all European temperate salt marshes (Bakker et al. 1997). Here, livestock grazing for agricultural purposes used to be common (Esselink et al. 2000). Since the 1980s, however, grazing was reduced in many of these salt marshes primarily for nature conservation reasons (Esselink et al. 2009). We expect grazing livestock to influence accretion rates in salt marshes in different ways: directly, by increasing soil compaction through trampling (Olsen et al. 2011); and indirectly by reducing above-ground biomass (Kiehl et al. 1996) and thus lowering the input of mineral sediments.

We studied effects of livestock grazing on the resilience of salt marshes to SLR by quantifying accretion and sediment deposition rates as well as soil compaction in grazed and adjacent ungrazed parts of four salt marshes along the mainland coast of the Wadden Sea. Furthermore, landward and seaward locations were sampled at each study site because distance to the sediment source was found to influence accretion in many studies before (Esselink et al. 1998, Reed et al. 1999, Bartholdy et al. 2004, but see Craft 2012 for a contrasting result).

We tested the following hypotheses:

(1) Vertical accretion rates are lower in grazed compared to ungrazed salt marshes. To prove this we calculated accretion rates by radionuclide dating of sediment horizons in soil cores.

(2) Sediment deposition rates are lower in grazed compared to ungrazed sites. This was investigated by calculating the yearly amount of settled sediment per unit area.

(3) Soil compaction is higher on grazed compared to ungrazed sites. This hypothesis was tested by comparing the dry bulk density of the soil, which was assumed to be a measure for grazing-induced soil compaction.

Materials and Methods

Study sites

The study was carried out on four different salt marshes in The Netherlands and Germany along the mainland coast of the European Wadden Sea, a shallow depositional coastal system, stretching from The Netherlands to Denmark (Fig. 8.1). The three German study sites are part of the Schleswig-Holstein Wadden Sea National Park, which was established in 1985. The Dutch study site is protected as a national nature conservation area. Traditionally, all study sites were used for intensive livestock grazing and are characterised by a history of coastal engineering. The construction of ditched sedimentation fields, enhancing sediment deposition and

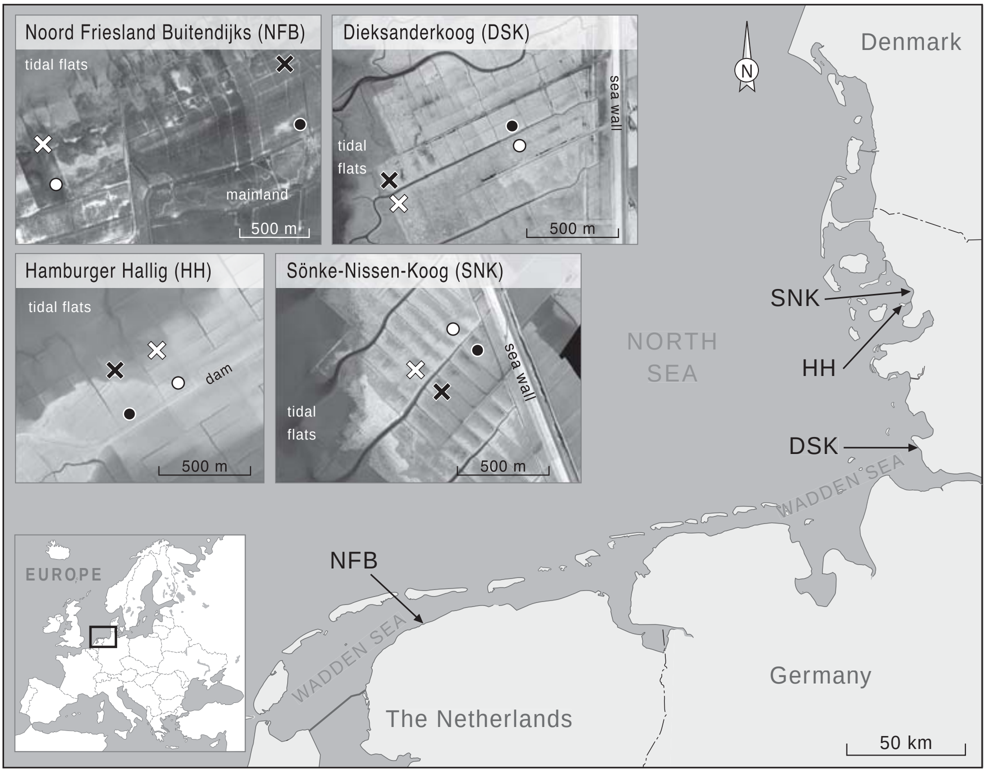

Figure 8.1 Location of the four study sites on the Wadden Sea mainland coast. Black markers= grazed salt marsh; white markers=ungrazed salt marsh; crosses=seaward sampling locations; dots=landward sampling locations; base maps: Amtliche Geobasisdaten Schleswig-Holstein, ©VermKatV-SH and Ministry of Agriculture, Nature and Food Quality, ©Slagboom en Peeters.

establishment of salt-marsh vegetation, led to an even distribution of ditches and a relatively flat topography (Esselink et al. 1998). With increasing importance of nature conservation, drainage and grazing were reduced or stopped in many Wadden Sea salt marshes since the 1980s (Esselink et al. 2009). Each of our study sites is subdivided into a grazed and an ungrazed part. Grazing treatments were underway for at least 20 years before sampling and have been maintained ever since. The change in grazing treatment led to a change in vegetation composition in most of the ungrazed and in some of the grazed parts of the study sites between 1988 and 2010 (Table 8.1; Esselink et al. 2009). Vegetation on ungrazed parts of the study sites generally developed from *Puccinellia maritima* or *Festuca rubra* types to the *Elymus athericus* type, which typically implied a development from rather short to high and biomass-rich canopies (Kiehl et al. 2001). Vegetation on grazed parts of the marshes often developed from *Puccinellia maritima* to *Festuca rubra* types or stayed the

Table 8.1 Key parameters of the study sites. Tidal amplitude data was retrieved from BSH (2011); NFB=Noord Friesland Buitendijks; DSK=Dieksanderkoog; HH=Hamburger Hallig; SNK=Sönke-Nissen-Koog; NAP=Normal Amsterdam Peil (Dutch Ordnance Datum); NHN=Normalhöhennull (German Ordnance Datum); MHT=mean high tide; TMAP=Trilateral Monitoring and Assessment Program (Esselink et al. 2009); SEB=sedimentation erosion bar. TMAP vegetation types were coded as follows: Agr (*Agrostis stolonifera* type), Atr/Puc (*Atriplex portulacoides* / *Puccinellia maritima* type), Ely (*Elymus athericus* type), Fes (*Festuca rubra* type), Puc (*Puccinellia maritima* type), Spa (*Spartina anglica* type).

Site	Sampling location	Treatment	Elevation	Elevation above mean high tide [m]	TMAP vegetation type in		Grazing animals	Grazing intensity	Distance to next creek [m]	Distance to marsh edge [m]	Literature		
					1988	2010					Literature Accretion rates [mm yr^{-1}]	Method used in Literature	Study
NFB	Landwards	Ungrazed (U)	1.55 m NAP	0.57	*Puc*	*Ely*	None		50	380	23.8	Plate	Nolte et al.
	(L)	Grazed (G)	1.74 m NAP	0.76	Puc	Agr	Horses	moderate	50	630	7.2		Unpubl.
	Seawards	Ungrazed (U)	1.29 m NAP	0.31	*Puc*	*Puc*	None		68	100	28.6		Data
	(S)	Grazed (G)	1.49 m NAP	0.51	*Puc*	*Puc*	Horses	moderate	100	160	9.2		
DSK	Landwards	Ungrazed (U)	2.11 m NHN	0.49	*Fes*	*Ely*	None		14	955	3.4	Levelling	WSV
	(L)	Grazed (G)	1.91 m NHN*	0.29	*Puc*	*Fes*	Sheep	intensive	48	920	5.2		2012
	Seawards	Ungrazed (U)	2.40 m NHN	0.78	*Puc*	*Ely*	None		74	290	9.1		
	(S)	Grazed (G)	2.25 m NHN*	0.63	*Spa*	*Ely*	Sheep	intensive	85	205	9.2		
HH	Landwards	Ungrazed (U)	2.13 m NHN	0.54	*Puc*	*Ely*	None		55	250	3.0-6.3	SEB	Stock 2011
	(L)	Grazed (G)	2.09 m NHN	0.5	*Puc*	*Fes*	Sheep	moderate	95	230			
	Seawards	Ungrazed (U)	1.92 m NHN	0.33	*Atr/Puc*	*Atr/Puc*	None		35	35	3.0-6.3		
	(S)	Grazed (G)	1.92 m NHN	0.33	*Puc*	*Fes*	Sheep	moderate	40	40			
SNK	Landwards	Ungrazed (U)	2.00 m NHN	0.41	Puc	Ely	None		46	525	7.7	Leveling	Suchrow
	(L)	Grazed (G)	2.07 m NHN	0.48	Puc	Puc	Sheep	intensive	51	685			et al. 2012
	Seawards	Ungrazed (U)	2.04 m NHN	0.45	Puc	Ely	None		47	340	7.7		
	(S)	Grazed (G)	2.04 m NHN	0.45	Puc	Puc	Sheep	intensive	48	450			

same (Esselink et al. 2009). Rates of vertical marsh growth between 7 and 43 mm yr^{-1} were reported for salt marshes at the Dutch coast (Dijkema 1997, Esselink et al. 1998, Hazelden and Boorman 1999, Dijkema et al. 2011), which is a higher range than values communicated for most salt marshes in Germany (6–26 mm yr^{-1}; Dittmann and Wilhelmsen 2004, Stock 2011, Suchrow et al. 2012).

The elevation of sampling locations was measured using a levelling instrument (Spectra precision® laser LL500 and laser receiver HR500 by Trimble) or extracted from a digital elevation model using the Software ArcGIS 10 (Table 8.1). The same software was used to assess the distance to the next creek and the distance to the marsh edge by means of an aerial photograph.

The salt marsh Noord-Friesland Buitendijks (NFB), The Netherlands (53°20'11", 5°43'40"), is exposed to a tidal range of about 2.1 m. The sedimentation fields, leading to marsh development, were installed in the years 1952 to 1960. Large parts of the area have been purchased by the NGO 'It Fryske Gea' for nature conservation. Drainage ditches have not been maintained since the year 2000 (Dijkema et al. 2011). The part of the site in which sampling took place is moderately grazed by horses (Dijkema et al. 2011). The ungrazed part was abandoned approximately 30 years ago and lies at a distance of 1.8 km to the grazed part.

Dieksanderkoog (DSK) at the mouth of the Elbe estuary, Germany, is a wide salt marsh, which stretches up to 2,000 m from the seawall to the intertidal flats (53°58'23", 8°53'8") and is exposed to a tidal range of 3 m. The marsh started to develop after 1935, when the present seawall and a system of sedimentation fields were constructed (Kohlus 2000). One part of the salt marsh is intensively grazed by sheep and an adjacent part remained ungrazed since the early 1990s (Stock et al. 2005). On the latter part, maintenance of the ditches was stopped after the abandonment of grazing. On the grazed part, however, ditches are still renewed every five years.

The study site Hamburger Hallig (HH) is situated behind a small remnant of a former island 3 km off the coast (54°36'8", 8°49'27"). The tidal range at this site is 3.4 m. After the construction of a dam connecting the island with the mainland in 1874, salt marshes began to expand alongside the dam (Palm et al. 2000). The whole salt marsh was intensively grazed by sheep until 1991. Since then, 26% of the area are moderately grazed and 21% are still intensively grazed, while grazing was abandoned on 53% of the area (Esselink et al. 2009).

The study site Sönke-Nissen-Koog (SNK) is situated 3.5 km north of HH (54°38'4", 8°50'2") and experiences the same tidal range (3.4 m). After the construction of the present seawall and adjacent sedimentation fields in 1925 (Kunz and Panten 1997), a salt marsh developed with a current extent of approximately 1,000 m. The study site is part of a grazing experiment (Kiehl et al. 1996), which started in 1988 and guarantees a continuous intensive grazing on the grazed part. The ungrazed part of the marsh is situated adjacent to the grazed one.

Core sampling

In 2010, we collected four soil cores from each of the study sites. NFB, HH and SNK were sampled in April; DSK was sampled in December. Two cores were taken from the ungrazed part and two from the grazed part of each site. One of the two cores per grazing treatment and site was collected at a sampling location close to the seawall (hereafter termed 'landwards') and one close to the intertidal flats (hereafter termed 'seawards'). Soil cores were taken by removing the vegetation at the sampling location and driving a PVC tube (11.8 cm inner diameter) down to a depth of 80 cm into the soil. After sampling, the tubes were sealed with plastic bags to avoid loss of soil moisture.

Core processing and soil properties

In the laboratory, each core was cut twice along its side in order to remove one half of the tube. For NFB and HH, processing of the cores was carried out at Groningen University. Here, the cores were cut into 2 cm sections. Each section of soil was weighed, dried in the oven at 105°C to constant weight, and then weighed again to determine soil moisture. Dry weight and volume per section were used to calculate dry bulk density (g cm^{-3}). The dried material was ground using a Culatti rotor mill to disaggregate the soil particles. The grain size was then analysed by laser diffractometry (Mastersizer S – long bench MAM 5005) assessing volumetric concentrations of different grain-size classes. Organic matter content was determined as the weight loss after ignition of a 5 g subsample of each section at 550°C for four hours. For DSK and SNK, processing of the cores was carried out at the University of Hamburg. Here, the cores were cut into 1 cm sections in the upper 24 cm and into 2 cm sections below. For SNK, sections below 40 cm were cut to 5 cm. Soil moisture, dry bulk density, and organic matter content were determined as described for NFB and HH, and samples were manually ground afterwards. Grain size distribution was analysed using a laser diffraction sensor (HELOS H2249).

In order to measure the activity of the radionuclide ^{137}Cs, the ground soil material of all samples was filled into 120 ml containers. Measurements were performed in the Laboratory for Radioisotopes at Göttingen University, Germany, for a minimum counting time of 250,000 seconds using a low-background coaxial Ge(Li)detector (Schuerch et al. 2012b). Because ^{137}Cs sorbs strongly onto small particles, the ^{137}Cs activity of each section was normalised to the mean organic matter content and mean percentage of grain sizes smaller than 20 μm of the whole core (Kirchner and Ehlers 1998).

The ^{137}Cs dating method

The ^{137}Cs radionuclide ($t_{1/2}$ = 30.2 years) is anthropogenic in origin and produced by nuclear fission. In Europe, sediment cores usually show two peaks of increased ^{137}Cs activity, which can be attributed to two historic nuclear events: The upper peak is usually related to the accident at the Chernobyl nuclear power plant in 1986, while the lower peak is caused by the nuclear bomb tests during the 1960s with its maximum in 1963 (Kirchner and Ehlers 1998). If only one peak was present in cores of our study, the ^{137}Cs activity below the peak was considered to relate the peak to either 1963 or to 1986. If the activity was approaching zero below the peak, the peak was regarded as resulting from 1963 and not from 1986 since anthropogenic emission of ^{137}Cs only started in the 1950s (Pennington et al. 1973).

Accretion and sediment deposition rates

Before calculating salt-marsh accretion rates, we corrected each core for sampling compaction. Sampling compaction was measured while taking the cores in the field. For doing this, the actual length of each soil core (distance upper to lower end of the core) was related to its original length (distance soil surface to lower end of the core) resulting in sampling compaction in %. Then, marsh accretion rates (mm yr^{-1}) were derived from the identified ^{137}Cs peak by dividing the respective depth by the time period since 1986 or 1963 (see Dyer et al. 2002).

To determine the input of sediment to a site, we calculated the sediment deposition rate (kg m^{-2} yr^{-1}; Callaway et al. 1996). For this, dry bulk density (ρ) and thickness of each section (a) above the soil depth with the identified ^{137}Cs peak were multiplied, summed up and divided by the years passed (t; Eq. 1). The sediment deposition rate includes both mineral sediment deposition and organic deposition.

$$\text{sediment deposition rate} = \frac{\sum_{i=1}^{n} (a_i * \rho_i)}{t} \qquad \text{(Eq. 1)}$$

Soil compaction (dry bulk density)

Dry bulk density was used as a proxy to assess soil compaction. We compared mean dry bulk densities above the identified ^{137}Cs peaks. Grazing-induced compaction is assumed to be an important parameter in influencing dry bulk density as found amongst others by Schrama et al. (2013).

Data Analysis

The data did not meet the assumptions of normality and homogeneity and therefore non-parametric tests were used. Wilcoxon signed-rank and Kruskal-Wallis tests were applied to compare site and core characteristics between sites, grazing treatments and among sampling locations. These site and core characteristics were elevation above MHT, distance to the marsh edge and to the next creek, as well as mean organic matter content and mean percentage of grain sizes smaller than 20 μm in the upper 50 cm of soil.

Differences in accretion rates, sediment deposition rates and dry bulk density between grazed and ungrazed parts were analysed with a Wilcoxon signed-rank test.

The same test was used for analysing differences between seaward and landward sampling locations. Differences among the four study sites were analysed with Kruskal-Wallis tests.

The relation of accretion rate, sediment deposition rate and dry bulk density to elevation above MHT, distance to the marsh edge, distance to the next creek, mean organic matter content and mean percentage of grain sizes smaller than 20 μm in the upper 50 cm of soil was tested with Spearman's rank correlations. Statistical significance in all tests was determined using a 95% confidence interval with the probability $P < 0.05$. All analyses were conducted with SPSS 19.

Results

Peak identification

In 14 out of the 16 cores, peaks of ^{137}Cs activity could be identified. Seven cores showed the expected pattern with two peaks (Fig. 8.2; Appendix A), which could be identified as 1986 and 1963, respectively. In five cores, we found a single peak only, which was identified as 1986. In two further cores, single peaks were found and identified as 1963 because the ^{137}Cs activity approached zero below the respective peak. No peak could be detected in the core of the seaward ungrazed sampling location at NFB. Here, it is likely that both the 1986- and 1963-peak were below the

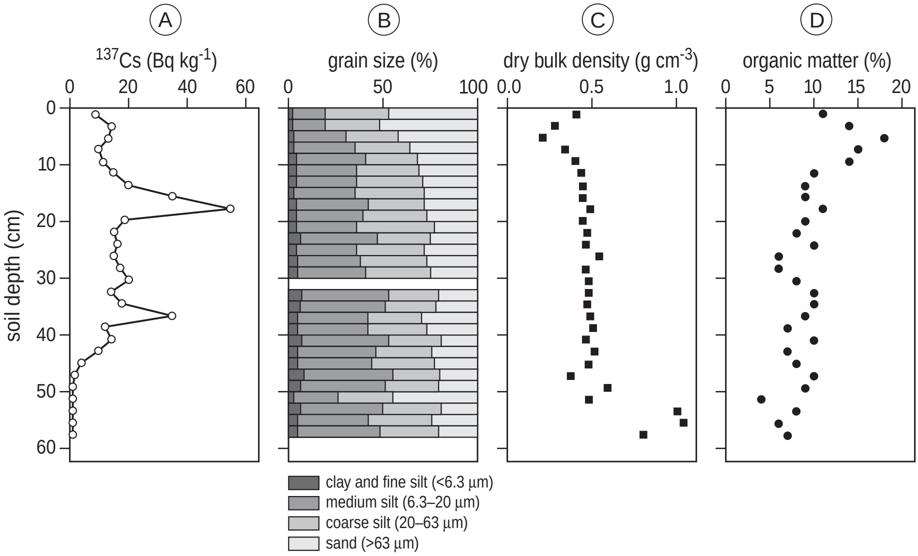

Figure 8.2 An example for the (A) ^{137}Cs activity, (B) grain size distribution, (C) dry bulk density, and (D) organic matter content for all depths in the core from the landward grazed sampling location at NFB. An overview of all 16 soil cores can be found in supporting information 1.

sampling depth of 80 cm. We therefore calculated a minimum accretion rate and sediment deposition rate for this core and used it for further analysis. In the core of the landward ungrazed sampling location at HH, a high activity of ^{137}Cs in a layer close to the marsh surface was found. This peak could not be clearly identified; its position was too shallow to be identified as the 1986-peak. We assume some disturbance in this core and excluded it from the calculation of accretion and sediment deposition rates and of mean dry bulk densities above the ^{137}Cs peak.

Site and core characteristics

Organic matter content, elevation above MHT, and distance to the marsh edge did not differ significantly between grazed and ungrazed parts of the marshes (Tables 8.1 and 8.2). The only difference was observed for the average distance to the next creek, which was slightly smaller for ungrazed parts (median 49 m, range 14–74 m) compared to grazed parts (median 51 m, range 40–100 m Z = –2.371; $P < 0.05$; n = 16; Wilcoxon-Test). Beside distance to the marsh edge, which is of course smaller for the seaward location, none of the abovementioned factors differed significantly between seaward and landward sampling locations.

Accretion rates

The mean accretion rate was 11.6 mm yr^{-1} and ranged from 5.4 to 34.6 mm yr^{-1} (Table 8.2). Generally, we found that the accretion rates calculated by ^{137}Cs dating were in accordance with literature data, except for a small number of values (Table 8.1). Rates did not significantly differ between the grazing treatments (Fig. 8.3).

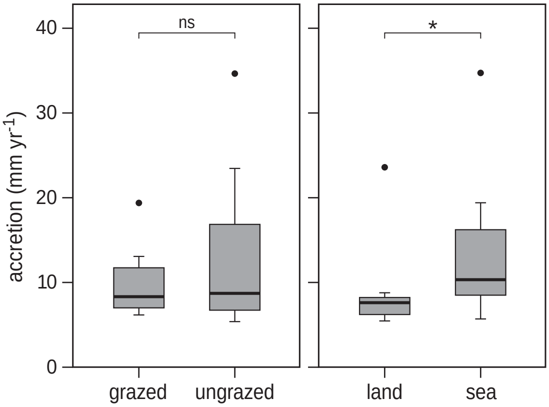

Figure 8.3 Accretion rates of grazed and ungrazed and of landward and seaward locations. Boxplots represent: median (middle line), interquartile range (box), 1.5 times interquartile range (bar) and outliers (dots). The grazing treatment had no significant effect (Z = 0.34; P = 0.74; n = 14; Wilcoxon-Test), while accretion rates were significantly higher in seaward compared to landward locations (Z = -2.37; $P < 0.05$; n = 14; Wilcoxon-Test).

Table 8.2 Mean proportion of grain sizes smaller than 20 μm and mean organic matter content in the upper 50 cm of each core, depth of the ^{137}Cs peaks, accretion rate, sediment deposition rate and mean dry bulk density above the identified peak.

Site	Orienation	Treatment	^{137}Cs 1986 depth [cm]	^{137}Cs 1960 depth [cm]	Mean % grain size <20 μm	Mean % organic matter	Accretion [mm yr^{-1}]	Reference year	Sediment deposition [kg m^{-2} yr^{-1}]	Sampling compact-ion [%]	Mean dry bulk density > peak [g cm^{-3}]
NFB	Landwards	Ungrazed (U)	56.1	none	45.79	9.72	2.34	1986	9.01	10	0.38
		Grazed (G)	17.9	36.8	40.4	9.37	0.75	1986	3.03	5	0.38
	Seawards (S)	Ungrazed (U)	none	none	37.69	8.75	3.46	1986	11.88	5	0.34
		Grazed (G)	46.4	none	41.39	9.26	1.93	1986	8.47	0.3	0.43
DSK	Landwards (L)	Ungrazed (U)	none	43.3	6.51	2.87	0.87	1963	8.88	10.96	0.98
		Grazed (G)	14.4	26.7	22.64	6.42	0.61	1963	5.69	6.72	0.91
	Seawards (S)	Ungrazed (U)	19.4	47.6	22.37	5.39	1.01	1963	9.17	10.74	0.89
		Grazed (G)	none	46.8	10.58	3.44	1.04	1963	11.59	4.14	1.09
HH	Landwards (L)	Ungrazed (U)	3.3	none	30.97	5.09	0.14	1986	0.68	8.66	0.38
		Grazed (G)	17.9	30.5	30.84	5.54	0.75	1986	3.5	5.12	0.44
	Seawards (S)	Ungrazed (U)	18.9	none	21.92	3.72	0.75	1986	4.01	11.11	0.48
		Grazed (G)	31.1	none	23.76	4.18	1.29	1986	7.48	7.21	0.56
SNK	Landwards (L)	Ungrazed (U)	12.9	none	40.88	10.24	0.54	1986	2.84	12.36	0.52
		Grazed (G)	15.2	53.4	32.53	7.29	0.63	1986	4.81	12.42	0.75
	Seawards (S)	Ungrazed (U)	14.5	33.7	30.25	6.91	0.56	1986	3.29	7.14	0.56
		Grazed (G)	21.4	49.7	26.99	7.47	0.89	1986	8.31	4.58	0.93

Highest values were achieved at the Dutch site NFB, where rates on the ungrazed parts were twice as high as on the grazed parts (medians 29.0 mm yr^{-1} and 13.4 mm yr^{-1}, respectively). The three German sites had all lower accretion rates of 8.2 mm yr^{-1} on average. In one further case we found a higher accretion rate in the ungrazed compared to the grazed part (DSK landwards; Table 8.2). The seaward locations at both HH and SNK showed the opposite pattern with higher accretion rates in the grazed compared to the ungrazed part. Accretion rates differed significantly between landward and seaward locations and were always higher at seaward locations (Fig. 8.3). We also found a negative correlation with distance to the marsh edge ($r_s = 0.54$; $P < 0.05$; $n = 15$). No significant correlations were found between accretion rate and distance to the next creek or to elevation above MHT.

Sediment deposition rates

The mean sediment deposition rate was 6.6 kg m^{-2} yr^{-1} and ranged from 2.8 to 11.9 kg m^{-2} yr^{-1}. It did not differ between the grazing treatments (Fig. 8.4). Also, differences between the study sites were not significant ($H = 6.57$; $P = 0.09$; $n = 15$; Kruskal-Wallis-Test). However, we found a trend of higher values at NFB. Here, a median of 10.4 kg m^{-2} yr^{-1} was deposited on ungrazed and 5.8 kg m^{-2} yr^{-1} on grazed parts. At all four study sites, sediment deposition rates were found to be higher at seaward compared to landward sampling locations (medians 8.4 and 4.8 kg m^{-2} yr^{-1}, respectively; Fig. 8.4).

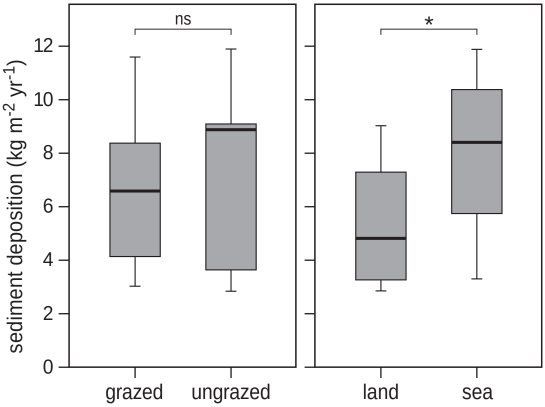

Figure 8.4 Sediment deposition rates of grazed and ungrazed and of landward and seaward locations. Boxplots represent: median (middle line), interquartile range (box), 1.5 times interquartile range (bar) and outliers (dots). The grazing treatment had no significant effect ($Z = 0.00$; $P = 1.0$; $n = 14$; Wilcoxon-Test), while sediment deposition rates were significantly higher in seaward compared to landward locations ($Z = -2.37$; $P < 0.05$; $n = 14$; Wilcoxon-Test).

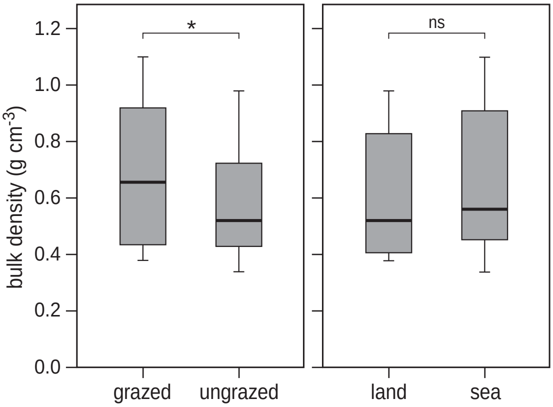

Figure 8.5 Mean dry bulk density above the identified ^{137}Cs peak of grazed and ungrazed and of landward and seaward locations. Peaks were identified to originate from 1986 (NFB, HH and SNK) and from 1963 (DSK). Boxplots represent: median (middle line), interquartile range (box), 1.5 times interquartile range (bar) and outliers (dots). Median dry bulk density was found to be significantly lower in ungrazed locations ($Z = -2.01$; $P < 0.05$; $n = 14$; Wilcoxon-Test), while no significant difference was found between landward and seaward locations ($Z = -1{,}82$; $P = 0.069$; $n = 14$; Wilcoxon-Test).

Compaction

Mean dry bulk density of sediment above the identified ^{137}Cs peak ranged from 0.34 to 1.10 g cm^{-3} and depended on the grazing treatment; it was significantly higher on grazed compared to ungrazed parts (medians 0.65 and 0.52 g cm^{-3}, respectively; Fig. 8.5). Mean dry bulk density increased with decreasing mean organic matter content in the upper 50 cm of the soil cores ($r_s = -0.68$; $P < 0.01$; $n = 15$). It further increased with decreasing mean percentage of soil particles smaller than 20 μm ($r_s = -0.76$; $P < 0.001$; $n = 15$).

Discussion

To our knowledge, this is the first study in which accretion and sediment deposition rates as well as soil compaction have been quantified for grazed and ungrazed salt marshes representing the whole geographical range of the Wadden Sea coast. Our results indicate that salt marsh soils were getting compacted by grazing, while accretion rates and sediment deposition rates were not affected by the grazing treatment. In areas with high minerogenic deposition rates like the Wadden Sea, the resilience of salt marshes to SLR thus seems not to be negatively influenced by livestock grazing.

Our hypotheses that accretion and sediment deposition rates would be higher on ungrazed salt marshes, was not supported by our results. However, we see a different outcome for the German marshes compared to the Dutch marsh, where our hypothesis was clearly supported. At all sites, accretion rates were well above rates of SLR mentioned in the introduction. As deep subsidence rates are low in the Wadden sea area (0.8 mm yr^{-1} for Dutch and 0.4 mm yr^{-1} for German sites (Veenstra 1980), it seems likely that most mainland Wadden Sea salt marshes outpace rates of current and projected SLR. Furthermore, if sea level rises, the frequency of inundations increases as well, initiating a positive feedback loop of enhanced sediment deposition on salt marshes (French 2006). However, if the rate of SLR would strongly accelerate in the future, salt marshes with low sediment supply might be endangered in the long term (Kirwan and Temmerman 2009).

Rather than depending on the grazing treatment or on elevation, as in other studies (*e.g.* Stoddart et al. 1989, Temmerman et al. 2003b), accretion and sediment deposition rates depended on the distance to the marsh edge, explaining large scale patterns of sediment deposition (see also Esselink et al. 1998, Reed et al. 1999, Bartholdy et al. 2004, but see Craft 2012 for a contrasting result). At NFB, the hypothesis of higher accretion and sediment deposition rates on the ungrazed part was supported, possibly due to a shorter distance to the marsh edge on ungrazed locations (Table 8.1).

One explanation for the unexpected results that do not support the hypothesis of lower accretion and sediment deposition rates in ungrazed marshes, might be the relative importance of small scale patterns of sediment deposition in Germany. At the Dutch site NFB, ditches are silted up and inundating water enters the marsh mainly from the marsh edge or the major creek and only during storm events. This flow pattern leads to a large scale sedimentation pattern with high sediment deposition rates closer to the marsh edge and major creeks. In contrast to NFB, inundating water enters the marshes in Germany mainly from the still intact ditch system. Consequently, sediment deposition is highest along the small ditches, thereby leading to the formation of levees. This small-scale pattern of sediment deposition might be amplified by vegetation, which can slow down currents and enhance sedimentation (*e.g.* Christiansen et al. 2000, Baustian et al. 2012, Temmerman et al. 2012). Vegetation structure differed considerably between the grazed and ungrazed parts of the study sites (Table 8.1); ungrazed salt marshes were covered by tall and dense vegetation, which can be expected to trap large amounts of sediment. Flow velocities at the creek edge are 2-4 times lower on a vegetated marsh than on a marsh with no or only short vegetation (Temmerman et al. 2012). Therefore, in a marsh with tall and dense vegetation, more sediment settles close to the ditch and does not reach the central part of the marsh, where the cores for this study were taken.

The hypothesis that compaction is higher on grazed sites than on ungrazed sites was supported by our findings. Mean dry bulk densities, which were used as an indicator for soil compaction, were significantly higher on grazed sites. Olsen et al. (2011) and Schrama et al. (2013) came to a similar conclusion. Soil compaction was especially pronounced at NFB. This very clear outcome might be caused by the livestock species used for grazing. While the German marshes are grazed by sheep, the study site at NFB is grazed by horses, which might cause more compaction because of their higher activity in comparison to cattle and sheep (Menard et al. 2002). In general, also organic matter content and grain size distribution can influence dry bulk densities (Kolker et al. 2009). However, since the mean organic matter content and the mean percentage of grain sizes smaller than 20 μm did not differ significantly between grazed and ungrazed parts of the study sites, these do not explain differences of mean dry bulk densities between the grazing treatments.

To conclude, accretion rates of the four investigated study sites were higher than the current rise in both sea level and MHT. No effect of grazing treatments on salt marsh resilience to SLR, measured as accretion and sediment deposition rates, was found because of contrasting results in different marshes. The influence of grazing on accretion rates, thus, is likely to be also affected by interactions of grazing with other biotic and abiotic processes. Meanwhile, an indication for an influence of grazing on marsh development is given by the increased soil compaction that was significantly higher on grazed compared to ungrazed marshes. For this reason, the effect of abiotic and biotic factors on accretion rates, the interaction of these factors and finally their alteration by livestock grazing should be further studied. This might be especially important in organogenic coastal systems (*e.g.* salt grasslands at the Baltic Sea coast; Callaway et al. 1997), where grazing for nature conservation (Sammul et al. 2012) might cause a larger degree of compaction compared to the minerogenic Wadden Sea salt marshes. In addition, small scale patterns of sediment deposition should be considered in future studies. If a prediction should be made about the marshes' future development, it should take the entire marsh into account (de Groot et al. 2011b). This could be done by combining methods with a high temporal resolution (*e.g.* ^{137}Cs dating) with methods with a high spatial resolution (*e.g.* sediment traps; Nolte et al. 2013b). In the face of a rising sea level, the question whether or not grazing as a tool for salt marsh management might influence sedimentation processes, is crucial to make sustainable management decisions. Models which aim to predict future marsh development therefore should seek to include the interplay between grazing and other factors influencing marsh accretion with respect to spatial patterns.

Acknowledgements

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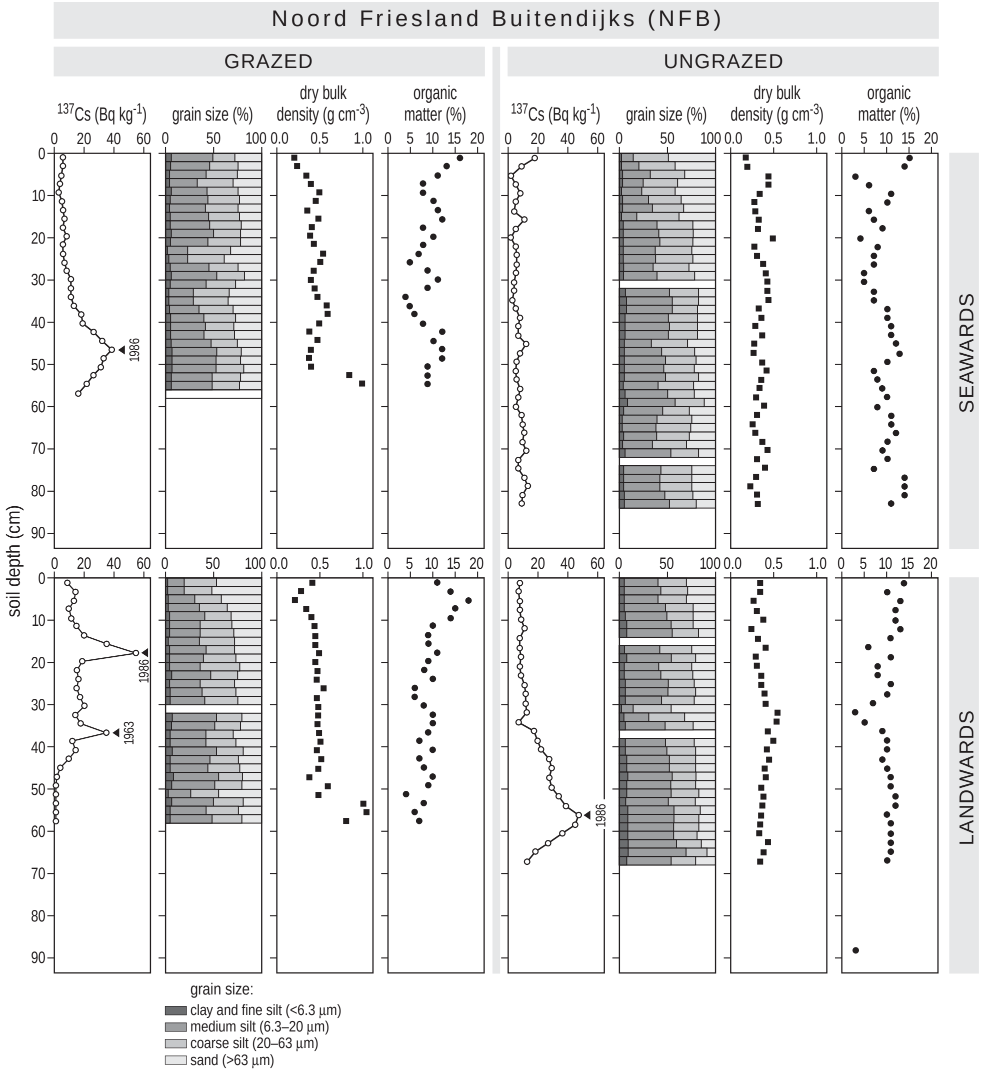
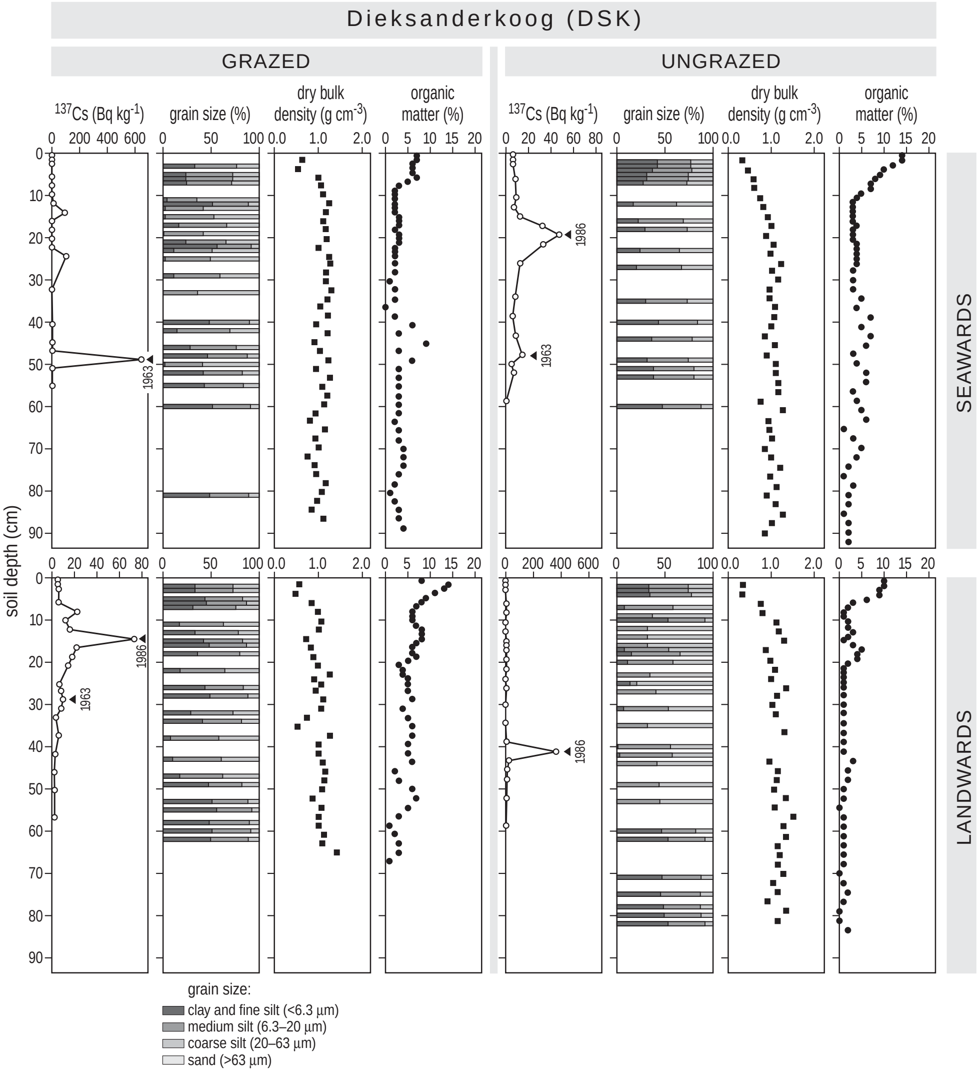
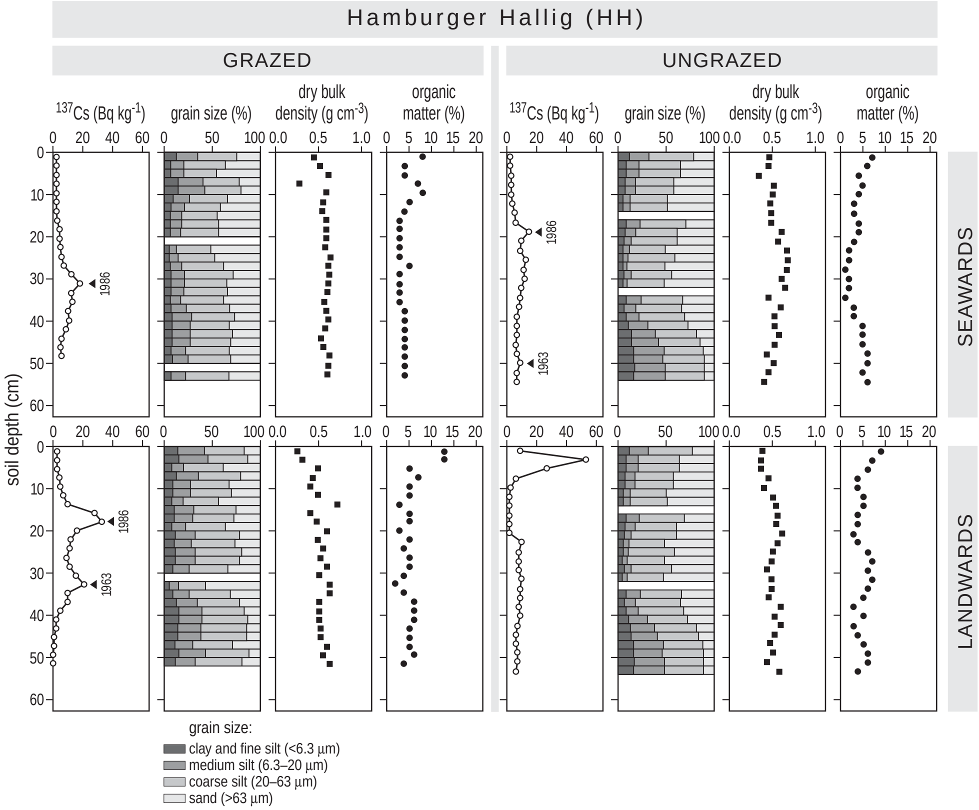
National Park of Schleswig-Holstein). Frauke Müller would like to thank ESTRADE (Estuary and Wetland Research Graduate School Hamburg as member of LExI (State Excellence Initiative) funded by the Hamburg Science and Research Foundation) for personal PhD funding and organisational support. We further thank our project partners Wadden Sea National Park Schleswig-Holstein and 'It Fryske Gea' for cooperation, supply of data and research permissions. Sincere thanks are further given to Katherina Meier, Jacob Hogendorf, Freek Mandema, Roel van Klink, Kerstin Hansen and Malte Schindler who assisted in the field and in the laboratory. We would like to thank Sigrid Suchrow, Martin Stock and Kees Dijkema, who supplied us with elevation data and reference data on accretion rates. Tom van der Spiet (University of Antwerp) and Sebastian Lindhorst (University of Hamburg) kindly analysed grain size distributions of the samples. Furthermore, we would like to thank Bernd Kopka and Rainer Schulz of the LARI Göttingen for their work. We thank Alma de Groot for valuable discussion during the Coastal Ecology Workshop 2012 and two anonymous reviewers for comments on an earlier version of this manuscript. Dick Visser is thanked for enhancing the figures and Tom Maxfield is thanked for revising the English language.

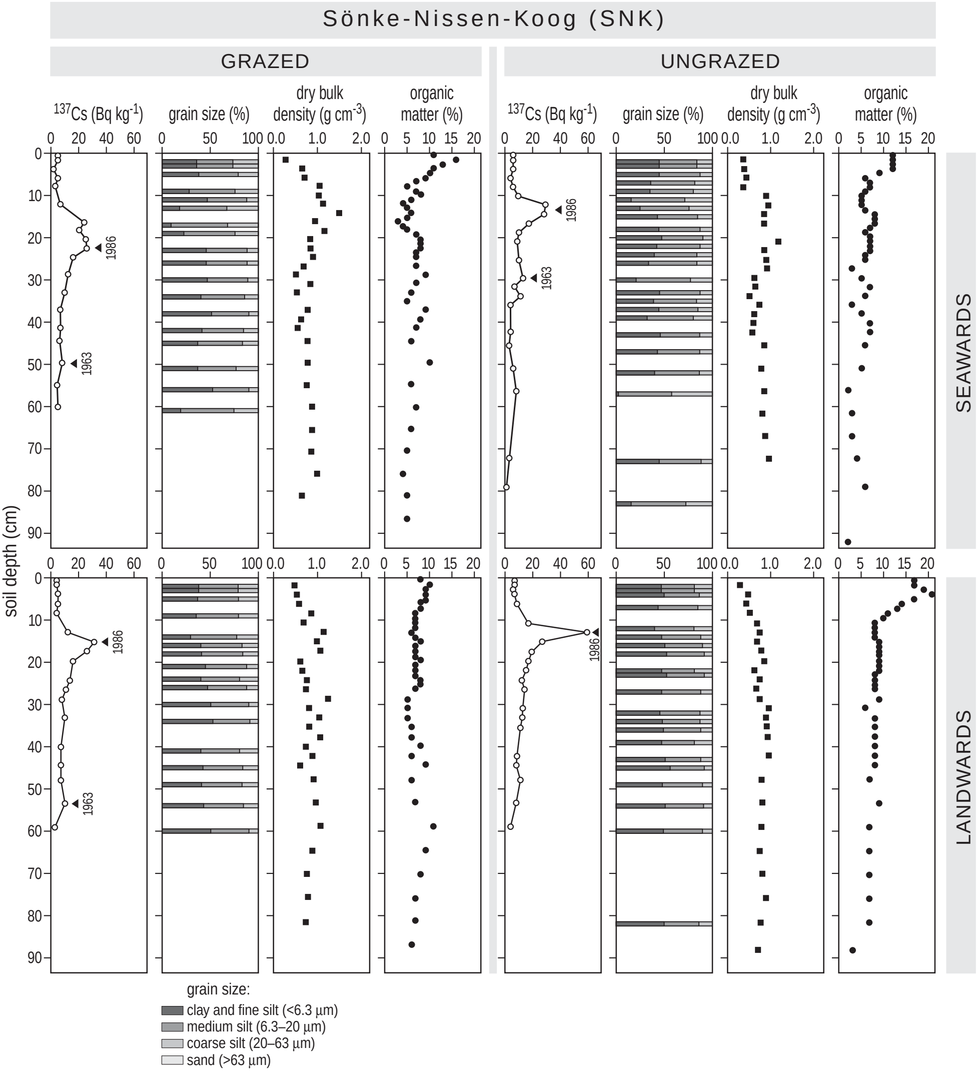
Appendix A

^{137}Cs activity, grain size distribution, dry bulk density, and organic matter content for all depths in the 16 cores. The peaks from 1986 and 1963 are indicated with arrows.




Dieksanderkoog (DSK)
GRAZED
UNGRAZED
^{137}Cs (Bq kg^{-1})
grain size (%)
dry bulk density (g cm^{-3})
organic matter (%)
0 200 400 600
0 50 100
0.0 1.0 2.0
0 5 10 15 20
0 20 40 60 80
soil depth (cm)
0 10 20 30 40 50 60 70 80 90
1963
1986
SEAWARDS
LANDWARDS
grain size:
clay and fine silt (<6.3 µm)
medium silt (6.3–20 µm)
coarse silt (20–63 µm)
sand (>63 µm)


Hamburger Hallig (HH)
GRAZED
UNGRAZED
137Cs (Bq kg-1)
grain size (%)
dry bulk density (g cm-3)
organic matter (%)
soil depth (cm)
1986
1963
SEAWARDS
LANDWARDS
grain size:
clay and fine silt (<6.3 µm)
medium silt (6.3–20 µm)
coarse silt (20–63 µm)
sand (>63 µm)


Sönke-Nissen-Koog (SNK)
GRAZED
UNGRAZED
^{137}Cs (Bq kg^{-1})
grain size (%)
dry bulk density (g cm^{-3})
organic matter (%)
soil depth (cm)
1986
1963
SEAWARDS
LANDWARDS
0 20 40 60
0 50 100
0.0 1.0 2.0
0 5 10 15 20
0 10 20 30 40 50 60 70 80 90
grain size:
clay and fine silt (<6.3 µm)
medium silt (6.3–20 µm)
coarse silt (20–63 µm)
sand (>63 µm)

Chapter nine

9

The effects of grazing as a nature management tool on different aspects of vegetation and accretion in a salt marsh – A synthesis

Stefanie Nolte

General introduction

In many grassland ecosystems, grazing with livestock is successfully used as a nature-management tool to increase or restore biodiversity (Rook et al. 2004, Metera et al. 2010). Many of these grassland ecosystems were traditionally used for agricultural purposes and are now abandoned because livestock grazing is no longer economically feasible (Rook et al. 2004). Among these previously intensively used areas are also western European coastal salt marshes. Here, large areas were abandoned for nature conservation purposes after the installation of nature protection areas such as National Parks (Bakker et al. 2003). Abandonment, however, led to a rapid succession of salt marshes resulting in large areas which are dominated by single plant species, mainly *Elytrigia atherica* (Bakker et al. 1993, Leendertse 1997, Bakker et al. 2003). *Elytrigia atherica* is a strong competitor (Kuijper et al. 2005) and areas dominated by this tall grass show very low plant species richness (Bos et al. 2002, Kleyer et al. 2003). The spread of *Elytrigia atherica* in abandoned marshes led to the question for salt-marsh management 'to graze or not to graze?' (Bakker et al. 2003). To answer this question, grazing experiments were installed along the German mainland coast (*e.g.* Andresen et al. 1990, Kiehl et al. 1996). No dominance of single competitive plant species such as *Elytrigia atherica* was detected and therefore the abandonment of marshes was further promoted (Kiehl et al. 1996). However, these results were based on a five year study and did therefore not quantify long-term effects (Bakker et al. 1996). *Elytrigia atherica* was found to invade the high marsh after nine, ten and eleven years and this might cause a loss of plant-species richness in the future (Schröder et al. 2002, Gettner 2003, Kiehl et al. 2007). It is argued, however, that a further spread of *Elytrigia atherica* may be prevented by a neglect of drainage ditches (Stock and Kiehl 2000, Gettner 2003, Kiehl et al. 2007), as a higher groundwater table is unfavourable for *Elytrigia atherica* (Kleyer et al. 2003, Davy et al. 2011). In contrast, a recommendation for grazing in low densities is given by other authors for both back-barrier (Bos et al. 2002, Bakker et al. 2003) and mainland marshes (Andresen et al. 1990, Bouchard et al. 2003). Kleyer et al. (2003), who also detected a repressing effect of a high groundwater table after eleven years of cessation of grazing, also recommend a low stocking density rather than no grazing. Which stocking density to apply in salt marshes is, however, still a point of consideration. The stocking density was also identified by Dumont et al. (2007a) as a key management variable when applying grazing as a nature-management tool. In addition to the stocking density, different livestock species may vary in their effect on vegetation (Olff and Ritchie 1998, Loucougaray et al. 2004). Yet another management strategy also needs further attention. Rotational grazing treatments, in which years of grazing are alternated with years without grazing, might be a good alternative to traditional management strategies. While in years without grazing the plants would be able to set seeds and breeding birds would be undisturbed, the vegetation succession would be slowed down in years with grazing, leading to a high plant-species richness. In addition to effects on the vegetation, the effect of different grazing treatments on sediment dynamics in salt marshes needs more attention (*e.g.* Andresen et al. 1990, Neuhaus et al. 1999, Stock 2011, Suchrow et al. 2012), as accelerated sea-level rise is a threat to coastal areas and marshes will only survive with sufficient accretion. Therefore, an experiment is required to study the effects of different stocking densities and livestock species, as well as rotational grazing treatments on the vegetation and accretion of salt marshes (Bakker et al. 2003, Kleyer et al. 2003).

Such an experiment was initiated on a mainland salt marsh using horses and cattle in two stocking densities. In this synthesis I want to summarize the results of the experiment with respect to different aspects of vegetation (de Bello et al. 2010) and relate these to the observed animal behaviour. Furthermore, I will address the effects of grazing on accretion in salt marshes. I also want to discuss the implication of the results for management and point out potential questions for further research. Finally, I will highlight the relevance of my results for management of other grassland systems.

Animal behaviour

To understand differences in the impact of livestock species on vegetation we need to understand the differences in their behaviour and combine behavioural and community ecology (Rook et al. 2004). Therefore, I compare the behaviour of horses and cattle with respect to diet choice, activity and spatial distribution in **chapter 2**. The results of this comparison form the baseline which helps us to understand the outcome of all chapters dealing with the effect of the two livestock species on vegetation (**chapter 3**, **4**, and **6**). When comparing livestock species, we found horses to include a higher amount of species with high fibre content in their diet (Gordon 1989, Duncan et al. 1990, Vulink 2001, Menard et al. 2002), such as the grass *Puccinellia maritima*, while cattle foraged more often on herbs such as *Aster tripolium*. Cattle graze more selective and the selectivity is supposed to have a strong effect on vegetation composition and structure (Metera et al. 2010). Additionally, the activity of livestock species differed. Horses spent more time grazing (Duncan et al. 1990) and travelled longer distances per day compared to cattle. This higher activity also influenced their spatial distribution pattern, for example horses utilized the entire area, while cattle showed a grazing gradient of decreasing local grazing intensity with increasing distance from the freshwater source (Fig. 9.1, Adler et al. 2001). In addition to the livestock species, stocking density is supposed to affect animal behaviour. In low sheep-grazing densities in an experiment in Germany a similar grazing gradient was observed, resulting in decreasing canopy height with increasing distance from the freshwater source (**chapter 5**, Kiehl et al. 1996). The stocking

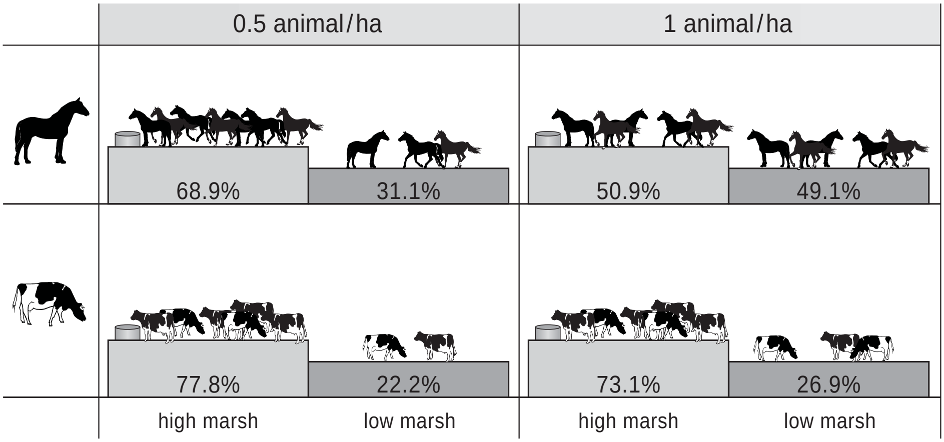


Figure 9.1 Spatial distribution of horses and cattle in two stocking densities within the low marsh and high marsh zone with the freshwater source. Numbers represent the percent of observed time animals spent on average in a grid cell in the low or high marsh (**chapter 2**).

density is influencing the selectivity of animals, as herbivores in high densities are likely to cause a depletion of preferred food plants and need to include less favoured species in their diet (Crawley 1983). We observed this difference between stocking densities in our study (**chapter 2**). It also influenced the spatial distribution, because in high densities animals were forced to walk further away from the freshwater source (**chapter 2** and **5**).

Target plant species and vegetation composition

The behavioural differences of diet choice, activity and spatial distribution between livestock species and stocking densities are likely to affect the vegetation on different scales. The smallest scale investigated in this study is the effect on the flower production of a target species as was suggested by Bakker et al. (1996) and de Bello et al. (2010). The target species chosen in this experiment was *Aster tripolium* (**chapter 3**), as this plant species was found to be selectively eaten (Jensen 1985, Kiehl et al. 1996). The higher amount of *Aster* in the diet choice of cattle (**chapter 2**) could lead to the expectation that *Aster* would produce fewer flowers in cattle-grazed treatments. However, the overall higher forage intake and activity of horses (**chapter 2**) brought us to the expectation that horses cause more damage to *Aster* plants and cause a stronger reduction of flowers. With respect to damage we found opposite trends at different stocking densities (Fig. 9.2). While cattle caused more damage at low densities, horses caused more damage at high densities. At low

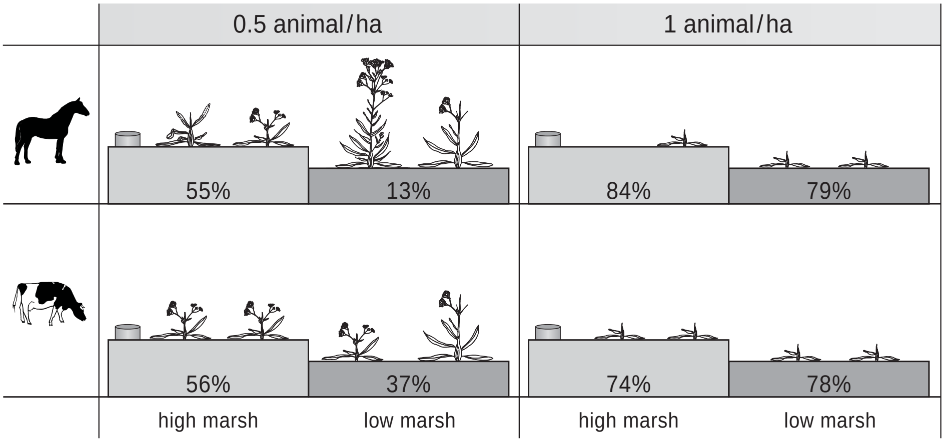


Figure 9.2 Mean damage of *Aster tripolium*-individuals in different livestock species and stocking densities treatments in the high and low marsh, respectively. The damage values were corrected for differences in treatments duration (see **chapter 3**).

stocking density, the higher selectivity of cattle for the preferred food plant caused more damage, whereas at high stocking densities, selective foraging by cattle became less important (Crawley 1983). At high stocking densities of horses, the more random damage increased due to both the higher forage intake and the higher activity. In low densities, the result of a higher number of flowers was well explained by the lower level of damage by horses in this treatment. In high densities, however, there was only a small difference between livestock species, probably because damaged plants were able to compensate for the loss of flowers. **Chapter 3** therefore shows clearly, how important the knowledge of behavioural differences in diet choice and activity between livestock species and stocking densities is to understand their effect on target plant species.

The effects on single plant species as described in **chapter 3** are likely to cause differences between plant-species composition and plant-species richness between treatments. Our expectation would be that the abundance of species that were frequently included in the diet (**chapter 2**) would either be reduced in permanent plots if these species were sensitive to grazing or be more abundant if the species were able to tolerate grazing. However, neither significant differences in species composition nor effects on the species composition change of permanent plots over time could be detected (**chapter 4**). Species composition was found to change slowly in fertile grasslands (Bullock et al. 1994), and therefore a long-term monitoring of at least ten years is required and recommended (Bakker et al. 1996). The plant-species richness was also found not to differ between treatments on various spatial scales (**Box 1**). A loss of plant species richness is often connected with the expansion of

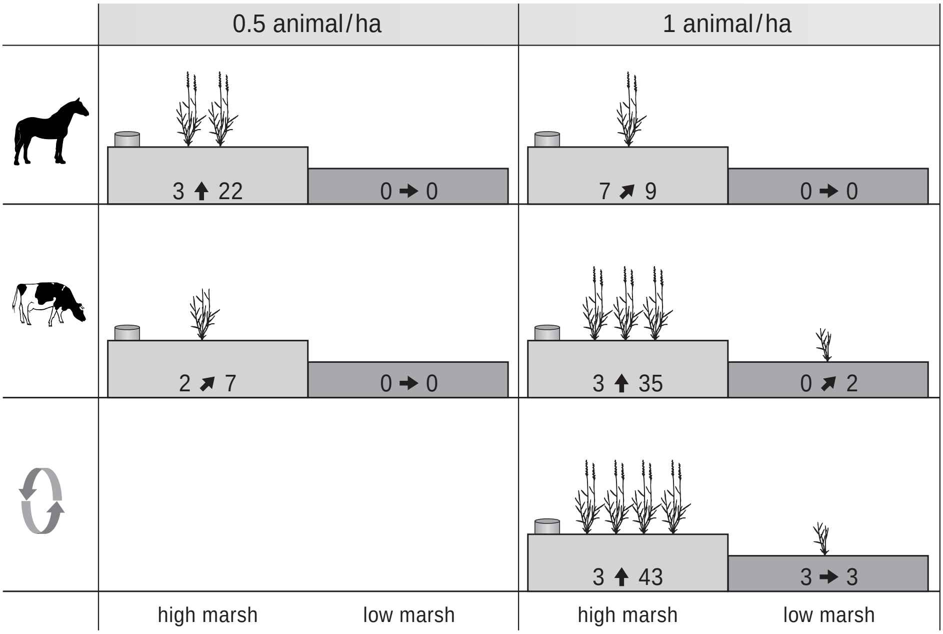


Figure 9.3 The mean cover percentage of *Elytrigia atherica* in permanent plots in year 0 and year 3 of the experimentwith grazing by different livestock species and stocking densities, and rotational grazing Arrows indicate the trends in relative change (↑ = strong increase; ↗ = increase; → = no change).

mono-specific stands of *Elytrigia atherica* (Bos et al. 2002, Kleyer et al. 2003), and therefore this species should be given special attention. A spread of *Elytrigia atherica* might be overlooked in permanent plot studies as long as the species does not invade any plot. Based on the behavioural differences between livestock species and densities (**chapter 2**) and first trends visible in the species composition (**chapter 4**), I would expect horses to be more effective than cattle and high stocking densities more effective than low densities in reducing or preventing the spread of *Elytrigia atherica*. A closer look at the cover percentage of *Elytrigia atherica* in permanent plots of the Mid and East Block shows an increase of *Elytrigia atherica* in all high marsh areas, but opposite trends in different stocking densities (Fig. 9.3). As expected based on the higher fibre content of the diet of horses (**chapter 2**) we found a stronger increase in cattle compared to horses, but only in high stocking densities. In contrast, under low stocking densities the *Elytrigia atherica* cover was increasing to a greater extent in horse-grazed plots. However, the increase of *Elytrigia atherica* seems not yet to cause any reduction of species numbers (**chapter 4** and **Box 1**), probably because the plots are not yet covered to a large extent by *Elytrigia atherica*. The strongest increase yet can interestingly be found in the rotational regime. Here the spread of *Elytrigia atherica* (Fig. 9.3) and the resulting tall canopy might have caused the trend of lesser plant species in permanent plots (**chapter 4**) and significantly lesser number of plant species in plots of smaller size (**Box 1**).

Vegetation structure

In addition to the classic monitoring of permanent plots (Bakker et al. 1996), it is also interesting to understand the effect of grazing on the vegetation structure (de Bello et al. 2010). A diverse vegetation structure is supposed to be the basis of high plant-species richness, as patches of tall and short canopy represent niches for different species of plants (Olofsson et al. 2008). Such a patchy vegetation structure may be induced by low stocking densities (Berg et al. 1997, de Knegt et al. 2008), because in low densities herbivores are able to select for preferred high-quality plant species and return to patches with high-quality regrowth (*e.g.* McNaughton 1979, McNaughton 1984, Adler et al. 2001). However, selectivity was found to differ between both livestock species and stocking densities (**chapter 2**, Crawley 1983). I investigated the effect of grazing on the vegetation structure on two scales.

On the large scale, the effect of various stocking densities on vegetation structure was investigated in a long-term sheep-grazing experiment in Germany (**chapter 5**). In high stocking densities, we expect the animals to be less selective and include a higher amount of tall canopy in their diet, thereby increasing the proportion of short canopy. As expected, we mainly found short canopy in high stocking densities (10 sheep/ha) and we found a high proportion of tall canopy in low densities (1.5 sheep/ha) and ungrazed marshes, while intermediate densities (3 and 4.5 sheep/ha) led to a mosaic of short and tall canopy. Similar results were described by Berg et al. (1997). Additionally, we found a gradient of increasing canopy height with increasing distance to the freshwater source. The same effect was observed for sheep by Kiehl et al. (1996) and for cattle by Andresen et al. (1990) and Esselink et al. (2002). The canopy height was also measured in the experiment in NFB every 25 metre along transects from the freshwater source to the end of each paddock in 2011 (Fig. 9.4). For cattle, the results show a very similar effect of stocking density on the formation of the gradient as described in **chapter 5** for sheep. While a clear gradient is visible in the 0.5 cattle/ha treatment, there is only a very small increase in canopy height with increasing distance to the freshwater source in the higher density cattle-grazing treatment. In contrast, horses seem to create a shorter canopy further away from the freshwater source when grazing in densities of 1.0 horses/ha. In lower stocking densities, the highest canopy is found at intermediate distances to the freshwater source with horses. These results are in line with the results of spatial distribution of the animals as described in **chapter 2** (Figs. 2.6 and 9.1).

The effect of different grazing treatments on the small-scale vegetation structure was investigated comparing two livestock species and stocking densities in the

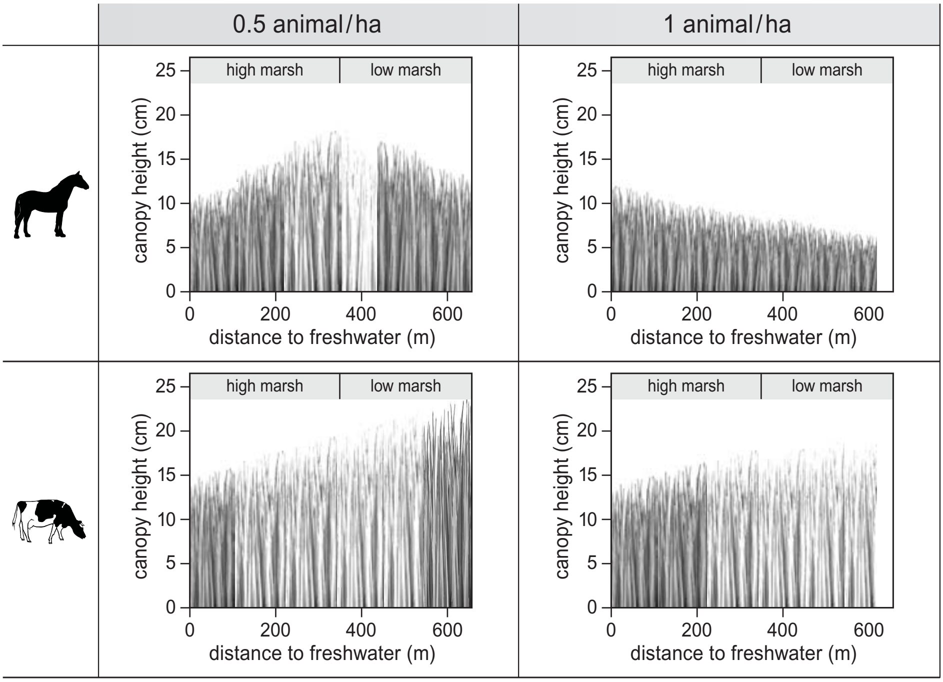


Figure 9.4 Canopy height along transects from the freshwater source to the end of each paddock for different livestock species and stocking density treatments in the high and low marsh, respectively.

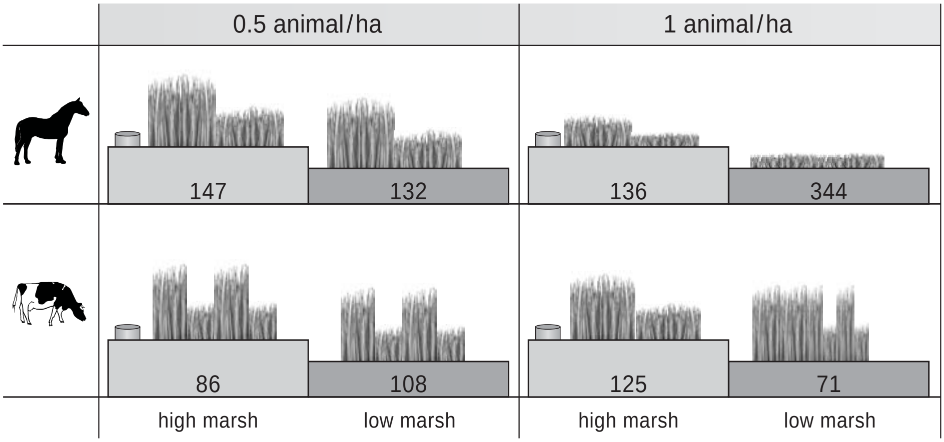


Figure 9.5 Average patch size in cm (range) for different livestock species and stocking density treatments in the high and low marsh, respectively.

experiment of NFB (**chapter 6**). Again, the results of the behavioural study (**chapter 2**) are useful for the interpretation of the vegetation structure results. Both the higher forage intake and trampling effect of horses, for example, explain why mean canopy height was shorter in horse grazed paddocks (Fig. 9.5). The higher forage intake probably also causes horses to be less selective on a plant-species base, including both high and low quality plant species in their diet. Less selective animals are therefore likely to induce larger patches and homogenize the natural pattern of undisturbed vegetation. Indeed, we found patch size to be larger in horse-grazed paddocks (Fig. 9.5). Additionally, anatomic differences between livestock species may contribute to this result. Horses, on the one hand, bite off parts of the plants with their set of incisors and thus creating a very short canopy (Gordon 1989). Cattle, on the other hand, rip off parts of the plants with their tongues (Gordon 1989), and thus create a small scale pattern of short, recently used, and tall canopy, which is still not tall enough to be ripped off by cattle. Although we found differences in mean canopy height and small-scale vegetation structure between treatments this seems not to influence the plant-species richness, yet. A shorter canopy structure is associated with a reduced competition for light (Olff and Ritchie 1998, Kuijper et al. 2005, Mayer et al. 2009), so that smaller species are not outcompeted by tall species such as *Elytrigia atherica*. This is one of the mechanisms how grazing increases plant species richness. In addition to the mean canopy height, a patchy vegetation structure provides niches for different plant species within tall canopy and short canopy patches (Olofsson et al. 2008). Both mechanisms seem not to have led to a difference in species richness between treatments, yet (**chapter 4** and **Box 1**).

Accretion

The observed effect of grazing on the vegetation structure might also affect the abiotics in salt marshes. For example, grazing was proposed to reduce the sediment-deposition rate by altering vegetation structure (Adam 2002). Many authors found that a dense vegetation structure reduces the water-flow velocity (Leonard and Luther 1995, Christiansen et al. 2000, Neumeier and Amos 2006) and thereby increased sediment-deposition rates (Townend et al. 2012). A reduced sediment-deposition rate is then leading to reduced accretion rates in grazed compared to ungrazed marshes. Andresen et al. (1990) found the accretion to decrease with increasing stocking rate and interpreted this as the effect of reduced turbulence in ungrazed marshes. Additionally, there might be a second pathway by which grazing livestock affects accretion rates (Fig. 9.6). Accretion in salt marshes consists of a mineral and an organic part (**chapter 7**). The sediments deposited from the inundating sea water contain the mineral part and the organic part is predominantly composed of autochthonous dead plant material such as litter and roots. The

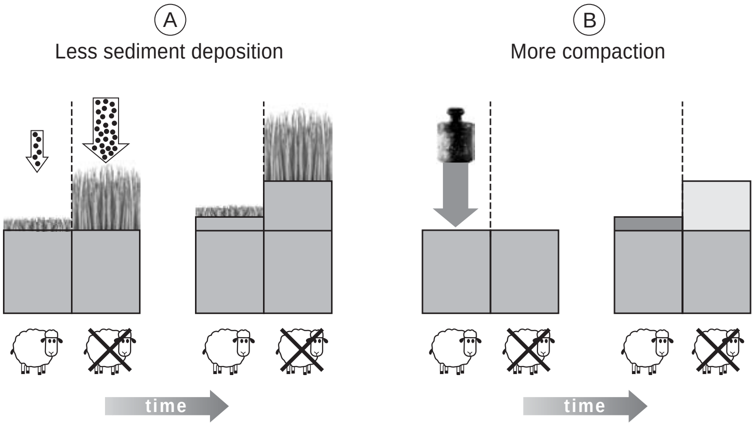


Figure 9.6 Mechanisms expected to cause a lower accretion rate in grazed salt-marshes. A) A short vegetation structure in grazed marshes is not able to reduce flow velocity of the incoming water and therefore sediment-deposition rates are low. B) In grazed marshes soil compaction is increased by livestock and therefore accretion rates are reduced while soil bulk density is higher.

accreted material is also subject to auto-compaction, which reduces the accretion rate (Cahoon et al. 1995, Bartholdy et al. 2010). The auto-compaction is caused by the soils own weight, but livestock was found to additionally increase soil compaction by trampling (Schrama et al. 2013). This soil compaction caused by trampling could therefore additionally decrease accretion rates.

We tested the hypothesis that accretion rates would be lower in grazed compared to ungrazed marshes because of increased soil compaction by trampling and reduced sediment deposition in short vegetation in **chapter 8**. By using the ^{137}Cs-method to date sediment in cores (**chapter 7**) we calculated the long-term accretion and sediment-deposition rates for grazed and ungrazed marshes in four different research areas. Neither accretion nor sediment-deposition rates were significantly different between grazed and ungrazed sites due to opposite trends in different marshes (**chapter 8**). Our results show how important it is to study mechanisms in a number of marshes before drawing general conclusions. In contrast to the accretion rate, the bulk density was significantly higher in the studied grazed marshes, which indicates a compacted soil. We conclude that accretion rates in grazed and ungrazed marshes do not follow a direct causality, but are influenced by other factors. Among those factors is the spatial distribution of sediment deposition (de Groot et al. 2011b), which is probably influenced by the spatial distribution of tall vegetation (Fig. 9.7). In tall vegetation the flow velocity is strongly reduced which probably causes most of the suspended sediment in the water to be deposited close to the creek with levee formation as a result. In contrast, short vegetation allows sediment to be transported further into the marsh and the spatial distribution of sediment deposition should be more evenly distributed (Temmerman et al. 2012). Seemingly contrasting

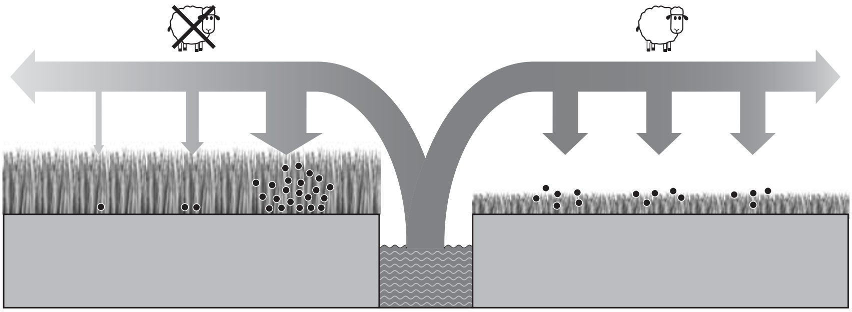


Figure 9.7 Tall vegetation is probably going to influence the spatial distribution of sediment deposition. In ungrazed marshes sediment settles close to the creek leading to the formation of a levee, whereas in grazed marshes the sediment is deposited more evenly. Therefore the effect of grazing on sediment deposition and accretion should be studied in a spatial context.

results are described by Esselink et al. (1998). They found a stronger levee formation in short vegetation created by a local high grazing intensity and almost no levee formation in tall vegetation in locally ungrazed areas. However, these grazed and ungrazed areas are not directly comparable as in **chapter 8**, because they result from a grazing gradient as described in **chapter 5**. Therefore, the ungrazed area is close to the marsh edge and the grazed area is further away from the marsh edge. The distance to the marsh edge has a negative effect on accretion rates and probably explains the results found by Esselink et al. (1998). Close to the marsh edge suspended sediment concentration is probably high and sediment is deposited close to the creek and also further away from it, leading to no clear levee formation even in tall vegetation. Further away from the marsh edge, however, suspended sediment concentration is likely lower and this lower amount of sediment in the water column probably settles already close to the creek, leading to a levee formation. Although suspended sediment concentration was not measured in the study by Esselink et al. (1998), they found higher mean accretion rates closer to the marsh edge and these might be caused by a higher suspended sediment concentration as hypothesized here. Additionally, areas close to the marsh edge will probably receive a higher amount of sediment from inundating water flowing directly from the marsh edge and the local spatial distribution of this sediment is likely to be less influenced by the position of the creek and will lead to no levee formation. Unfortunately, the spatial distribution of sediment deposition cannot be analysed using the ^{137}Cs-method (**chapter 7**). A general conclusion which can be drawn from this study is that all marshes studied irrespective of whether they were grazed or not, had accretion rates which should enable them to outpace the current rate of sea-level rise.

Implications for management

In order to successfully use grazing as a nature-management tool, it is crucial to first consider the options and define a target (Bakker et al. 2002, Rook et al. 2004). The choice of an appropriate grazing management for this target then needs information on the effect of different treatments on the ecosystem. I investigated the effect of livestock grazing on various aspects of vegetation and accretion in salt marshes and the results can be used by nature-conservation agencies to choose the appropriate grazing treatment to reach their management target.

The most important general result is that livestock units may not be the ideal way to measure for grazing intensity when different livestock species are involved (**chapter 2**). The effect of the same stocking density of cattle and horses in an area can be quite different, not only because of differences in diet choice and selectivity, but mainly because of differences in their total forage requirements and the resulting activity, which is also influenced by social behaviour (**chapter 3**). If possible, I suggest that future management schemes should for example calculate average hours per day spent grazing and use the measure of grazing hours per unit area to compare grazing intensities rather than livestock units. As grazing time is not the only possible difference between livestock species affecting management outcomes, the calculation of activity could also be done by calculating an average distance travelled per day and hectare. These calculations would ideally be based on behavioural studies of livestock within the management area, but could also be estimated using available data for common livestock species. As livestock units are still very common

Table 9.1 Overview of effects of grazing treatments on the potential management targets studied. Strong positive effects are indicated by '++' and positive effects by '+', whereas negative effects are indicated by '-' and strong negative effects by '--'. For example 0.5 cattle/ha increased vegetation structure patchiness, while 1.0 horses/ha led to a decrease in patchiness and a homogeneous short sward. If no effect was found the result is represented by '0' and unclear results due to the short duration of the study by '?'. Symbols in brackets mean that recommendations are based on trends and need further testing.

		Horses		Cattle		Rotational
	Chapter	0.5/ha	1.0/ha	0.5/ha	1.0/ha	
Flower production (*Aster*) short term	3	+	-	0	0	?
Flower production (*Aster*) long term	4	(-)	(--)	(++)	(+)	(?)
Species richness	4	?	?	?	?	-
Reduction *Elytrigia atherica*	4	(+)	(++)	(-)	0	(-)
Canopy height	6	0	--	+	0	(++)
Patchiness	6	+	-	++	+	?

in management and will probably be used in the future, it should be remembered that if one cattle is represented by one LU, one horse should be seen as approximately 1.7 LU according to the results of **chapter 2**. However, to gain a better understanding of the causes of changes in the ecosystem with respect to different management regimes I suggest experiments and monitoring schemes which take both behavioural ecology and community ecology of the target group into account as suggested by Rook et al. (2004) and shown in the present study. Additionally, it needs to be remembered, that these are stocking densities per unit area and that the actual local grazing intensity might differ greatly, because of differences in spatial distribution (**chapter 2**).

The results of **chapter 3**, **4** and **6**, which can be applied for the management of salt marshes, are summarized in table 9.1. If a large number of flowers of the target plant *Aster* is the management goal, the results would recommend a low stocking density of horses (**chapter 3**). This recommendation is given with the constraint that the study in **chapter 3** analysed the short-term effect of grazing treatments. The results of **chapter 4**, which encompass three years of data, show that the longer-term population dynamics of *Aster* might be affected by treatments in a different way as found in **chapter 3**. In Fig. 4.3 we see a trend that *Aster* is more common in cattle- compared to horse-grazed treatment. It is possible, that the effects on *Aster* we saw in the first year of the study, when the situation in paddocks was comparable, might have changed into a different direction. After some years, the effect of higher forage intake and higher activity of horses could be additive, because of the increasing depletion of forage. Therefore, the effect of higher selectivity of cattle observed in the first year might play a smaller role after situations changed and paddocks were less comparable. Therefore, I would recommend based on the long-term permanent plot data to apply cattle rather than horses if a high number of *Aster* flowers is the long-term management target.

The most common management target in nature conservation is the conservation of species richness (*e.g.* Bakker et al. 2006, Pajunen et al. 2008, Dumont et al. 2009, Mayer et al. 2009, de Bello et al. 2010). Also in salt marshes the effect of grazing on plant species richness is a frequent research topic (*e.g.* Kleyer et al. 2003, Kiehl et al. 2007, Milotic et al. 2010). We studied the effect of different grazing treatments on plant species richness on a fixed scale of the size of permanent plots (**chapter 4**) and on a variety of other spatial scales (**Box 1**). No differences between livestock species could be found thus far and, therefore, I can give no recommendation for management, but advise to base decisions on long-term monitoring. We found, however, an effect of different treatments on mean canopy height and small-scale vegetation-structure patchiness (**chapter 6**). The management target with respect to canopy height can be very different. While geese prefer a short canopy of high quality grass for grazing (van der Graaf et al. 2002, Bos et al. 2005), a tall canopy might increase the number of available niches for invertebrates. Therefore I give no recommendation for management, but only summarize that a short canopy height can be found in high rather than low and stocking densities (**chapter 5** and **6**) and horse grazed compared to cattle grazed treatments (**chapter 6**). With respect to a high variation in vegetation structure, which is supposed to increase biodiversity (Olofsson et al. 2008), I would advise to use cattle, rather than horses.

With respect to different stocking densities we analysed the effect on plant species richness in the grazing experiment in Noord-Friesland Buitendijks, as well as in two long-term experiments in Germany (**Box 1**). At all sites stocking density had no effect on number of plant species. In the high marsh (Friedrichskoog) there was a trend of lower number of species in the high compared to the low stocking density in small plots. This example shows how important it is to decide on which scale you want to conserve and monitor plant species richness, because the outcome could depend on the plot size. The still relatively high number of species in the plots with high stocking density was attributed to an input of seeds of grazing sensitive species from adjacent ungrazed treatments (Kiehl et al. 2007). This is a good example of how a spatially diverse management can be used to increase the value of a whole area. By dividing large areas into smaller sections (*e.g.* 60 ha), a number of contrasting management targets like suitability for geese and a high plant species richness can be accommodated within one area.

The loss of plant species richness in salt marshes is often correlated with the spread of communities dominated by *Atriplex portulacoides* or *Elytrigia atherica* (Bakker et al. 1993, Leendertse et al. 1997, Bakker et al. 2003), and therefore the reduction of *Elytrigia atherica* cover might be another management target. While *Elytrigia atherica* is common in the study site *Atriplex portulacoides* is rare, because its growth is prohibited probably by the high concentration of small soil particles and a lack of drainage leading to anoxic conditions. Grazing is probably not limiting the spread of *Atriplex portulacoides*, as this species is also rare in an adjacent ungrazed marsh. We found both livestock species to spend a large amount of time in the *Elytrigia atherica* vegetation type. Horses are, however, frequently observed grazing there, cattle mainly use these elevated dry areas for resting and ruminating (**chapter 2**). This would be in line with the trend in Fig. 4.3 indicating *Elytrigia atherica* to be more common in cattle-grazed plots. Also in Fig 9.3 we found an on average higher cover of *Elytrigia atherica* in cattle-grazed treatments, even though there are opposite trends in different densities. While in low densities there seems to be more increase in the horse-grazed treatment compared to the cattle grazed treatment, in high densities we found the opposite result (Fig. 9.3). Therefore, I would recommend grazing with horses if an already existing dominance of *Elytrigia atherica* is supposed to be reduced. Metera et al. (2010) also recommended horse grazing to remove tall low-quality grasses. However, as grazing with horses might have negative effects on other management targets and switching from horse to cattle grazing after a short period might be technically difficult for managers, I would recommend a higher density than 1.0 cattle/ ha to reduce *Elytrigia atherica*. If *Elytrigia atherica* is present, but not dominating large areas, I would recommend 1.0 cattle/ha. Cattle grazing in densities of 0.5 cattle/ha should only be applied if *Elytrigia atherica* is rare or absent (Bakker et al. 2003).

As an additional management option we investigated the effect of rotational grazing on plant-species richness (**chapter 4** and **Box 1**), because data were available for three years of experimental grazing. We found a lower plant-species richness in the rotational treatment compared to the 1.0 cattle/ha treatment. This is in line with an increase of *Elytrigia atherica* observed in the permanent plots (Fig. 9.3), which was previously found to be the reason for a loss in plant species richness (Bakker et al. 1993, Leendertse et al. 1997, Bakker et al. 2003). Therefore, I would not recommend rotational grazing in the studied stocking density and frequency if the nature management goal is a high plant species richness and a reduction of *Elytrigia atherica*. However, it is possible that other rotational treatments with *e.g.* higher stocking densities in grazed periods or other grazing frequencies like two grazed years followed by one ungrazed year, would create more positive results. I would thus not generally advise against rotational treatments.

The results of this study are generally applicable to all mainland marshes in the Wadden Sea. It should, however, be noticed, that the plant species composition can differ between marshes. While our study area contained little of for example the high-marsh grass *Festuca rubra*, this species is more abundant in other marshes (Kiehl et al. 1996). Therefore the diet composition of livestock species is probably also going to differ between areas depending on the available forage. The availability of single species and the resulting abundance in the diet is likely to affect the outcome of studies investigating target species (*e.g.* **chapter 3**). However, the higher amount of high-fibre plant species in the diet of horses is a general phenomenon (Gordon 1989, Duncan et al. 1990, Vulink 2001, Menard et al. 2002) and horses were found to reduce the amount of tall, low quality plant species also in other systems (Metera et al. 2010). Therefore our recommendation with respect to the spread of the tall grass Elytrigia atheirca, can be generalized for all mainland marshes and back-barrier marshes. Also the effects on patchiness were irrespective of species composition and the mechanisms causing the differences in patchiness, like selectivity of the two livestock species, are likely also to affect salt marshes with a different species composition in a similar way.

Further research

A further monitoring of the observed trends in the experiment is recommended to verify our results and study long-term developments. As observed in the German grazing experiments results after 5 years of grazing (Kiehl et al. 1996) should only be

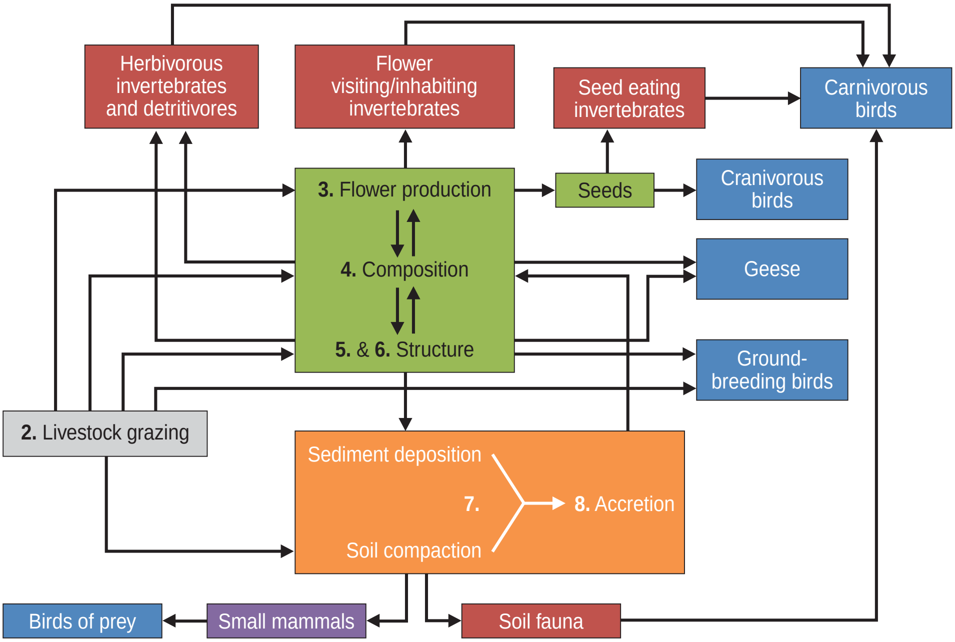


Figure 9.8 Schematic overview of possible direct and indirect effect of livestock grazing on different groups of organisms.

seen as preliminary, because an invasion of *Elytrigia atherica* was detected in other studies only after approximately a decade (Schröder et al. 2002, Gettner 2003, Kiehl et al. 2007). To study the effect of different treatments on the spread of *Elytrigia atherica*, I furthermore recommend a repeated mapping of vegetation types *e.g.* Bakker et al. 2002, Bouchard et al. 2003) or distribution of plant species in transects (Esselink et al. 2000, van Duin et al. 2007) in addition to permanent plots. Furthermore, it would be interesting to investigate the dynamics of the vegetation structure patches (Berg et al. 1997) to see how light competition in tall vegetation and a diverse vegetation structure indeed lead to increased plant species richness.

A longer time series of measurements is also required to draw sound conclusions on the effect of rotational grazing. Although first results in this study seem not to be in favour of a rotational treatment, it still holds interesting possibilities for nature management in *e.g.* a potential increase in flower and seed production in years without grazing. Different options of rotational management with respect to stocking density and rotation frequency need to be studied and tested for their applicability in different marshes before final conclusions can be drawn.

In addition to the effect of different livestock species and stocking densities on the vegetation, both direct and indirect effects of treatments on other organisms (Fig. 9.8) should be investigated (Metera et al. 2010). For example, the protection of birds is a frequent focus of nature management. Bird groups of interest in salt marshes are migratory geese, wintering songbirds, and ground-breeding birds. Geese were found to be facilitated by grazing livestock, because the large animals keep the vegetation structure short and thus promote the growth of high-quality plant species, the constant regrowth of protein rich new shoots, and repress the spread of the avoided grass *Elytrigia atherica* (van der Graaf et al. 2002, Bos et al. 2005). Following this result it is necessary to investigate the effect of different grazing treatments on geese (Mandema et al. 2013). Breeding birds were also found to benefit from livestock grazing to a certain extent (Bakker et al. 1993, Adam 2002, Doody 2008, Metera et al. 2010). On the one hand, grazing livestock indirectly benefits breeding birds by the creation of a preferred vegetation structure. On the other hand, the negative direct effect of livestock trampling nests might be more important (Beintema and Müskens 1987). To allow managers to apply appropriate grazing treatments further research on breeding birds is necessary including both the vegetation structure and trampling risks in different treatments. Breeding birds including their young, and among them many songbirds are foraging on invertebrates. The abundance and accessibility of their food is likely to depend on various characteristics of the vegetation, which in turn is altered by grazing animals (Fig. 9.8, **chapter 5** and **6**). Such complex effects on food webs should also be included in management decisions if the protection of animal species is the management target, and further information about these interactions are necessary. First studies investigating the abundance and diversity of invertebrates in grazed and ungrazed salt marshes are available (Pétillon et al. 2007, Rickert et al. 2012), while multitrophic studies (Schrama et al. 2012) are still lacking for grazed salt marshes.

In addition to the protection of biodiversity, ecosystem services became a research focus in the past years. For salt marshes, ecosystem services such as coastal protection, carbon sequestration and tourism should be investigated and included in management schemes. Coastal protection has long been identified as a function of salt marshes and their role in the dissipation of waves (Möller 2006) as well as the potential use of plants as ecosystem engineers were studied (Borsje et al. 2011). Yet, salt marshes can only perform this function in the future if they are able to outpace sea-level rise by accretion. Our study showed no effect of grazing on accretion, but this needs to be investigated in a higher spatial resolution to take spatial patterns of sediment deposition into account (de Groot et al. 2011b). Additionally, the effect of different livestock species on accretion rates and patterns needs further attention, as behavioural differences might be an important factor. For example, the more active horses (**chapter 2**, Duncan et al. 1990) might cause more soil compaction and therefore reduce the accretion stronger than other livestock species. Also the effect of vegetation structure patterns created by different treatments (**chapter 5** and **6**, Kiehl et al. 1996, Esselink et al. 1998, 2000) should be incorporated into studies investigating the pattern of accretion.

Accretion rates and increased soil compaction by livestock might also affect the capability for carbon sequestration in salt marshes (Olsen et al. 2011). For example, soil compaction and the resulting lack of oxygen in the soil (Jensen 1985) might increase the storage of carbon. A similar effect was found in a clayey back-barrier marsh where grazing decreased nitrogen mineralization (Schrama et al. 2013).

Another aspect of salt marshes hardly studied is their value for tourism. Large numbers of tourists visit the Wadden Sea National Parks and nature areas in Denmark, Germany and the Netherlands every year. These tourists might value other salt-marsh characteristics than nature managers based on a more aesthetical background. Yet, this ecosystem service of salt marshes needs to be quantified to take it into account into management decisions.

Conclusions and relevance for other systems

The general findings of this study are not only applicable for salt marshes along the Wadden Sea or the Baltic coast (Sammul et al. 2012), but for all grassland systems in which livestock species are used as a tool for nature management. Among those systems are for example previously extensively-used grasslands which are now abandoned (Metera et al. 2010). Also the management of grasslands where large herbivores have disappeared due to human interference such as the North American prairies (Knapp et al. 1999, Damhoureyeh and Hartnett 2002, Derner et al. 2009) needs careful consideration of both herbivore species and stocking densities. In addition to the accepted importance of stocking density as a key variable in management schemes (Dumont et al. 2007a, b), I was able to identify differential effects of two livestock species on vegetation. Therefore, I would emphasize that livestock species should be carefully chosen with respect to the management target (Metera et al. 2010). The ideal case includes knowledge of the livestock species' behaviour with respect to diet composition, activity and spatial distribution. I also advocate quantifying grazing intensities as average daily grazing hours/area or average distance travelled daily/ha instead of livestock units/area, as animals of different species but similar size might have different forage intake requirements.

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General introduction

Grazing with livestock is successfully used as a nature-management tool to increase or restore biodiversity in many grassland ecosystems. Among these ecosystems are Western European coastal salt marshes which were traditionally intensively grazed. Grazing was abandoned however, in large areas, because it was either no longer economically feasible for farmers or for nature conservation after the installation of nature protection areas. This abandonment led to a rapid succession of salt marshes resulting in large areas dominated by single plant species, mainly the tall grass *Elytrigia atherica*, and a loss in plant-species diversity. This development led to the question for salt-marsh management "to graze or not to graze?". To answer this question, grazing experiments were installed along the German mainland coast. Here, *Elytrigia* was found to invade the high marsh after approximately ten years and this development might cause a loss of plant species diversity in the future. Therefore, grazing in low or moderate stocking densities is nowadays recommended for nature conservation to slow down succession and preserve species-rich early succession stages. Which grazing management to apply in salt marshes is, however, still a point of consideration. In addition to the stocking density, different livestock species may also vary in their effect on vegetation. Therefore, an experiment was required to study the effects of different stocking densities and livestock species on the vegetation of salt marshes. Such an experiment was conducted on the mainland salt marsh of Noord-Friesland Buitendijks (NFB), The Netherlands. The experimental setup consisted of three blocks, in which five different grazing treatments were installed. Each block included parts of the high-marsh zone, where a freshwater source was situated, and a low-marsh zone. The grazing treatments included grazing with horses in two stocking densities (0.5 and 1.0 animal/ha), grazing with cattle in two stocking densities (0.5 and 1.0 animal/ha) and a rotational regime with 1.0 cattle/ha during one year followed by a fallow year. The results of the experiment after three years are summarised here.

Animal behaviour

In order to understand differences in the impact of livestock species on vegetation, we need to understand the differences in their behaviour and have to combine behavioural and community ecology. Therefore, we studied the behaviour of horses and cattle with respect to diet choice, activity and spatial distribution in **chapter 2**. When comparing livestock species, we found horses to include a higher amount of plant species with high fibre content in their diet such as grasses, while cattle foraged more often on herbs. Cattle grazed more selective and the selectivity is supposed to have a strong effect on vegetation composition and structure. Additionally, the activity of livestock species differed. Horses spent more time grazing and travelled longer distances per day compared to cattle. This higher activity also influenced their spatial distribution pattern, for example horses utilized the entire area, while cattle showed a grazing gradient of decreasing local grazing intensity with increasing distance from the freshwater source. Furthermore, we observed stocking density to influence the selectivity of animals and the spatial distribution, because in high densities animals were forced to walk further away from the freshwater source (**chapter 2** and **5**).

Target plant species and vegetation composition

The behavioural differences of diet choice, activity and spatial distribution between livestock species and stocking densities are likely to affect the vegetation on different scales: the plant species level, the community level, and the vegetation-structure level. We investigated the effect on the flower production of a target plant species, namely *Aster tripolium* (**chapter 3**). A higher amount of *Aster* was found in the diet choice of cattle (**chapter 2**) and this result could lead to the expectation that *Aster* would produce fewer flowers in cattle-grazed treatments. However, the overall higher forage intake and activity of horses (**chapter 2**) brought us to the expectation that horses cause more damage to *Aster* plants and cause a stronger reduction of flowers. We found opposite trends in different stocking densities with respect to damage. While cattle caused more damage in low densities, horses caused more damage in high densities. The higher selectivity of cattle for the preferred food plant caused more damage in low stocking densities. In high densities selective foraging by cattle became less important and the more random damage caused by the higher forage intake and activity of horses increased. In low densities, the result of a higher number of flowers was well explained by the lesser damage by horses in this treatment. In high densities, however, there was only a small difference between livestock species, probably because damaged plants were able to compensate for the loss of flowers. **Chapter 3** therefore shows clearly, how important the knowledge of behavioural differences in diet choice and activity between livestock species and stocking densities is to understand their influence on target plant species.

The differences in animal behaviour are also likely to cause differences in plant-species composition and plant species number among treatments. However, no significant differences in species composition and no influence on the species composition change of permanent plots over time could be detected (**chapter 4**). The plant-species diversity was also found not to differ between treatments on various spatial scales (**Box 1**). A loss of plant-species diversity is often connected with the expansion of *Elytrigia atherica*, and therefore this species should be given special attention. Based on the behavioural differences between livestock species and densities (**chapter 2**) and first trends visible in the species composition (**chapter 4**) we would expect horses to be more effective than cattle and high densities more effective than low densities in reducing or preventing the spread of *Elytrigia*. A closer look at the cover percentage of *Elytrigia* in permanent plots in two out of the three experimental blocks showed an increase of *Elytrigia* in all high marsh areas, but opposite trends in different densities. As might have been expected based on the higher fibre content of the diet of horses (**chapter 2**), we found a stronger increase in cattle compared to horses, but only in high stocking densities.

Vegetation structure

In addition to the classic monitoring of permanent plots, we studied the effect of grazing on the vegetation structure. A diverse vegetation structure is supposed to be the basis of high plant-species diversity, as patches of tall and short canopy represent niches for different species of plants. We investigated the effect of grazing on the vegetation structure on two scales.

On the large scale, the effect of various stocking densities on vegetation structure was investigated in a long-term sheep-grazing experiment in Germany (**chapter 5**). We mainly found short canopy in high stocking densities and a high proportion of tall canopy in low densities, while intermediate densities led to a mosaic of short and tall canopy. Additionally, we found a gradient of increasing canopy height with increasing distance to the freshwater source. The same effect was observed for cattle in **chapter 2**.

The effect of different grazing treatments on the small-scale vegetation structure was investigated comparing two livestock species and stocking densities in the experiment NFB (**chapter 6**). Here, the higher forage intake of horses, for example, explains why mean canopy height was shorter in horse-grazed paddocks. This higher forage intake probably also caused horses to be less selective on a plant species base, including both high and low-quality plant species in their diet. Less selective animals were therefore likely to create larger patches and homogenize the pattern of undisturbed vegetation. Indeed, we found patch size to be larger in horse grazed paddocks (Fig. 9.4). Although we found differences in in small-scale vegetation structure between treatments this seems not to influence the plant-species diversity, yet. **(chapter 4)**.

Vertical accretion

The observed effect of grazing on the vegetation structure might also affect the abiotic conditions in salt marshes. For example, grazing was proposed to reduce the sediment-deposition rate by altering vegetation structure. A dense vegetation structure reduces the water flow velocity and thereby would indirectly lead to increased sediment-deposition rates. Therefore, the short canopy in grazed areas should lead to a reduced sediment-deposition rate which would then lead to reduced accretion rates in grazed compared to ungrazed marshes. Additionally, there might be a second pathway by which grazing livestock effects accretion rates. The accreted material is subject to auto-compaction, which reduces the accretion rate. The auto-compaction is caused by the soils own weight, but livestock was found to additionally increase soil compaction by trampling. This soil compaction caused by trampling could result in an additional reduction of accretion rates.

We tested the hypothesis that accretion rates would be lower in grazed compared to ungrazed marshes because of increased soil compaction by trampling and reduced sediment deposition in short vegetation in **chapter 8**. By using the ^{137}Cs-method to date sediment in soil cores (**chapter 7**) we calculated the long-term accretion and sediment-deposition rates for grazed and ungrazed marshes in four different research areas. Neither accretion nor sediment-deposition rates were significantly different between grazed and ungrazed sites due to opposite trends in different marshes (**chapter 8**). In contrast to the accretion rate, the bulk density was significantly higher in the studied grazed marshes, which indicates a compacted soil. We conclude that accretion rates in grazed and ungrazed marshes do not follow a direct causality, but are influenced by other factors such as the spatial distribution of sediment deposition. A general conclusion which can be drawn from this study is that all marshes included in our study, irrespective of whether they were grazed or not, had accretion rates which should enable them to outpace the current rate of sea-level rise.

Implications for management

In order to successfully use grazing as a nature-management tool, it is crucial to first define a target. We investigated the effect of different livestock grazing treatments on various aspects of vegetation and accretion to enable managers to choose the appropriate management for the chosen target. The most important general result is that livestock units may not be the ideal way to measure grazing intensity when different livestock species are involved (**chapter 2**). The effect of the same stocking density of cattle and horses in an area can be quite different mainly because of differences in their total forage requirements and the resulting activity (*e.g.* **chapter 3**). If possible, I suggest that future management schemes should calculate average hours per day spent grazing and use the measure of grazing hours per unit area to compare stocking densities. As livestock units are still very common in management and will probably be used in the future, it should be remembered that if one cattle is represented by one LU, one horse should be seen as approximately 1.7 LU. Additionally, it needs to be remembered, that these are stocking densities per unit area and that the actual local grazing intensity might differ greatly, because of differences in spatial distribution (**chapter 2**).

If the management goal is a large number of flowers of the target plant *Aster*, the results would recommend a low density of horses (**chapter 3**). This recommendation is given with the constraint that the study in **chapter 3** analysed the short-term effect of grazing treatments. The results of **chapter 4**, which encompass three years of data, show that the long-term population dynamics of *Aster* might be affected by treatments in a different way as was found in **chapter 3**. We would expect the results of **chapter 3** to be applicable to other salt-marsh species which are selectively eaten by cattle such as *Triglochin maritima* (**chapter 4**).

The most common management target in nature conservation is the conservation of species richness. No differences in the effect on plant species richness between livestock species could be found thus far and, therefore, we can give no recommendation for management, but advise to base decisions on long-term monitoring. We did, however, find an effect of different treatments on small-scale vegetation-structure patchiness (**chapter 6**). As a diverse vegetation structure is supposed to increase biodiversity, *i.e.* species-richness of plants and different groups of animals, we would advise to use cattle, rather than horses to increase structural diversity.

With respect to different stocking densities we analysed the effect on plant species richness in the grazing experiment in Friesland, as well as in two long-term experiments in Germany (**Box 1**). At all sites stocking density had no effect on the number of species. The still relatively high number of species in the plots with high stocking density was attributed to an input of seeds of grazing sensitive species from adjacent ungrazed treatments. This is a good example of how a spatially diverse management can be used to increase the conservation value of a whole area. By dividing large areas into smaller sections, a number of contrasting management targets like suitability for geese and a high plant species diversity can be accommodated within a single area.

The loss of plant-species diversity in salt marshes is often correlated with the spread of *Elytrigia atherica*, and therefore the reduction of *Elytrigia* cover might be another management target. We found both livestock species to spend a large amount of time in the *Elytrigia* vegetation type. However, while horses are frequently observed grazing there, cattle mainly use these elevated dry areas for resting and ruminating (**chapter 2**). Therefore, we would recommend grazing with horses if an already existing dominance of *Elytrigia* is supposed to be reduced.

As an additional management option we investigated the effect of rotational grazing on plant-species richness (**chapter 4** and **Box 1**). We found lower plant-species richness in the rotational treatment compared to the 1.0 cattle/ha treatment. This is in line with an increase of *Elytrigia* observed in the permanent plots, which was previously found to be the reason for a loss in plant-species richness. Therefore, we would not recommend rotational grazing in the studied stocking density and frequency if the nature management goal is a high plant species richness and a reduction of *Elytrigia*. However, it is possible that other rotational treatments with *e.g.* higher stocking densities in grazed periods or other grazing frequencies like two grazed years followed by one fallow year, would create more positive results.

Further research

A further monitoring of the observed trends in the experiment is advisable to verify our results and study long-term developments. To study the effect of different treatments on the spread of *Elytrigia atherica*, we furthermore recommend a repeated mapping of vegetation types in addition to permanent plots. Furthermore, it would be interesting to investigate the dynamics of the vegetation structure patches to see how competition for light in tall vegetation and a diverse vegetation structure leads to increased plant species richness. A longer time series of measurements is also required to draw sound conclusions on the effect of rotational grazing. Furthermore, different options of rotational management with respect to stocking density and grazing frequency need to be studied and tested for their applicability in different marshes before final conclusions can be drawn.

In addition to the effect of different livestock species and stocking densities on the vegetation, both direct and indirect effects of treatments on other organisms *e.g.* birds should be investigated. Furthermore, the effect of different livestock species on accretion rates and patterns needs further attention, as behavioural differences might be an important factor. For example, the more active horses might cause more soil compaction and therefore reduce the accretion stronger than other livestock species. Also the effect of vegetation structure patterns created by different treatments should be incorporated into studies investigating the pattern of accretion.

Conclusions and relevance for other systems

The findings of this study are not only applicable for salt marshes along the Wadden Sea or the Baltic coast, but for all grassland systems in which livestock species are used as a tool for nature management. Among those systems are for example previously extensively-used grasslands which are now abandoned and grasslands in which large herbivores have disappeared due to human interference. In addition to the accepted importance of stocking density as a key variable in management schemes, we were able to identify differential effects of two livestock species on vegetation. Therefore, we emphasize that livestock species should be carefully chosen with respect to the management target.

Samenvatting

Algemene introductie

Beweiding wordt succesvol ingezet als een vorm van management om biodiversiteit te verhogen of te restaureren in veel grasland ecosystemen. Tussen deze ecosystemen zitten ook West-Europese kwelders, die in het verleden intensief begraasd werden. Na de aanleg van natuurgebieden werd in grote gebieden de beweiding afgeschaft, omdat het niet langer een economisch voordeel had voor boeren en voor het natuurbeheer. Deze afschaffing leidde tot een snelle opeenvolging van kweldervegetatie en resulteerde in gebieden die gedomineerd worden door enkele plantensoorten, voornamelijk door het gras *Elytrigia atherica*, en verlies van soortenrijkdom. Deze ontwikkeling leidde tot de vraag “beweiden of niet beweiden?”. Om deze vraag te beantwoorden werden beweidingexperimenten aangelegd langs de Duitse kust. Na ongeveer tien jaar bleek *Elytrigia atherica* de hoge kwelder over te nemen en deze ontwikkeling kan uiteindelijk een verlies van soorten veroorzaken. Daarom wordt beweiding in middelmatige en lage dichtheden vandaag de dag aanbevolen aan natuurbeheerders om successie te vertragen en soortenrijkdom van de vroege successiestadia te behouden. Welk soort management in kwelders moet worden aangehouden is desondanks nog steeds een punt van discussie. Behalve verschillende beweidingdichtheden kunnen verschillende soorten vee ook een verschillend effect hebben op de vegetatie van de kwelders. Daarom was een experiment nodig om de effecten van verschillende soorten vee en beweidingdichtheden op de vegetatie te bestuderen. Dit experiment werd uitgevoerd op de vastelands kwelder Noord-Friesland Buitendijks (NFB), Nederland. De opzet van het experiment was drie blokken, waarin vijf verschillende beweidingregimes werden toegepast. Ieder blok bestond uit een hoge kwelderzone, waar waterbakken voor de dieren stonden, en een lage kwelderzone. De beweidingregimes bestonden uit beweiding met paarden in twee dichtheden (0.5 en 1.0 dier/ha), begrazing met koeien in twee dichtheden (0.5 en 1.0 dier/ha) en een roulatiesysteem waar het ene jaar 1.0 koe/ha graast en het jaar erna dit stuk grond braak ligt. Hier worden de resultaten na drie jaar onderzoek beschreven.

Gedrag van dieren

Om de verschillende invloeden van beweiding op plantensoorten te kunnen begrijpen, moeten we de verschillen in het gedrag van grazers begrijpen en moeten we gedragsbiologie combineren met gemeenschapsecologie. Daarom hebben we het gedrag van de paarden en koeien bestudeerd met betrekking tot dieet keuze, activiteit en ruimtelijke verdeling van de dieren in **hoofdstuk 2**. Toen de verschillende grazers werden vergeleken vonden we dat paarden meer planten met een hoog vezelgehalte in hun dieet hebben. Terwijl koeien vaker kruidige planten aten. Koeien grazen meer selectief en de selectiviteit heeft waarschijnlijk een groot effect op soortensamenstelling en structuur. Daarbij komt dat de activiteit van de grazers verschilde. Paarden brachten meer tijd door met grazen en legden grotere afstanden af vergeleken met de koeien. Deze hogere activiteit beïnvloedt ook de ruimtelijke verdeling van de dieren. Bijvoorbeeld, paarden gebruiken het hele gebied terwijl koeien een begrazingsgradiënt vertoonden met een afname in begrazingsdruk hoe verder men van de waterbak af komt. Verder hebben we de beweidingdichtheden bekeken om de selectiviteit van de grazers in de ruimte te beïnvloeden, omdat in hogere dichtheden de dieren worden gedwongen zich verder van de waterbakken af te bewegen (**hoofdstuk 2** en **5**).

Doelsoorten en vegetatiesamenstelling

De verschillen tussen de verschillende soorten grazers in gedrag, dieet keuze, activiteit en ruimtelijke verdeling, beïnvloeden de vegetatiesamenstelling waarschijnlijk op verschillende niveaus: op soortniveau, gemeenschapsniveau en op het niveau van de vegetatiestructuur. We onderzochten het effect op de productie van bloemen van een doelsoort, *Aster tripolium* (**hoofdstuk 3**). In het dieet van koeien werd meer *Aster tripolium* gevonden (**hoofdstuk 2**) en dit suggereert dat er minder *Aster*-bloemen worden geproduceerd in met koeien beweide gebieden. Desondanks, doet de over het algemeen hogere voedselinname van paarden en hun grotere activiteit, vermoeden dat deze een grotere schade aan *Aster* planten toebrengen en dat er daardoor minder bloemen zouden kunnen zijn. We vonden tegengestelde resultaten in lage en hoge dichtheden van grazers. In gebieden met lage dichtheden was er meer schade bij de koeien en in hoge dichtheden was er meer schade bij de paarden. De hogere selectiviteit van de koeien in dieetkeuze veroorzaakte meer schade aan *Aster*-planten in de lage dichtheden. In hoge dichtheden werd de selectiviteit van koeien minder belangrijk en werd de schade meer willekeurig toegebracht door de hogere voedselinname en activiteit van de paarden. In lage dichtheden werd de grotere hoeveelheid bloemen goed verklaard doordat er minder schade werd toegebracht door paarden. In hogere dichtheden was slechts een klein verschil tussen de verschillende grazers waar te nemen, waarschijnlijk omdat beschadigde planten het verlies aan bloemen konden compenseren. **Hoofdstuk 3** Laat daarom goed zien hoe belangrijk het is om kennis te hebben van de verschillen in gedrag van grazers en hun dichtheden om hun invloed op planten te begrijpen.

De verschillen in gedrag van dieren zijn waarschijnlijk ook van belang voor vegetatiesamenstelling en aantallen planten bij verschillende behandelingen. Toch werden er geen significante verschillen gevonden in vegetatiesamenstelling, en er kon geen invloed op de verandering van die samenstelling in de vaste kwadraten worden waargenomen in de drie jaar van het onderzoek (**hoofdstuk 4**). Diversiteit van planten soorten bleek ook niet te verschillen in de verschillende behandelingen, ook niet op verschillende ruimtelijke schalen (**Box 1**). Verlies van diversiteit in plantensoorten wordt vaak geassocieerd met toename van *Elytrigia atherica* en daarom heeft deze soort extra in de aandacht gestaan. Gebaseerd op de verschillen zijn in gedrag van de grazers en hun dichtheden (**hoofdstuk 2**) en de eerste trends die gevonden in de vegetatiesamenstelling (**hoofdstuk 4**) verwachten we dat paarden effectiever zijn dan koeien en hogere veedichtheden effectiever dan lagere dichtheden in het reduceren en voorkomen van de spreiding van *Elytrigia atherica*. Een meer gedetailleerde blik op het bedekkingspercentage van *Elytrigia* in permanente kwadraten laat een toename van dit gras zien in twee van de drie blokken op de hoge kwelder, maar tegengestelde trends bij de verschillende veedichtheden. Zoals verwacht mag worden op basis van de hogere vezelconcentratie in het dieet van paarden (**hoofdstuk 2**), vonden we een sterkere toename van *Elytrigia* bij de koeien in vergelijking met begrazing door paarden, maar alleen in de hogere dichtheden.

Vegetatie structuur

Bovenop de klassieke monitoring van permanente kwadraten, hebben we ook het effect van begrazing op de vegetatie structuur onderzocht. Een diverse vegetatiestructuur wordt gezien als de basis van diversiteit bij hogere planten, omdat plekken met hoge of korte vegetatie verschillende niches representeren voor verschillende soorten planten. We onderzochten de effecten van begrazing op de vegetatiestructuur op twee schalen.

Op de grote schaal werd het effect van verschillende begrazingsdichtheden van schapen op vegetatie structuur onderzocht door middel van een lange-termijn experiment in Duitsland (**hoofdstuk 5**). We vonden vooral korte vegetatiestructuren bij de hoge begrazingsdichtheden en een hoge proportie van hoge vegetatie bij de lage begrazingsdichtheden, terwijl de tussenliggende dichtheid tot een mozaïek van korte en hoge vegetatie leidde. Daarbovenop vonden we een gradiënt van toenemende vegetatiehoogte bij toenemende afstand tot de drinkbak. Hetzelfde effect was voor koeien waargenomen in **hoofdstuk 2**.

Door de verschillende grazers en hun verschillende dichtheden te vergelijken werd het effect van de verschillende beweidingregimes op de vegetatiestructuur op kleine schaal onderzocht in NFB (**hoofdstuk 6**). Hier verklaart bijvoorbeeld de hogere voedsel inname van paarden waarom de gemiddelde vegetatiehoogte korter is in de paardenblokken. Deze hogere voedselinname is waarschijnlijk ook de reden dat paarden minder selectief zijn in welke soorten planten ze eten, en eten ze planten van zowel hoge als lage kwaliteit. Minder selectieve grazers veroorzaken daardoor waarschijnlijk grotere homogene plekken. We vonden inderdaad grotere 'patches' in de met paarden beweide blokken (fig. 9.14). Hoewel we verschillen vonden tussen de verschillende behandelingen in de vegetatiestructuur op kleine schaal bleek dit geen invloed te hebben op de diversiteit van de planten, tenminste nu nog niet.

Verticale opslibbing

De waargenomen effecten van beweiding op de vegetatiestructuur kan ook de abiotische condities van kwelders beïnvloeden. Bijvoorbeeld, beweiding wordt gezien als een factor die sedimentafzetting reduceert doordat het de vegetatie structuur veranderd. Een dichte vegetatiestructuur vermindert de stromingsnelheid van water en draagt zo indirect mee aan toegenomen opslibbing van sediment. De korte vegetatiestructuur in beweide gebieden leidt dan tot minder sediment afzetting en daardoor tot minder opslibbing in vergelijking met onbeweide kwelders. Daarbij komt dat er nog een tweede manier is waardoor grazers effect kunnen hebben op de opslibbing; het opgeslibte sediment is onderhevig aan bodemverdichting, wat de opslibbing verminderd. De bodemverdichting wordt veroorzaakt door het gewicht van de grond zelf, maar grazers dragen extra bij door vertrapping van de grond. Deze extra bodemverdichting, veroorzaakt door de vertrapping, kan resulteren in een grotere vermindering van de opslibbing.

De hypothese, dat opslibbing in beweide gebieden lager is dan onbeweide gebieden door vertrapping en lagere vegetatie, hebben we getest in **hoofdstuk 8**. Door afgezette sedimentlagen in een boorkern te dateren, door middel van de ^{137}CS-methode (**hoofdstuk 7**), hebben we de lange-termijn opslibbing en sediment afzetting ratios berekend voor de onbeweide en beweide gebieden in vier onderzoeksgebieden. Er was, noch in opslibbing, noch in sedimentafzetting, een significant verschil tussen onbeweide en beweide gebieden door tegengestelde trends in de verschillende gebieden (**hoofdstuk 8**). In tegenstelling tot de opslibbing was de dichtheid van de grond wel significant hoger in de beweide kwelders, dit geeft een meer verdichtte grond aan. We concluderen dat de opslibbing op beweide en onbeweide kwelders niet een directe oorzaak heeft, maar beïnvloed wordt door andere factoren zoals de ruimtelijke verspreiding van sedimentafzetting in het gebied. Een algemene conclusie die we kunnen trekken is dat alle kwelders, zowel beweid als onbeweid, genoeg opslibbing hebben die het mogelijk maakt om toekomstige zeespiegelstijging te kunnen bijhouden.

Implicaties voor management

Om beweiding succesvol als een management tool te kunnen gebruiken, is het cruciaal om eerst een doel te definiëren. We onderzochten de effecten van verschillende grazers en dichtheden van grazers op verschillende aspecten van vegetatie en opslibbing om managers te helpen met het kiezen van de juiste management voor het gekozen doel.

Het meest belangrijke algemene resultaat is dat de eenheid voor begrazing (LU) niet het beste middel is om beweidingintensiteit te meten wanneer er verschillende grazers in het spel zijn (**hoofdstuk 2**). De effecten van verschillende dichtheden van paarden en koeien kan in hetzelfde gebied heel anders zijn vooral vanwege de verschillende voedselbehoeften en de daardoor resulterende verschillen in activiteit van de grazers (*e.g.* **hoofdstuk 3**). Indien mogelijk, stellen we voor dat toekomstige plannen voor natuurbeheer gemiddelde beweidinguren berekenen en de beweidinguren per eenheid ruimte gebruiken om beweidingdichtheden te vergelijken. Omdat LU op dit moment gebruikelijk is in natuurbeheer en waarschijnlijk in de toekomst ook belangrijk blijven is het goed om, als 1 koe wordt gerepresentateerd door één LU, ervan uit te gaan dat één paard dan moet worden gezien als 1.7 LU. Daarbij komt dat dit beweidingdichtheden zijn per eenheid ruimte en dat de echte locale beweidingdichtheid sterk kan variëren door de verschillen in ruimtelijke verspreiding van de grazers (**hoofdstuk 2**).

Als het management doel bestaat uit een grote hoeveelheid van de doelsoort *Aster tripolium*, is de resulterende aanbeveling een lage dichtheid van paarden (hoofdstuk 3). Deze aanbeveling wordt gegeven onder voorbehoud dat **hoofdstuk 3** alleen de korte-termijn effecten van beweidingdruk analyseert. De resultaten van **hoofdstuk 4**, die drie jaar onderzoeksdata omvatten, laten zien dat op de lange termijn de verschillende beweidingregimes de populatie dynamiek van *Aster tripolium* op andere wijze zouden kunnen beïnvloeden dan wat in **hoofdstuk 3** werd gevonden. We zouden kunnen verwachten dat de resultaten van **hoofdstuk 4** ook op andere kweldersoorten, zoals *Triglochin maritima*, van toepassing zijn, wanneer deze soorten selectief worden gegeten door koeien (**hoofdstuk 4**).

Het meest algemene management doel in natuurbehoud is het behoud van diversiteit. Tussen de verschillende grazers werd tot nu toe geen effect gevonden op deze diversiteit. Daarom is het niet mogelijk om hier voor management een aanbeveling te geven, maar we adviseren om beslissingen op lange-termijn monitoring te baseren. We vonden echter wel een effect van de verschillende behandelingen op vegetatiestructuren op kleine schaal (**hoofdstuk 6**). Omdat een variatie aan vegetatiestructuren waarschijnlijk biodiversiteit verhoogt, i.e. soorten rijkdom van planten en verschillende groepen dieren, adviseren we om koeien te gebruiken en geen paarden om de diversiteit aan vegetatiestructuur te verhogen.

Met betrekking tot verschillende veedichtheden hebben we de effecten op plantensoorten rijkdom geanalyseerd in het beweidingexperiment in Friesland, en in twee lange-termijn experimenten in Duitsland (**Box 1**). In alle gebieden had de dichtheid van het vee geen effect op het aantal soorten. Het relatief hoge aantal soorten in de kwadraten wordt gezien als het gevolg van de toevoer van zaden van plantensoorten die gevoelig zijn voor beweiding uit nabijgelegen onbeweide gebieden. Dit is een goed voorbeeld hoe management dat de beschikbare ruimte op verschillende manieren gebruikt, de natuurwaarde van een heel gebied kan verhogen. Door een groot gebied in meerdere gebieden te verdelen, is er een mogelijkheid om een aantal tegengestelde natuurdoelen, zoals geschiktheid voor ganzen en een hoge plantendiversiteit, te behalen in één gebied.

Het verlies van diversiteit van planten in kwelders is vaak gecorreleerd met de verspreiding van *Elytrigia atherica*, en daardoor kan de verlaging van *Elytrigia*-bedekking een ander doel zijn in management. We vonden dat beide grazers een behoorlijke tijd in de *Elytrigia* vegetatie doorbrachten. Desondanks gebruikten koeien deze plekken om te rusten en te herkauwen, terwijl paarden er vaak grazend werden geobserveerd (**hoofdstuk 2**). Hierdoor bevelen we beweiding met paarden aan als er een hoge bedekking van *Elytrigia* is die gereduceerd moet worden.

Als een bijkomstige optie voor het natuurbeheer hebben we het effect van wisselende beweiding en braakligging op soorten rijkdom onderzocht (**hoofdstuk 4** en **box 1**). We vonden minder soorten diversiteit in de roulatiebehandeling dan in de 1.0 koe/ha behandeling. Dit is in overeenstemming met de toename van *Elytrigia* in de permanente kwadraten, die eerder al de oorzaak was gebleken van verlies van soorten. Daarom adviseren we geen roulatieregime met de onderzochte veedichtheden en beweidingfrequentie aan, als het doel een hoge diversiteit van plantensoorten en een afname van *Elytrigia* is. Het is echter wel mogelijk dat andere roulatieregimes met, bijvoorbeeld, hogere veedichtheden en andere frequenties zoals twee jaar beweid en één jaar onbeweid, positievere resultaten oplevert.

Vervolg onderzoek

Een verdere monitoring van de geobserveerde tendensen in het experiment is noodzakelijk om onze resultaten te verifiëren en lange termijn effecten te bestuderen. Om het effect van de verschillende behandelingen op de verspreiding van *Elytrigia* te bestuderen, bevelen we het voortzetten van de vegetatiekartering aan, ter aanvulling op het opnemen van de permanente kwadraten. Verder is het interessant om de dynamiek van de vegetatiestructuur te onderzoeken om te kijken hoe de competitie voor licht in hoge vegetatie, en diversiteit in vegetatiestructuur leidt tot een hogere soortenrijkdom. Een langere tijdserie van de metingen is ook nodig om goede conclusies te kunnen trekken over de roulatiebehandeling. Daarbij komt dat het nodig is om verschillende roulatiebehandelingen met elkaar te vergelijken en uit te proberen in verschillende kwelders om tot goede conclusies en aanbevelingen te kunnen komen.

Ter aanvulling op het effect, van de verschillende grazers en beweidingdichtheden, op de vegetatie, moeten directe en indirecte effecten van de behandelingen op andere organismen, *e.g.* vogels, worden onderzocht. Verder moet er aandacht worden besteed aan de effecten van verschillende soorten grazers op opslibbing- hoeveelheid en patronen, omdat verschillen in gedrag hierin een belangrijke rol kunnen spelen. Als voorbeeld, de meer actieve paarden kunnen meer bodemverdichting veroorzaken en daardoor de opslibbing sterker verminderen dan andere grazers. Ook het effect van verschillende patronen in vegetatiestructuur bij verschillende behandelingen zullen moeten worden geïncorporeerd in vervolgonderzoek.

Conclusies en relevantie voor andere systemen

De bevindingen van dit onderzoek zijn niet alleen toepasbaar in kwelders in de Waddenzee of aan de Baltische kust, maar voor alle graslanden waar vee en andere grazers worden gebruikt als instrument voor natuurbeheer. Onder deze systemen zitten bijvoorbeeld tot voor kort extensief gebruikte graslanden, die nu buiten beheer zijn, en graslanden waar grote herbivoren verdwenen zijn door menselijke storing. Aanvullend op het geaccepteerde belang van beweidingdichtheid als een instrument in natuurbeheer, waren we in staat om verschillende effecten van twee soorten grazers op de vegetatie te ontrafelen. Daarom benadrukken we dat er een zorgvuldige keuze moet worden gemaakt voor soorten grazers die passen bij het doel van het natuurbeheer.

Zusammenfassung

Allgemeine Einleitung

Nutztierbeweidung wird im Natur-Management erfolgreich als Werkzeug genutzt, um die Biodiversität von Grünland-Ökosystemen zu erhöhen oder wiederherzustellen. Zu diesen Ökosystemen gehören auch die westeuropäischen Salzwiesen, welche traditionell intensiv beweidet wurden. Die Beweidung wurde hier jedoch in großen Gebieten auf Grund mangelnder Rentabilität für Landwirte oder als Maßnahme zum Naturschutz in Schutzgebieten aufgegeben. Diese Beweidungsaufgabe führte häufig zu einer raschen Sukzession und resultierte in der großflächigen Dominanz einzelner Pflanzenarten, darunter vor allem das hohe Gras *Elytrigia atherica*, sowie dem damit einhergehenden Verlust der Pflanzenbiodiversität. Diese Entwicklung führte zu der folgenden Frage für das Management von Salzwiesen: “Beweiden oder nicht Beweiden?“. Um diese Frage beantworten zu können, wurden entlang der deutschen Festlandsküste Beweidungsexperimente eingerichtet. In diesen Experimenten wurde beobachten, dass *Elytrigia* die hohe Salzwiese nach etwa zehn Jahren besiedelt und diese Entwicklung wird wahrscheinlich in Zukunft zu einem Verlust von Pflanzenbiodiversität führen. Aus diesem Grund lautet die Empfehlung für den Naturschutz in Salzwiesen inzwischen Beweidung mit geringen oder moderaten Dichten um die Sukzession zu verlangsamen und artenreiche Sukzessionsstadien zu erhalten. Welches Beweidungsmanagement jedoch genau angewendet werden soll, benötigt stets noch verschiedene Überlegungen. Zusätzlich zur Beweidungsdichte, können nämlich auch verschiedene Nutztierarten unterschiedliche Einflüsse auf die Vegetation haben. Aus diesem Grund wurde ein Experiment benötigt, in dem der Einfluss verschiedener Beweidungsintensitäten und Nutztierarten auf die Vegetation der Salzwiese untersucht wird. Solch ein Experiment wurde auf der Festlandssalzwiese Noord-Friesland Buitendijks (NFB) in den Niederlanden ausgeführt. Der Aufbau des Experiments bestand aus drei Blocks, in denen jeweils alle fünf verschiedenen Treatments angewendet wurden. Jeder Block enthielt einen Teil der hohen Salzwiese, in dem sich auch eine Trinkwasserstelle für die Tiere befand, und einen Teil der unteren Salzwiese. Die Beweidungstreatments bestanden aus: Beweidung mit Pferden (jeweils 0.5 und 1.0 Tiere/ha) und Beweidung mit Kühen (jeweils 0.5 und 1.0 Tiere/ha), sowie eine Rotationsbeweidung, in der sich Jahre mit Kuhbeweidung (1.0 Tier/ha) und unbeweidete Jahre abwechselten. Die Resultate dieses Beweidungsexperiments werden hier zusammengefasst.

Verhalten der Tiere

Um die unterschiedlichen Einflüsse der Nutztierarten auf die Vegetation besser zu verstehen, sollten wir zunächst die Unterschiede im Verhalten der Tiere kennen und daraufhin die Verhaltensökologie der Tiere und die Synökologie der Pflanzen miteinander kombinieren. Deshalb untersuchten wir zunächst das Verhalten von Pferden und Kühen im Hinblick auf deren Diätzusammenstellung, Aktivität und räumliche Verteilung (**Kapitel 2**). Beim Vergleich der Nutztierarten stellten wir fest, dass Pferde einen größeren Anteil Pflanzenarten mit hohem Faseranteil fraßen, während Kühe mehr krautige Pflanzen bevorzugten. Außerdem fraßen Kühe selektiv, und die Selektivität soll einen großen Einfluss auf die Vegetationszusammensetzung und -struktur haben. Zusätzlich unterschied sich auch die generelle Aktivität der Nutztierarten. So verbrachten etwa Pferde einen größeren Anteil des Tages mit Grasen und legten längere Strecken zurück als Kühe. Diese erhöhte Aktivität bei Pferden beeinflusst auch das räumliche Verteilungsmuster der Tiere. Während zum Beispiel Pferde die gesamte zur Verfügung stehende Fläche nutzen, zeigten Kühe einen deutlichen Beweidungsgradienten mit einer abnehmenden lokalen Beweidungsintensität mit zunehmender Entfernung zum Trinkwasser. Des Weiteren fanden wir einen Einfluss der Beweidungsdichte auf die Selektivität der Tiere und deren räumliche Verteilung, denn in höheren Anzahlen werden die Tiere gezwungen sich weiter vom Trinkwasser zu entfernen (**Kapitel 2** und **5**).

Modellpflanzenart und Vegetationszusammensetzung

Die Unterschiede in Diätzusammenstellung, Aktivität und räumlicher Verteilung zwischen Nutztierarten und zwischen Beweidungsdichten beeinflussen die Vegetation der Salzwiese wahrscheinlich auf verschiedenen Ebenen: einzelne Pflanzenarten, die Artenzusammensetzung der Pfanzengemeinschaft und die Vegetationsstruktur. Auf der Ebene einzelner Pflanzenarten untersuchten wir den Einfluss von verschiedenen Beweidungstreatments auf die Blütenproduktion der Beispielpflanze *Aster tripolium* (**Kapitel 3**). Ein hoher Anteil *Aster* befand sich in der Diät von Kühen (**Kapitel 2**) und dieses Resultat gibt zu der Annahme Anlass, dass diese Pflanzen in von Kühen beweideten Salzwiesen weniger Blüten produzieren würden. Da jedoch Pferde eine höhere Gesamtnahrungsaufnahme und eine höhere generelle Aktivität zeigten (**Kapitel 2**), kamen wir zu der Annahme, dass Pferde die *Aster*-Pflanzen in höherem Maße beschädigen werden und auch zu einer stärkeren Reduktion der Blütenanzahl führen. Die Ergebnisse des Schadens an Pflanzen zeigten jedoch gegensätzliche Trends in den Beweidungsdichten. Während in niedrigen Dichten Kühe mehr Schaden verursachten, waren die Schäden in hohen Dichten bei Pferden grösser. Der Grund für die stärkere Beschädigung durch Kühe in geringen Dichten ist die höhere Selektivität der Kühe für bevorzugte Pflanzen. In höheren Dichten dagegen spielt die Selektivität der Kühe eine geringere Rolle als die zufällige Beschädigung der Pflanzen durch die generell höhere Nahrungsaufnahme und Aktivität der Pferde. In geringen

Beweidungsdichten kann die gefundene höhere Anzahl Blüten bei Pferden durch die geringere Beschädigung durch die Tiere in diesem Treatment erklärt werden. Dagegen fand sich in höheren Beweidungsdichten nur ein geringer Unterschied zwischen den Nutztierarten im Zusammenhang mit der Anzahl der Blüten, wahrscheinlich weil beschädigte Pflanzen in der Lage waren den frühen Verlust von Blütenknospen zu kompensieren. **Kapitel 3** zeigt also deutlich, wie wichtig das Wissen über Verhaltensunterschiede in Diätzusammenstellung und Aktivität zwischen Nutztierarten ist um ihren unterschiedlichen Einfluss auf einzelne Pflanzen zu verstehen.

Die genannten Unterschiede im Verhalten führen wahrscheinlich auch zu Unterschieden in Artenzusammenstellung und Artenzahl der Pflanzen zwischen den Treatments. Bis jetzt konnte jedoch kein signifikanter Unterschied in der Artenzusammensetzung und kein Einfluss auf die zeitliche Änderung der Artenzusammensetzung in Dauerflächen festgestellt werden (**Kapitel 2**). Es wurden des Weiteren auf unterschiedlich großen Flächen keine Unterschiede in Pflanzendiversität zwischen den Treatments gefunden (**Box 1**). Der Verlust an Pflanzendiversität geht jedoch oft einher mit der Ausbreitung von *Elytrigia atherica*, und deshalb sollte diese Pflanze gesondert betrachtet werden. Basierend auf den Unterschieden zwischen Nutztierarten und Beweidungsdichten in der Diätzusammenstellung (**Kapitel 2**) und den ersten sichtbaren Trends in der Artenzusammenstellung (**Kapitel 4**) würden wir erwarten, dass Pferde effektiver als Kühe und hohe Beweidungsdichten effektiver als niedrige Beweidungsdichten im Vorbeugen einer *Elytrigia*-Ausbreitung sind. Betrachtet man den Bedeckungsgrad von *Elytrigia* in den Dauerflächen findet man in zwei von drei Blocks eine Ausbreitung von *Elytrigia* in der hohen Salzwiese. Allerdings zeigen sich gegensätzliche Trends in unterschiedlichen Beweidungsdichten. Wie auf der Basis des höheren Faseranteils im Futter der Pferde (**Kapitel 2**) erwartet werden konnte, zeigte sich eine stärkere Zunahme von *Elytrigia* bei Kühen im Vergleich zu Pferden, allerdings nur in höheren Beweidungsdichten.

Vegetationsstruktur

Zusätzlich zum klassischen Monitoring von Dauerflächen, untersuchten wir den Effekt der Beweidung auch auf die Vegetationsstruktur. Eine diverse Vegetationsstruktur soll förderlich für eine hohe Pflanzendiversität sein, da abwechselnde Stellen, sogenannte Patches, mit kurzer und hoher Vegetationshöhe Nischen für verschiedene Pflanzenarten bieten. Wir untersuchten den Effekt von Beweidung auf die Vegetationsstruktur auf zwei unterschiedlichen Skalen.

Auf der großen Skala wurde der Einfluss von verschiedenen Beweidungsdichten auf die Vegetationsstruktur innerhalb eines Langzeit-Beweidungsexperiments mit Schafen in Deutschland untersucht (**Kapitel 5**). Hier fanden wir vor allem eine geringe Vegetationshöhe in höheren Beweidungsdichten und eine höhere Vegetationshöhe in geringeren Dichten, während mittlere Beweidungsdichten zu einem Mosaik von hoher und kurzer Vegetation führten. Zusätzlich fanden wir einen Gradienten von höher werdender Vegetation mit zunehmendem Abstand vom Frischwasser. Dieser Effekt wurde auch bei Kühen beobachtet (**Kapitel 2**).

Den Einfluss der unterschiedlichen Beweidungstreatments auf die kleinskalige Vegetationsstruktur wurde anhand des Beweidungsexperiment NFB für zwei unterschiedliche Nutztierarten und Beweidungsdichten untersucht (**Kapitel 6**). Die mittlere Vegetationshöhe war hier deutlich niedriger bei Pferden im Vergleich zu Kühen, wahrscheinlich auf Grund des höheren täglichen Futterbedarfs der Pferde. Dieser höhere tägliche Futterbedarf ist wahrscheinlich ebenso der Grund für die geringere Selektivität der Pferde im Zusammenhang mit der Wahl von Futterpflanzen und führt dazu, dass Pferde einen hohen Anteil von Pflanzen sowohl schlechter als auch guter Qualität fressen. Aus diesem Grund führt die Beweidung mit weniger selektiven Tieren auch zu größeren Patches und einer Homogenisierung der vorhandenen Vegetationsstruktur. In der Tat konnten wir in von Pferden beweideten Teilen der Marsch die größeren Patches beobachten. Trotz dieser kleinskaligen Unterschiede der Vegetationsstruktur konnten wir bisher keinen Einfluss auf die Diversität der Pflanzen feststellen.

Sedimentakkretion

Der beobachtete Einfluss von Beweidung auf die Vegetationsstruktur könnte sich indirekt auch auf die abiotischen Bedingungen in Salzwiesen auswirken. So wurde zum Beispiel angenommen, dass Beweidung die Sedimentationsrate indirekt durch die Verringerung der Vegetationsstruktur beeinflusst, denn eine dichte Vegetationsstruktur verringert die Fließgeschwindigkeit des Wassers und damit die Sedimentationsrate. Aus diesem Grund sollte eine sehr kurze Vegetationsstruktur in beweideten Gebieten zu geringeren Akkretionsraten führen als in unbeweideten Gebieten. Zusätzlich gibt es eine zweite direkte Weise in der Beweidung die Akkretionsrate verringern könnte. Das Sediment in Salzwiesen wird auf Grund seines Eigengewichts im Laufe der Zeit immer kompakter gelagert. Dieser Vorgang verringert die Akkretionsrate. Nutztiere könnten die Sedimente jedoch zusätzlich durch Betreten kompaktieren und somit die Akkretionsrate zusätzlich verringern.

Wir testeten die Hypothese, dass Akkretionsraten, auf Grund von Kompaktion und verringertem Sedimenteintrag in kurzer Vegetation, kleiner in beweideten im Vergleich zu unbeweideten Gebieten sind (**Kapitel 8**). Dazu wurden Akkretionsraten und Sedimentdepositionsraten für beweidete und unbeweidete Flächen in vier Untersuchungsgebieten mit Hilfe der ^{137}Cs-Methode (**Kapitel 7**) berechnet. Weder Akkretions- noch Sedimentdepositionsraten unterschieden sich signifikant zwischen beweideten und unbeweideten Flächen auf Grund von gegensätzlichen Trends in den Untersuchungsgebieten (**Kapitel 8**). Im Gegensatz zur Akkretionsrate war die Bodendichte in beweideten Gebieten signifikant höher, was auf eine Kompaktion des Bodens durch die Tiere hindeutet. Wir schlussfolgern aus diesen Ergebnissen, dass die Akkretionsrate in beweideten und unbeweideten Flächen nicht von direkten Kausalitäten abgeleitet werden kann, sondern durch eine Anzahl Faktoren wie z.B. die räumliche Verteilung der Sedimentdeposition bestimmt wird. Im Allgemeinen konnte jedoch festgestellt werden, dass die Akkretionsrate in sowohl beweideten wie auch unbeweideten Marschen über dem jetzigen Meeresspiegelanstieg liegen.

Anwendungen im Naturmanagement

Die wichtigste Grundlage für den erfolgreichen Einsatz von Beweidung als Werkzeug im Naturmanagement ist die Definition von klaren Zielsetzungen. Wir untersuchten den Einfluss von verschiedenen Beweidungsformen auf die Vegetation und Akkretion um Managern zu ermöglichen ein adäquates Management für das Erreichen von Zielsetzungen zu wählen. Dabei ist das wichtigste allgemeine Resultat, dass es sich bei Nutzvieheinheiten nicht um die optimale Einheit handelt um den Beweidungsdruck festzulegen wenn verschiedene Nutztierarten involviert sind (**Kapitel 2**). Der Effekt der gleichen Beweidungsdichte von Pferden und Kühen in einem Gebiet kann sich sehr unterscheiden, da sich die Tiere in ihrem Futterbedarf und der daraus resultierenden Aktivität unterscheiden (z.B. **Kapitel 3**). Sofern möglich, schlage ich deshalb vor, das zukünftige Pläne im Naturmanagement die durchschnittlichen täglichen Weidestunden berechnen sollten und die Einheit Weidestunden pro Fläche nutzen um Beweidungsdichten zu vergleichen. Da Nutzvieheinheiten jedoch vielfach in Gebrauch sind, und dies wahrscheinlich auch bleiben werden, sollte beachtet werden, dass wenn eine Kuh eine Nutzvieheinheit repräsentiert, ein Pferd als ungefähr 1,7 Nutzvieheinheiten angesehen werden sollte. Zusätzlich sollte nicht vergessen werden, dass sich die Beweidungsdichte pro Fläche und die wirkliche lokale Beweidungsintensität auf Grund von Unterschieden in der räumlichen Verbreitung der Tiere stark unterscheiden können (**Kapitel 2**).

Wenn das Ziel des Managements eine hohe Anzahl von Blüten, z.B. der Art *Aster tripolium*, sein sollte, dann würden wir auf Grund der Ergebnisse in **Kapitel 3** eine Beweidung mit Pferden in geringer Beweidungsdichte empfehlen. Diese Empfehlung wird allerdings mit der Einschränkung gegeben, dass es sich bei diesen Ergebnissen um kurzzeitige Einflüsse im Experiment handelt. Im Gegensatz dazu zeigen die Ergebnisse in **Kapitel 4**, das auf lange Frist die Populationsdynamik von *Aster* anders beeinflusst wird als in **Kapitel 3**. Wir gehen davon aus, dass sich die Ergebnisse der Beispielpflanze *Aster* auch auf andere Arten der Salzwiese wie z.B. *Triglochin maritimum* anwenden lassen die selektiv von Kühen gefressen werde (**Kapitel 4**).

Eines der häufigsten Ziele im Naturmanagement ist die Erhaltung einer hohen Artenzahl. Zum jetzigen Zeitpunkt konnte noch kein Einfluss der Beweidungstreatments auf die Artenzahl festgestellt werden (**Kapitel 5**) und deshalb können wir noch keine Empfehlung in dieser Hinsicht geben, sprechen allerdings die Empfehlung aus eine Entscheidung auf Langzeitbeobachtungen zu stützen. Im Gegensatz zur Artenzahl konnte jedoch ein Effekt der verschiedenen Treatments auf die kleinskalige Vegetationsstruktur festgestellt werden (**Kapitel 6**). Da eine abwechslungsreiche Vegetationsstruktur sich jedoch positiv auf die Biodiversität, sowohl im Hinblick auf Pflanzen als auch verschiedene Gruppen von Tieren, auswirken soll, würden wir Kühe und keine Pferde empfehlen um die strukturelle Diversität zu erhöhen.

Mit Hinblick auf unterschiedliche Beweidungsintensitäten haben wir deren Einfluss sowohl in Friesland (NFB), als auch in einem Langzeitexperiment in Deutschland untersucht (**Box 1**). In allen Fällen hatte die Beweidungsintensität keinen Einfluss auf die Artenzahl. Dabei erklärt sich die immer noch relative hohe Artenzahl in intensiv beweideten Gebieten vor allem durch den Sameneintrag aus benachbarten unbeweideten Gebieten. Dies ist ein gutes Beispiel wie ein räumlich unterschiedliches Management die Wertigkeit eines ganzen Gebietes für den Naturschutz erhöhen kann. Indem ein großes Gebiet in mehrere kleinere geteilt wird, ist es möglich dass unterschiedliche Managementstrategien Anwendung finden und so gegensätzliche Ziele wie etwa eine hohe Anzahl Gänse und eine hohe Pflanzendiversität innerhalb eines Gebietes erreicht werden können.

Der Verlust der Pflanzendiversität geht in Salzwiesen oft mit der Ausbreitung von *Elytrigia atherica* einher, und aus diesem Grund könnte die Eindämmung dieses Grases ein weiteres Ziel des Managements sein. Wir konnten feststellen, dass beide Nutztierarten einen großen Teil ihrer Zeit im *Elytrigia*-Vegetationstyp verbringen. Während Pferde dort jedoch häufiger beim Grasen beobachtet wurden, nutzen Kühe diese leicht erhöhte und vergleichsweise trockene Zone dagegen überwiegend zum Liegen und Wiederkäuen (**Kapitel 2**). Aus diesem Grund empfehlen wir Beweidung mit Pferden, soll eine bereits bestehende Dominanz von *Elytrigia* verringert werden.

Eine weitere Option für das Management von Salzwiesen die in dieser Studie untersucht wurde ist die Wechselbeweidung und deren Einfluss auf die Pflanzendiversität (**Kapitel 4** und **Box 1**). Dabei wurde eine geringere Pflanzendiversität unter Wechselbeweidung im Vergleich zu 1,0 Kühen/ha gefunden. Dieses Ergebnis deckt sich mit einer Zunahme von *Elytrigia* in den Dauerflächen, welche bereits in anderen Studien als Grund für einen Verlust an Pflanzendiversität identifiziert wurde. Aus diesem Grund würden wir Wechselbeweidung in der hier untersuchten Beweidungsdichte und Wechselfrequenz nicht empfehlen, sollte das Managementziel eine hohe Pflanzendiversität und die Eindämmung von *Elytrigia* sein. Es ist jedoch möglich, dass andere Wechselbeweidungsregimes mit z.B. einer höheren Beweidungsdichte oder Wechselfrequenz zu positiveren Resultaten führen würden.

Weitere Untersuchungen

Ein weiteres Monitoring der beobachteten Entwicklungen wäre sehr zu empfehlen um die gefundenen Resultate zu verifizieren und um die Langzeitentwicklung zu untersuchen. Außerdem sollte die Ausbreitung von *Elytrigia atherica* im Experiment weiter untersucht werden, am besten an Hand von wiederholten Vegetationskartierungen. Des Weiteren wäre es interessant die Entwicklung der Patches in der Vegetation weiter zu beobachten und zu untersuchen ob sich diese auf die Pflanzendiversität auswirken. Auch für die Schlussfolgerungen über den Einfluss der Wechselbeweidung wäre eine längere Messreihe vorteilhaft. Zusätzlich sollte der Einfluss von verschiedenen Optionen der Wechselbeweidung in Hinsicht auf Beweidungsdichte und Wechselfrequenz untersucht werden um endgültige Schlussfolgerungen zu ziehen.

Zusätzlich zu dem hier untersuchten Einfluss von verschiedenen Nutztierarten und Beweidungsdichten auf die Vegetation sollten sowohl direkte wie auch indirekte Effekte auf andere Organismengruppen wie z.B. Vögel untersucht werden. Des Weiteren verdient der Einfluss von unterschiedlichen Nutztierarten auf die Akkretion weitere Aufmerksamkeit, da Unterschiede im Verhalten der Tiere diese beeinflussen könnten. So könnten z.B. die aktiveren Pferde zu einer stärkeren Kompaktion des Bodens beitragen als andere Arten. Außerdem sollten die durch die Beweidung entstandenen räumlichen Unterschiede in der Vegetationsstruktur in Studien der Verteilung von Sediment mit einbezogen werden.

Schlussfolgerungen und Relevanz für andere Systeme

Die Ergebnisse dieser Untersuchung lassen sich nicht nur auf Salzwiesen entlang der Nord- und Ostseeküsten anwenden, sondern auch auf alle Graslandsysteme in denen Nutztiere als Werkzeug im Naturmanagement eingesetzt werden. Darunter finden sich z.B. Gebiete, die früher extensiv genutzt wurden und jetzt aufgegeben wurden oder Grasländer in denen die natürlich vorkommenden Herbivoren auf Grund von menschlichen Einflüssen verschwunden sind. Zusätzlich zu der anerkannten Wichtigkeit der Beweidungsdichte, konnten wir auch Unterschiede im Einfluss verschiedener Nutztierarten auf die Vegetation feststellen. Also möchten wir betonen, dass die Nutztierart mit Hinblick auf das Ziel des Managements sorgfältig ausgesucht werden sollte.

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