Effects of vegetation patterns and grazers on tidal marshes

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NIOZ Royal Netherlands Institute for Sea Research

This PhD project was carried out at the Community and Conservation Ecology group, which is part of the Groningen Institute for Evolutionary Life Science (GELIFES) at the University of Groningen, The Netherlands. The research was conducted in cooperation with the Spatial Ecology Group at the Royal Netherlands Institute for Sea Research (NIOZ-Yerseke), The Netherlands.

This project was funded by the Dutch Organization for Scientific Research (NWO-ZKO), project number 83908320. It was further supported by the Schure-Beijerinck-Popping fonds.

The printing of this thesis was partially funded by the University of Groningen and the Faculty of Mathematics and Natural Science.

Lay-out & figures:	Dick Visser
Cover:	Kelly Elschot & Dick Visser
Photo's:	Kelly Elschot, cover 4th photo & chapter 2, Irene van Schrojenstein Lantman
Printed by:	CPI- Koninklijke Wöhrmann, Zutphen

ISBN: 978-90-367-8088-9
ISBN: 978-90-367-8087-2 (electronic version)

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groningen

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Proefschrift

ter verkrijging van de graad van doctor aan de
Rijksuniversiteit Groningen
op gezag van de
rector magnificus prof. dr. E. Sterken
en volgens besluit van het College voor Promoties.

De openbare verdediging zal plaatsvinden op

vrijdag 18 september 2015 om 11:00 uur

door

Kelly Elschot

geboren op 9 november 1980
te Zelhem

Promotores
Prof. dr. J.P. Bakker
Prof. dr. S. Temmerman
Prof. dr. J. van de Koppel
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General introduction

Kelly Elschot

INTRODUCTION

Circa 40% of the global terrestrial area is covered by grasslands (White et al. 2000) and many of them are being grazed by wildlife as well as domestic livestock for agricultural uses (Kemp and Michalk 2007). All these grazers have large impacts on the functioning of grassland ecosystems (Olff and Ritchie 1998). They can control the vegetation top-down, which generally boosts local plant diversity (Bos et al. 2002, Bakker et al. 2006). Meanwhile, presence and abundance of the grazers is for a large part controlled bottom-up by the primary production of the local vegetation (e.g. White 2008; Center and Dray 2010). These animal-plant interactions have remained an important subject in ecology (e.g. McNaughton 1985; Olff and Ritchie 1998). Next to intense livestock grazing, changing environmental conditions and human impact has lead to populations of native grazers reducing in some ecosystems (De Visser et al. 2011), while they are increasing in other ecosystems (e.g. Fox et al. 2005). With these global changes in grazing pressures, it is important to understand their role within ecosystems. We need to understand how they impact vegetation characteristics, the interactions between grazers and vegetation and how they affect important ecosystem processes. In this thesis I studied this, using tidal marshes as a model ecosystem.

Tidal marshes are highly dynamic ecosystems that form the natural transitions between land and sea (Allen 2000). They are important feeding and breeding habitats for many different grazers, e.g. large populations of migrating geese use them as feeding and wintering habitats (Madsen et al. 1999). Other small grazers, such as snails (Silliman et al. 2005), hare and rabbits, are present year-round (Kuijper and Bakker 2005). Additionally, many European marshes are grazed by livestock (Kiehl et al. 1996, Bouchard et al. 2003). This can be for management purposes, to maintain plant diversity, or for agricultural purposes. Grazers are known to have large impacts on tidal marshes. They reduce vegetation height (Bos et al. 2002), alter the species composition (Bakker 1989, Andresen et al. 1990, Di Bella et al. 2013), increase plant diversity (Olff and Ritchie 1998, Loucougaray et al. 2004), induce patchiness (Bos et al. 2004, Nolte et al. 2013a), alter nutrient cycling (Van Wijnen et al. 1999, Olsen et al. 2011) and change local abiotic conditions in the soil (Schrama et al. 2013a). In extreme cases, grazers can degrade entire marsh areas and regeneration is expected to take decades, if regeneration is even possible (Esselink et al. 1997, Mclaren and Jefferies 2004, Silliman et al. 2005).

For conservation purposes, we need to understand how grazer presence impact important marsh characteristics, and how this in turn could affect grazer abundance. In this thesis I had the unique possibility to use long-term field-based experiments together with long-term datasets, to study the role of grazers in tidal marshes and how their presence is affected by small-scale heterogeneity in the marsh platform. I included different spatial scales (few m^2 vs. km^2) as well as different grazer types (small grazers vs.

large grazers and above-ground grazing vs. below-ground grubbing). I studied these, throughout ecosystem development. Overall, the studies contribute to understanding the impact of grazers on tidal marshes and the mechanisms driving grazer abundance, which were the core themes of the funding program.

MARSH SUCCESSION AND GRAZER ABUNDANCE THROUGHOUT ECOSYSTEM DEVELOPMENT

Local productivity, plant composition and grazer presence changes with marsh succession (Olff et al. 1997). Initially, marsh development starts when pioneer vegetation successfully establishes on a coarse-grained (sandy) intertidal flat. At this stage, pioneer species have to cope with saline, low fertile and often waterlogged environmental conditions (Davy et al. 2011). Presence of pioneer vegetation stabilizes the soil and enables nutrient-rich fine-grained sediment (silt) to accumulate on top of the coarse-grained substrate (Olff et al. 1997). Ultimately, the morphology of the marsh platform largely depends on these strong feedbacks between vegetation and tidally introduced sediment (Allen 2000, Temmerman et al. 2003a, Neumeier and Amos 2006b). With the incoming fine-grained sediment, nutrients accumulate on the marsh surface resulting in an increasing productivity as well as increasing surface elevation with age of the marsh (Olff et al. 1997). Local abiotic stress reduces and the pioneer vegetation gets replaced by later-successional species (Olff et al. 1997). Generally, when productivity continues to increase, mono-stands of the tall grass Sea couch, *Elytrigia atherica*, are formed and plant diversity becomes reduced (Gray and Bunce 1972, Olff et al. 1997, Veeneklaas et al. 2013).

A general theory in ecology is that either top-down or bottom-up control within plant-animal interactions changes with local productivity of an ecosystem (Hairston et al. 1960, Oksanen et al. 1981, Van De Koppel et al. 1996). At young successional stages, nutrient availability is still relatively low and limited biomass production results in low grazer abundance (Oksanen et al. 1981, Van De Koppel et al. 1996, Kuijper and Bakker 2005). Hence, grazer abundance is controlled bottom-up by limited primary production. With increasing age, both productivity and primary production increase resulting in marshes to become more suitable for a higher number of small grazers (Van De Koppel et al. 1996). At this point, grazers will control the local plant community top-down (Van Der Wal et al. 2000c). When nutrient availability and primary production increase further, palatable species get replaced by more tall and unpalatable plant species and herbivores are controlled bottom-up again due to low plant quality (Van De Koppel et al. 1996, Van Der Wal et al. 2000a). Only grazing by larger grazers (livestock) can bring back early-successional plant species and make marshes suitable for small grazers, such as hare and goose, again (Kuijper et al. 2008).

THESIS OUTLINE

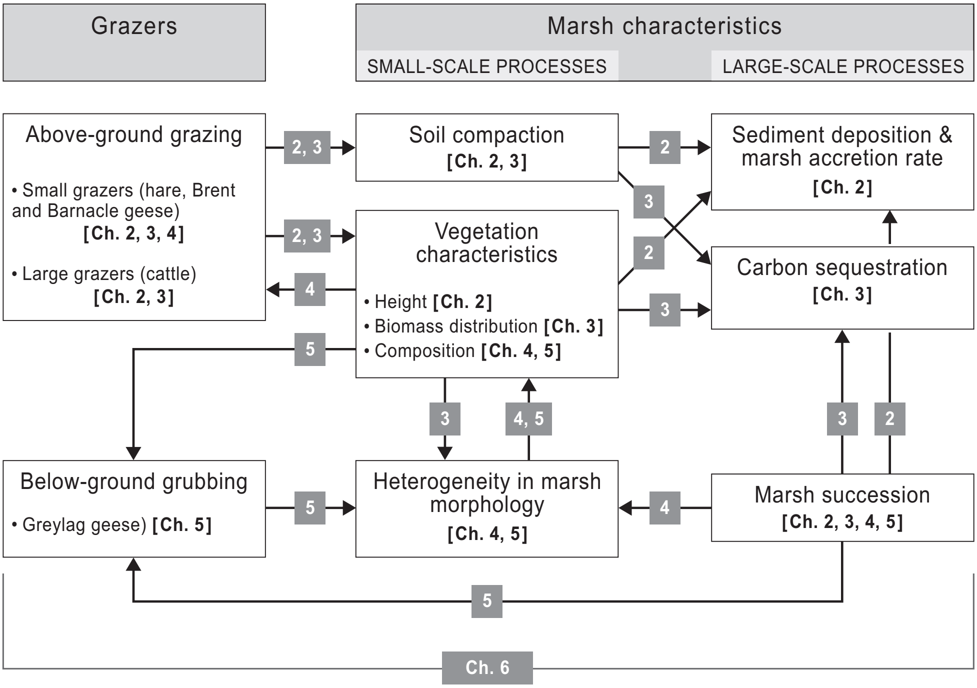

Figure 1.1. A schematic overview of the different interactions studied in this thesis. Numbers in the scheme represent the different chapters

In this study, I want to increase our general understanding of grazer- plant interactions and how they interact with their environment. I used long-term field experiments and long-term datasets to study the role of different grazer types in tidal marshes. I included: 1) below-ground grubbing by Greylag goose, 2) above-ground grazing by small grazers (Brent goose, *Branta bernicla*, Barnacle goose, *Branta leucopsis*, and hare, *Lepus europaeus*) and 3) above-ground grazing by large grazers (cattle). Additionally, I wanted to determine how heterogeneity in marsh morphology affects the presence of small grazers.

I divided this study in three main questions:

1. What is the effect of long-term, above-ground grazing on the local marsh vegetation, sediment accretion rates and carbon sequestration?
2. What is the effect of topographic heterogeneity on the local marsh vegetation and grazer presence?
3. What is the long-term effect of below-ground grubbing on the marsh vegetation and how this in turn affects grazer abundance?

These questions are introduced in detail in the following sections. Additionally, figure 1.1 gives a schematic overview of the different interactions studied in this thesis with the corresponding chapters.

1. **What is the effect of long-term, above-ground grazing on the local marsh vegetation, sediment accretion rates and carbon sequestration?**

Firstly, we focussed on the effects of above-ground grazing by small grazers and large grazers in a salt marsh. We determined how they affected salt-marsh accretion and carbon sequestration (**chapters 2 and 3**), using a long-term field experiment located on a back-barrier tidal marsh. Grazers have already been excluded for at least 16 years along a natural chronosequence present on Schiermonnikoog (NL), ranging from young (15 years old) to mature (120 years old) marshes. Along this chronosequence, small grazers (hare, Barnacle goose and Brent goose) were excluded on 15, 30, 45 and 55 yrs-old marshes. Large grazers (cattle) were excluded on the mature 120 yrs-old marsh (Kuijper and Bakker 2005).

In **chapter 2** we focussed on the effect of these grazers on vegetation height and marsh accretion rates. Due to global climate change, an accelerated sea-level rise is expected (Church and White 2011) and this poses a threat to coastal ecosystems, such as tidal marshes (FitzGerald et al. 2008). A sufficient marsh accretion rate will enable tidal marshes to keep up with an increasing sea level. Although many studies tried to estimate whether marshes are able to keep pace (Van Wijnen and Bakker 2001, Kirwan and Megonigal 2013), the impact of grazers on marsh accretion rates has received little attention so far. Tall and stiff vegetation is known to trap more tidally introduced sediment compared to short and/or more flexible vegetation (Peralta et al. 2008). When grazers reduce the vegetation height, this could negatively affect the marsh accretion rates (Neuhaus et al. 1999, Suchrow et al. 2012, Nolte et al. 2013c).

In **chapter 3** we used the same experimental set-up as in **chapter 2**. Here, we determined the effects of long-term grazing on carbon sequestration in tidal marshes. Several studies showed that marshes can sequester large amounts of carbon (Chmura et al. 2003, Mcleod et al. 2011, Kirwan and Mudd 2012). However, the impact of grazers has remained relatively unclear. Studies both showed positive (Yu and Chmura 2010) as well as negative (Morris and Jensen 1998) effects of grazers on carbon sequestration in marshes. We determined the impact of both small and large grazers on carbon accumulation. Additionally, we studied several abiotic conditions in the soil, such as bulk density and redox potential. Ultimately, we proposed a conceptual framework to clarify how grazers can impact carbon accumulation in ecosystems.

2. **What is the effect of topographic heterogeneity on the local marsh vegetation and grazer presence?**

In **chapter 4** we determined how small-scale topographic heterogeneity affects plant diversity and grazer abundance throughout long-term ecosystem development. Environmental heterogeneity can strongly boost plant diversity (Ricklefs 1977, Stein et al. 2014) and alter ecosystem functioning (Hooper et al. 2005). In several European marshes small-scale heterogeneity in the marsh morphology is described in literature (Gray and Bunce 1972, Allen 2000). However, how it is formed and its impact on plant diversity and grazer presence has remained unclear. In **box I** we studied the formation of these patterns using four different European marshes. As mentioned previously, studies conducted on homogeneous marsh showed that grazer presence increased with productivity of the marsh until an optimum was reached at marshes of intermediate productivity (Van De Koppel et al. 1996). Thereafter, the numbers of grazers decreased again. In **chapter 4** we determined whether the abundance of small grazers along the chronosequence was affected when small-scale topographic heterogeneity was present and how it impacted plant diversity.

3. **What is the long-term effect of below-ground grubbing on the local marsh vegetation and how this in turn affects grazer abundance?**

In **chapter 5** we studied the effects of below-ground grubbing by Greylag geese on plant composition and grazer abundance. By grubbing belowground for storage organs of the local vegetation, migratory geese can create bare patches in the marsh vegetation (Mclaren and Jefferies 2004). In extreme cases, they can even degrade large marsh areas (Jefferies et al. 2006, Peterson et al. 2013). In this chapter, we wanted to determine how bare patches created by Greylag geese regenerate and whether this top-down control by grubbing Greylag geese reduced their own abundance by reducing their food resources. We included different spatial scales, to estimate the importance of local-scale top-down control by herbivores (few square metres) vs. the landscape-scale bottom-up control by natural succession through marsh accretion (few square kilometres). We used a 40-year time-series of aerial photographs to study the regeneration of bare patches created by the grubbing greylag geese.

In **chapter 6** I summarized my main conclusions and how they fit with current knowledge in marsh ecology.

STUDY SITES

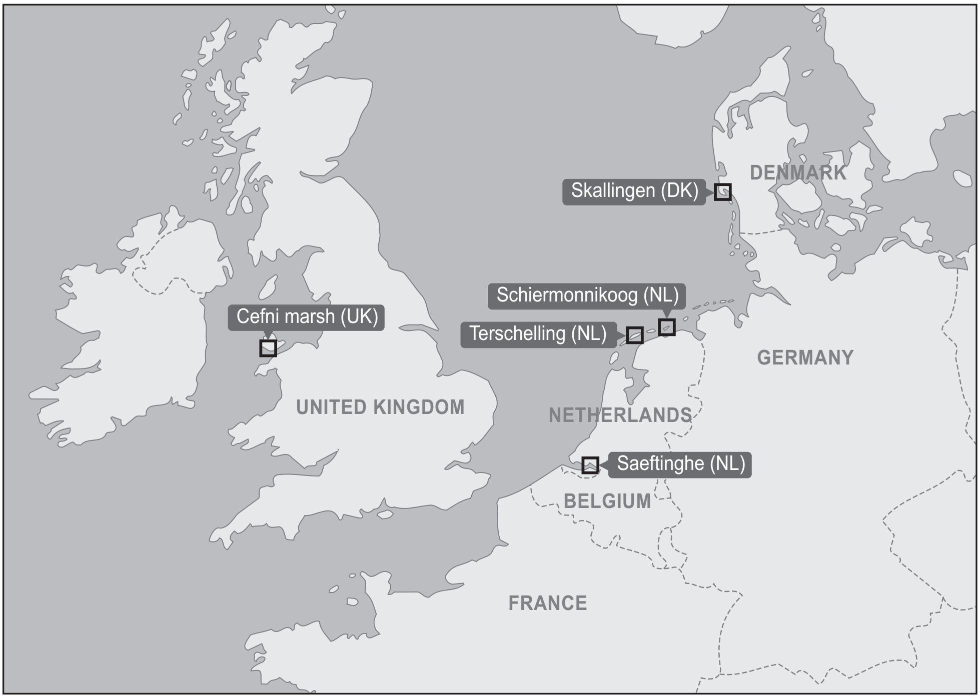

Figure 1.2. Five European tidal marshes (black squares) that were included in this thesis.

To answer the questions posed in this thesis, I needed to include five different marshes located along the North Sea and the Irish Sea (Fig. 1.2). These marshes were selected for their contrasting and unique features. All study sites feature small-scale patterns of topographic heterogeneity. Schiermonnikoog, harbours elevated hummocks on which hare and geese graze on above-ground plant parts. These hummocks alternate with lower elevated depressions. For reasons of generalization, these patterns were compared to marshes on Terschelling and Skallingen. To gain insight in the development of these hummocks, I studied a gradient of bare soil with hummocks located on the bare intertidal flat on the Cefni marsh in Wales. All these marshes were sandy with relatively low productivity. The marsh of Saeftinghe has a thick layer of fine-grained sediment and a high productivity. Large geese grub on below-ground plant parts in small bare patches. Long-term successional features, including the interaction between herbivores and vegetation, marsh accretion rate and carbon sequestration rate, could be derived from a natural chronosequence on the marsh of Schiermonnikoog. Aerial photographs of the marsh of Saeftinghe, allowed for the study of long-term interactions between herbivores and the marsh vegetation change. The study sites are discussed in more detail in the next section.

The island of **Schiermonnikoog** has a large back-barrier marsh (Fig. 1.2, 53°30'N, 6°10'E, 2.3 m tidal range) and is located in the Wadden Sea (The Netherlands, **chapters 2, 3 and 4**). Along the island a natural chronosequence exists, ranging from young (+ 15 years) marshes on the eastside of the island towards older (+ 120 years) marshes on the Westside of the island (Olff et al. 1997). This allowed me to study processes along a natural productivity and age gradient. In summer, only the oldest marshes in the west (185 ha) are grazed by cattle (Bos et al. 2002). The younger marshes in the east (1450 ha) have never been grazed by cattle, but are very important for small grazers. They are used for winter- and spring staging by several migratory birds such as Barnacle goose, *Branta leucopsis*, and Brent goose, *Branta bernicla*. Another important small grazer present on this marsh is the European brown hare, *Lepus europaeus*.

The **Cefni marsh** is an estuarine marsh located inside the Cefni Bay (Fig. 1.2, United Kingdom, 53°10'N, 4°23'W, with tidal range of 4.7 m). Due to continuous expansion from the south northward into the bay, a large pioneer zone is present in front of the Cefni marsh. Salt-marsh development only started since the 1960s (Packham and Liddle 1970). In the pioneer zone I studied higher elevated hummocks of varying sizes and heights, dominated by pioneer vegetation (**chapter 4**).

The island of **Terschelling** (The Netherlands, 53°26'N, 5°28'E, 2.0 m tidal range), and the peninsula of **Skallingen** (Denmark, 55°30'N, 8°20'E, tidal range of 1.3 m) were included as study sites (**Box 1**). I observed similar small-scale topographic heterogeneity as I studied on Schiermonnikoog and on the Cefni marsh (Fig. 1.2, **chapter 4**). Both Terschelling and Skallingen (Van Wijnen and Bakker 1997) have a back-barrier marsh. On both marshes I only used the cattle ungrazed marsh.

Saeftinghe (The Netherlands, **chapter 5**) is a large, high productive brackish marsh located in the Western Scheldt estuary (Fig. 1.2, 51°21'N, 4°11'E). Tidal range is estimated between 4 and 5 m (Temmerman et al. 2004). It is the largest marsh in Western Europe, approximately 2800 ha in size, and is an important feeding habitat for a large population of Greylag goose, *Anser anser*. A small part near the seawall is grazed by cattle, but the largest part is ungrazed by large herbivores. Only since the 1980s has this area become an important staging site for Greylag geese. Goose numbers have been increasing rapidly until about 2000, but thereafter a decrease in population size has been recorded (Castelijns et al. 1998, Castelijns and Jacobusse 2010). The geese grub below ground for storage organs of preferably Sea club-rush *Bolboschoenus maritimus* and Common cordgrass *Spartina anglica* (Amat 1995, Esselink et al. 1997, Bakker et al. 1999). By grubbing they create large bare and degraded patches that may take decades to recover (Mclaren and Jefferies 2004). I studied the dynamic of these patches using aerial photographs since the 1980s. All scientific names for the marsh' flora used in this thesis follow Van der Meijden (2005).

2

Effects of long-term grazing on sediment deposition and salt-marsh accretion rates

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Published as:
Elschot K, Bouma TJ, Temmerman S & Bakker JP (2013)
Effects of long-term grazing on sediment deposition and salt-marsh accretion rates.
Estuarine, Coastal and Shelf Science 133:109-115.

ABSTRACT

Many studies have tried to predict whether coastal marshes will be able to keep up with future acceleration of sea-level rise by estimating marsh accretion rates. However, the number of studies focussing on the long-term effects of herbivores on vegetation structure and subsequent effects on marsh accretion has been limited. Deposition of fine-grained, mineral sediment during tidal inundations, together with organic matter accumulation from the local vegetation, positively affects accretion rates of marsh surfaces. Tall vegetation can enhance sediment deposition by reducing current flow and wave action. Herbivores shorten vegetation height and this could potentially reduce sediment deposition. In this study, we estimated the effects of herbivores on *i*) vegetation height, *ii*) sediment deposition and *iii*) resulting marsh accretion after long-term (at least 16 years) herbivore exclusion of both small (*i.e.* hare and goose) and large grazers (*i.e.* cattle) for marshes of different ages. Firstly, our results showed that both small and large herbivores can have a major impact on vegetation height. Secondly, grazing processes did not affect sediment deposition. Finally, trampling by large grazers affected marsh accretion rates by compacting the soil. In many European marshes, grazing is used as a tool in nature management as well as for agricultural purposes. Thus, we propose soil compaction by large grazers should be taken in account when estimating the ability of coastal systems to cope with an accelerating sea-level rise.

INTRODUCTION

Global climate change threatens many different ecosystems and human habitats worldwide (Warren et al., 2010). One of the most striking and evident threats concerns the effect of accelerating rates of sea-level rise (Woodworth et al., 2011), which could cause flooding of many coastal habitats in the nearby future (FitzGerald et al., 2008). Coastal habitats, such as tidal marshes, provide many important ecosystem services including coastal protection of inland areas against tidal and storm-surge flooding (Costanza et al., 2008; Gedan et al., 2010; Temmerman et al., 2012b) and staging sites for migrating waterfowl (Madsen et al., 1999). Tidal marshes accumulate fine-grained, mineral sediment thereby enhancing marsh accretion rates, which in turn may enable marshes to keep pace with accelerating sea-level rise (Cahoon and Reed, 1995; Kirwan and Temmerman, 2009; Stralberg et al., 2011). However, previous studies assessing the ability of marshes to keep up with accelerating sea-level rise found contradicting results. Some marshes have been predicted to become submerged (Bakker et al., 1993; van Wijnen and Bakker, 2001; Kirwan and Temmerman, 2009; Kirwan et al., 2010; Stralberg et al., 2011), whereas other marshes have been predicted to be able to keep pace with the accelerating sea-level rise (Bakker et al., 1993; Neuhaus et al., 1999; Morris et al., 2002; Temmerman et al., 2004). So far, the main focuses have been on abiotic controls of marsh accretion rates and the effects of local vegetation on sediment deposition, whereas indirect effects by grazers on the sedimentation process have received much less attention (with exceptions of Andresen et al., 1990, Neuhaus et al., 1999, Suchrow et al., 2012).

Important processes affecting accretion rates of tidal marshes identified so far include: tidal-driven deposition of mineral sediment that was suspended in the water column on the marsh surface (especially silt and clay); organic matter accumulation (from local vegetation); erosion; and auto-compaction of the soil sediment (Cahoon et al., 2006). Both deposition of mineral sediment and organic matter accumulation can enhance marsh accretion (Day et al., 2011; Suchrow et al., 2012) and are influenced by marsh vegetation. Firstly, aboveground vegetation can positively affect sediment deposition (Mudd et al., 2010; Day et al., 2011). As inundating water flows over the marsh surface, the vegetation offers resistance and reduces velocity of the tidal current (Christiansen et al., 2000; Neumeier and Amos, 2006a, 2006b; Temmerman et al., 2012a), thereby enhancing the settling of suspended sediment from the water column onto the marsh surface (Mudd et al., 2010). Tall, stiff vegetation can decrease current velocities more efficiently, which can result in a more positive effect on sediment deposition (Peralta et al., 2008). Secondly, belowground roots form an important part of the organic matter accumulating in the soil (Nyman et al., 2006; Neubauer, 2008). With respect to processes that reduce accretion rates, erosion is generally not significant in marshes because the aboveground vegetation canopy diminishes flow velocities and belowground roots consolidate sediment, thus increasing their resistance to disturbance (*e.g.* Howes et al., 2010). However, auto-compaction of the deposited sediment can be a significant process that reduces marsh accretion rates. Thick layers of fine-grained sediments on older marshes can auto-compact due to age, weight and drought (Cahoon et al., 1995, 2011; Allen, 2000; Bartholdy et al., 2010).

As mentioned previously, presence of vegetation on the marsh can enhance sediment accretion rates and this will positively affect the ability of marshes to keep pace with the accelerating rate of sea-level rise. When grazers are present in a system, they generally change vegetation structure, most notably reducing vegetation height (Bakker, 1989; Andresen et al., 1990; Bos et al., 2002). There are many different grazers present on marshes ranging from small (*e.g.* hare and different goose species) (Madsen et al., 1999; van der Wal et al., 2000b) to large species (*e.g.* cattle and sheep). Livestock are used for nature management practices as well as for agricultural purposes (Bakker, 1989; Kiehl et al., 1996). By grazing, herbivores can create short dense 'grazing lawns' consisting of short highly palatable vegetation (Bos et al., 2002, 2004). This could negatively impact sediment deposition as the grazers remove the tall vegetation needed to reduce current velocities so that suspended sediment can settle on the marsh surface. Additionally, grazing has been shown to alter the grain size of particles found at the local scale (Yang et al., 2008).

In this study, we quantified the effects of grazers on *i*) vegetation height, *ii*) sediment deposition and iii) resulting marsh accretion rates. To achieve this, we compared plots that had been grazed over the long term with those that had been excluded from grazing by either small herbivores (*i.e.* hares and geese; 16 years of exclusion using wire mesh exclosures) or large herbivores (*i.e.* cattle; 22 years). Ultimately, we want to test two hypotheses: 1) Grazing by both small and large herbivores will shorten vegetation height, thereby reducing rates of sediment deposition; 2) Large herbivores will compact the soil by trampling, thereby reducing marsh accretion rates.

MATERIALS AND METHODS

Definition of terms

For clarification purposes, we will first define the terms used in this paper. For sediment characteristics, we used similar terms as those defined in a review by Nolte et al., (2013), who in turn adapted most of their terminology from Cahoon et al., (1995) and Van Wijnen and Bakker (2001). The terms commonly used in this paper are sediment deposition, total deposited sediment, fine-grained sediment layer thickness, (auto-) compaction, bulk density and marsh accretion rate. Marsh formation starts when pioneer vegetation establishes on a coarse-grained sandy plain (hereafter referred to as the base elevation) and fine-grained sediment is slowly deposited on the marsh surface (hereafter referred to as sediment deposition (g cm^{-2})). Total deposited sediment (g cm^{-2}) is used to refer to all the sediment accumulated on the marsh surface since marsh formation. The thickness of the layer containing sediment deposited since marsh formation is referred to as the fine-grained sediment layer thickness (cm). Increasing age and thickness of the layer will generally result in auto-compaction. Under the influence of its own weight, the bulk density (g cm^{-3}) will increase and the fine-grained sediment layer will decrease in thickness. Ultimately, a combination of total deposited sediment, compaction of the sediment and root material added from the local vegetation will determine the marsh accretion rate (increase in surface elevation in mm yr^{-1}). It is this accretion rate which determines whether a marsh can keep up with accelerating rates of sea-level rise.

Study site

This study was carried out on the back-barrier marsh of the island of Schiermonnikoog located in the Dutch Wadden Sea (Fig. 2.1, 53°30'N, 6°10'E). Tidal range is approximately 2.3 m and extreme high tides (*i.e.* tides reaching higher than 1.3 m above MHT) occur approximately 5 times each year. This back-barrier marsh was formed when large dune formation prevented the bare sand flat behind them from being frequently inundated by tidal water from the North Sea and daily inundations only continued from the gentler waters from the south side of the island. This reduction in the current velocities of the inundating water allowed pioneer vegetation to establish on the bare sand flat and fine-

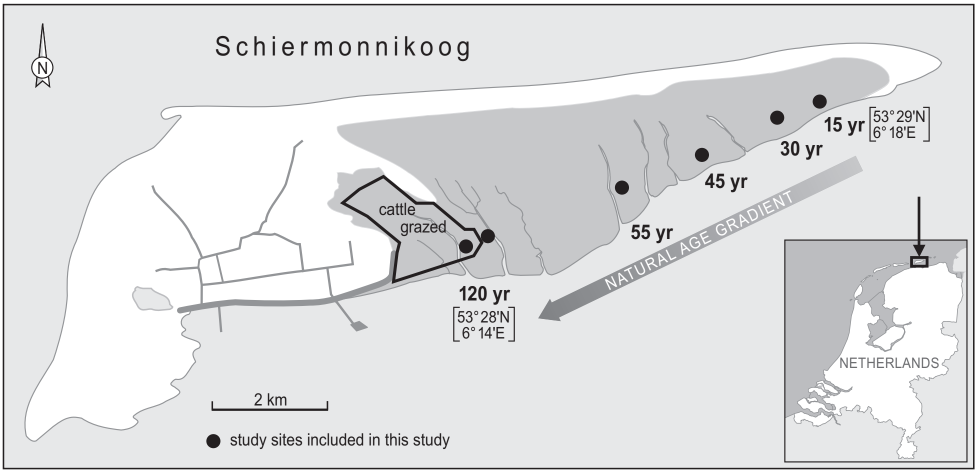

Figure 2.1. A map is shown of the eastern part of the back-barrier marsh of Schiermonnikoog (grey area), including the natural successional gradient. Each study site is indicated with a black dot, representing an exclosure and approximate age of the site is shown. The most western marshes are grazed by cattle (indicated with the black line) and the eastern marshes are only grazed by hares and geese.

grained sediment to be deposited on the marsh surface (Olff et al., 1997). Changing sea currents caused the island to extend eastward, resulting in a natural successional gradient ranging from older marshes in the west to younger marshes in the east (Olff et al., 1997). The marsh soils consist of a relatively thin fine-grained sediment layer containing silt and sand deposited on top of the sandy substrate. The thickness of this fine-grained sediment layer ranges from 7 cm in the 15-year-old marsh to 15-20 cm in the 120-year-old marsh. A clear transition between coarse- and fine-grained sediment allowed us to collect and identify the entire fine-grained sediment layer which had accumulated since the beginning of marsh development.

The most western and oldest marshes (185 ha, about 120 years old) are grazed by cattle in summer with a stocking rate of approximately 0.5 individual per ha (Bos et al., 2002). These marshes were grazed until 1958, ungrazed between 1958 and 1988, and partly grazed again thereafter. The more eastern, younger marshes (1450 ha) have never been grazed by cattle and have remained relatively undisturbed by human impact. As a winter- and spring-staging area, Schiermonnikoog is important for many different migratory birds such as Barnacle (*Branta leucopsis*) and Brent geese (*Branta bernicla*). In addition to these two geese species, the brown hare (*Lepus europaeu*) is the third important small herbivore present on Schiermonnikoog. In contrast to the migratory geese, hares graze on the salt marsh for the entire year. The highest grazing intensity by geese and hares is found at marshes of intermediate age (about 30 years) (van de Koppel et al., 1996), where the density of highly nutritious plant species is highest (Olff et al., 1997). Higher productivity ultimately results in a homogeneous cover of a tall stiff grass species, *Elytrigia atherica*, on the high marsh and a tall shrub, *Atriplex portulacoides*, on the low marsh (Olff et al., 1997). Both species are relatively unpalatable and the small grazers are evicted by succession (van der Wal et al., 2000a).

Experimental set-up

Along the natural succession gradient, four sites which differ in age and productivity (Olff et al., 1997) were selected to study the effect of small grazers on vegetation height and sediment deposition. On these sites, exclosures (6 m × 6 m) were set-up in 1994, which excluded grazing by both hares and geese. Each exclosure consisted of wire mesh on the sides (approximately 1 m high) to prevent geese and hares from entering the exclosures from the side and ropes crossed over the exclosures to prevent geese from flying in (for further details see Kuijper and Bakker 2005). The age of each site was calculated from the first establishment of vegetation using a time series of aerial photographs by Olff et al., (1997). We assumed that once vegetation had established, fine-grained sediment started accumulating on the marsh surface. In 2010, the respective ages for each of the study sites were approximately 15, 30, 45 and 55 years (for further details see Olff et al., 1997). Note that exclosures had been set-up at the youngest site when the marsh was still at the pioneer stage. The exclosures were located at base elevations of 20 ± 2, 33 ± 3, 39 ± 1 and 21 ± 1 cm above MHT at respectively for the 15-, 30-, 45- and 55-year-old marshes. Control plots were set up at least 10 m from the exclosure at similar base elevations.

To study the effect of large grazers, a fifth site was selected on the edge of the cattle-grazed area, which was approximately 120 years old. Sediment samples were taken on both sides of the cattle fence at a base elevation of 40 ± 1 cm above MHT. This set-up allowed us to determine the effects of both small and large grazers, although historical constraints necessitated an unbalanced experimental design: with or without small grazers at the 15-, 30-, 45- and 55-year-old marshes and with or without large grazers at the 120-year-old marsh.

Vegetation height and herbivore pressure

Vegetation height was estimated in July 2012 by dropping a foam disk (diameter = 40 cm) surrounding a vertical ruler onto the vegetation from a specific height (Stewart et al., 2001). Height of the vegetation was estimated to the nearest centimetre on the vertical ruler that the disk came to rest on top of the vegetation. We randomly dropped the disk ten times inside and outside each exclosure. Stewart et al., (2001) concluded this method is appropriate when estimating the effects of vertebrate grazing in medium-tall swards.

As a measure of grazing pressure, we estimated the number of droppings of both hares and geese per 4m^2 plot at each study site in November 2010. Sample size ranged between 15 and 30 plots per site. These measurements were taken ten days after an extreme high tide that had flushed away all old droppings. Counting the number of droppings is a good method to estimate herbivore pressure for both geese (Owen, 1971) and hares (Langbein et al., 1999).

Soil properties

In June 2010, we sampled ten cores per site (diameter 10 cm) containing the entire fine-grained sediment layer. Of these ten cores, five were taken inside and five outside the exclosures. The thickest fine-grained sediment layer found was 17 cm. Length of the sampled core was compared with the depth of the hole left in the soil surface to exclude samples that had been compacted during sampling. To collect the cores, a Tullgren soil corer was used allowing us to sample with minimal compaction (Van Straalen and Rijninks 1982). If compaction was more than 0.5 cm, the core was discarded and a new one was taken. The total fine-grained sediment layer thickness was estimated at the same locations as the cores for the soil samples. We took the mean of four replicate measurements with a smaller soil corer (gouge type with diameter = 1 cm).

Lab analyses

From each collected core, two slices of 5 cm were taken to determine bulk density (g cm^{-3}); one each from the top and deeper part of the fine-grained sediment layer. Due to a limited fine-grained sediment layer thickness of approximately 7 cm at the youngest site, only the top layer could be sampled. The first 0.5 cm of each core was discarded to avoid samples containing very high root density. To avoid contamination of the fine-grained sediment with coarser sandy sediment, the bottom few centimetres near the underlying sandy substrate were also not used for analysis. Additionally, we avoided sampling locally occurring thin sand-layer incursions (generally of a few millimetres thick) within the fine-grained sediment layer, which had been created by wash-overs during storms (de Groot et al., 2011; Rodriquez et al., 2013). From each slice, four smaller sub-cores (diameter = 2.1 cm) were taken, which were weighed and freeze dried. Dry bulk densities of the sediment were determined by taking the mean value of all four sub-cores. Of the four sub-cores, one was chosen randomly to use for particle size analysis. All roots greater than 1mm were removed from the sample using a 1 mm sieve. Samples were analyzed using laser diffraction with a Malvern mastersizer (model APA 2000). Detection range is between 0.02 and 1000 µm.

Data analyses

Effects of small grazers and large grazers were analyzed separately due to the unbalanced design of this study (+/- small grazers at 4 young sites and +/- large grazers at the oldest site). Effects of marsh age on different vegetation and sediment characteristics were analyzed with ANOVAs using both site and grazing as categorical explanatory variables. If the interaction effect was not significant, we simplified the model by removing the interaction effect. Following the ANOVAs, differences within each site were tested with Tukey-tests. Effects of large grazers on the oldest site were tested with t-tests. If necessary, data were transformed when either variance was unequal or data were not normally distributed. All data were analyzed using R, version 2.13.0 (R Development Core Team 2011).

RESULTS

Grazing intensity, vegetation height and soil properties along the age gradient

Dropping counts (m^{-2}) of both hares and geese showed highest grazing intensity at sites of intermediate age (Fig. 2.2). Hares showed an optimum at the 30-year-old marsh while geese showed an optimum at the 45- and 55-year-old marshes. The vegetation height (Fig. 2.3A) and total deposited fine-grained sediment (g cm^{-2}) on the marsh surface (Fig. 2.3B) were significantly different between study sites and increased with age of the marsh (statistics are shown in Table 2.1). Meanwhile, bulk density (g cm^{-3}) decreased with age in both the top and lower soil layers (Fig. 2.3C and D). The fine-grained sediment layer thickness (cm) (Fig. 2.3E) increased with age, while particle size in the top layer did not change with age of the marsh (Fig. 2.3F). Particle size did differ significantly between sites but no clear trend is shown along the age gradient (Fig. 2.3F).

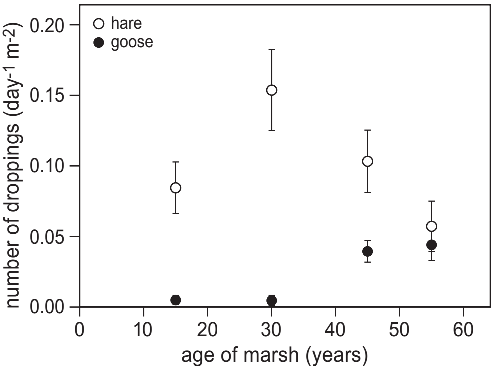

Figure 2.2. Herbivore activity (droppings day^{-1} m^{-2}) estimated in November 2010. Activity of both geese and hares are shown along the natural age gradient.

Table 2.1. Results of statistical tests of vegetation and sedimentation characteristics inside and outside exclosures. Along the successional gradient, small grazers were excluded and analyzed with ANOVAs, using age and grazing as categorical predictor variables. To simplify the model, the interaction effects were removed when they were not significant. Large grazers were excluded on the 120-year-old marsh and the response variables were analyzed using two tailed t-tests. Percentage particles < 63 µm are shown for only the top 5 cm of the fine-grained sediment layer. P < 0.05 is considered significant and indicated in bold.

	Small grazers			**Large grazers**
	Age	Grazing	Age*grazing	Grazing
Vegetation height	**$F_{(3,72)} = 7.78$** **$p < 0.001$**	**$F_{(1,72)} = 7.39$** **$p < 0.01$**	**$F_{(3,72)} = 5.10$** **$p < 0.01$**	**$t_{(11.6)} = 10.58$** **$p < 0.001$**
Total sediment accumulated	**$F_{(3,35)} = 53.07$** **$p < 0.001$**	$F_{(1,35)} = 0.03$ $p = 0.87$	n.s.*	$t_{(8.0)} = 1.78$ $p = 0.11$
Fine-grained sediment layer thickness	**$F_{(3,35)} = 105.80$** **$p < 0.001$**	$F_{(1,35)} = 0.08$ $p = 0.78$	n.s.*	**$t_{(7.2)} = -2.54$** **$p = 0.04$**
Bulk density layer 0.5-5.5 cm	**$F_{(3,35)} = 23.94$** **$p < 0.001$**	$F_{(1,35)} = 3.00$ $p = 0.09$	n.s.*	**$t_{(6.4)} = 7.00$** **$p < 0.001$**
Bulk density layer 5.5-10.5 cm	**$F_{(2,26)} = 26.67$** **$p < 0.001$**	$F_{(1,26)} = 2.62$ $p = 0.12$	n.s.*	$t_{(6.9)} = -0.35$ $p = 0.74$
Percentage particles <63µm	**$F_{(3,32)} = 6.28$** **$p < 0.01$**	$F_{(1,32)} = 1.07$ $p = 0.31$	**$F_{(3,32)} = 5.24$** **$p < 0.01$**	**$t_{(6.0)} = -11.27$** **$p < 0.001$**

*n.s. = not significant

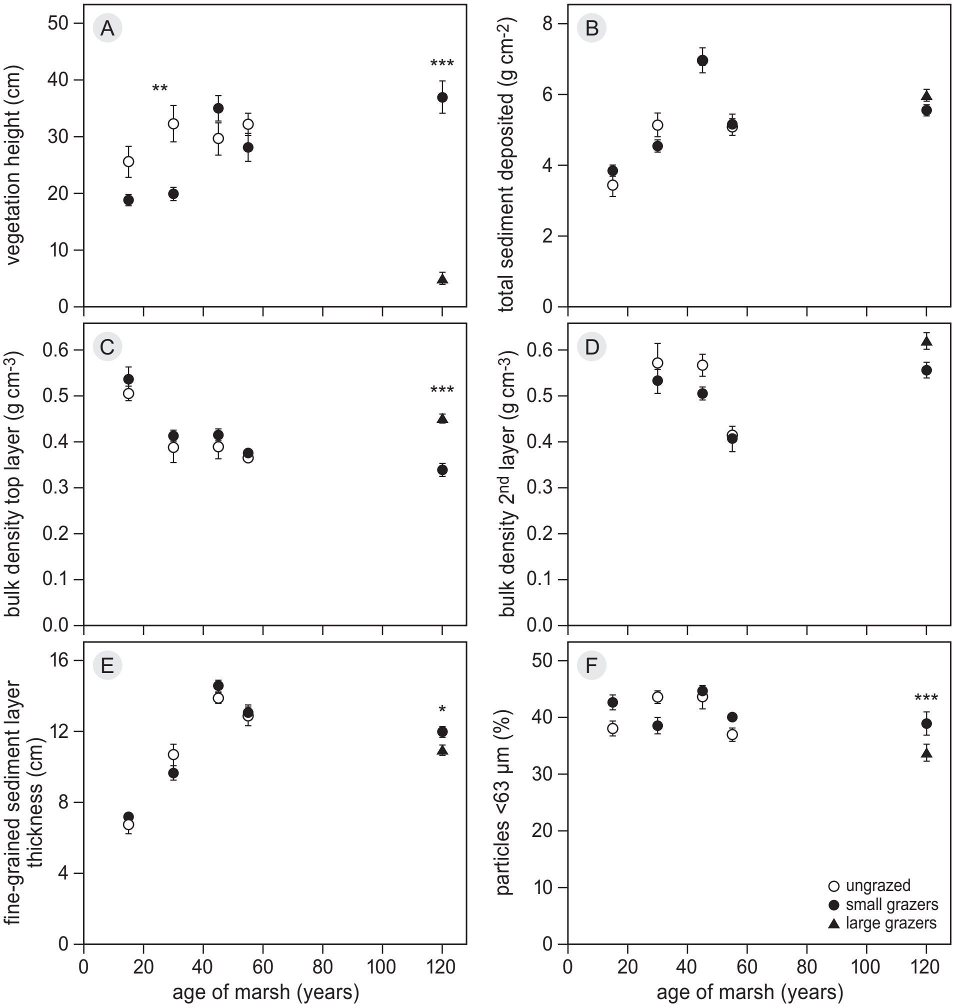

Figure 2.3. Differences in vegetation height and soil properties estimated inside and outside the exclosures along the successional gradient. In marshes between 15 and 55 years of age, small grazers have been excluded for 16 years; in the 120-year-old marsh, large grazers have been excluded for 22 years. Significant differences per site are shown by: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Effects of small grazers on vegetation height and soil properties

Presence of small grazers significantly decreased vegetation height at the 30-year-old site from 32.3 ± 3.2 to 19.9 ± 1.17 cm (Fig. 2.3A). However, grazing did not affect any sediment or soil property estimated in this study (Fig. 2.3B-2.3F, statistics are shown in table 2.1). Sixteen years of excluding small grazers did not significantly change the amount of deposited sediment (Fig. 2.3B), dry bulk densities in top or deeper fine-grained sediment layer (Fig. 2.3C and D), fine-grained sediment layer thickness (Fig. 2.3E) or particle size of the deposited sediment (Fig. 2.3F). Even at the youngest marsh site of approximately 15 years of age, where both treatments had been present since marsh formation, no significant effect of small grazers was found. We did find a significant interaction effect between site and grazing for particle size, but there was no clear trend and grazing in 15-year-old marsh showed the opposite effect from that in the 30-year-old marsh (Fig. 2.3F).

Effects of large grazers on vegetation height and soil properties

Even though we found large, significant differences between vegetation height in the cattle-grazed (5.0 ± 1.1 cm) and ungrazed marsh (37.0 ± 2.8 cm) (Fig. 2.3A), sediment deposition was not affected. Cattle presence did, however, significantly increase bulk density in the top layer from 0.33 ± 0.03 to 0.45 ± 0.01 g cm^{-3}, but not in the deeper layer (Fig. 2.3C and D). This resulted in a significant decrease in the fine-grained sediment layer thickness (Fig. 2.3E) from 12.0 ± 0.3 to 11.0 ± 0.2 cm. Furthermore, we found significant differences in the particle size of the deposited sediment inside and outside the cattle-grazed marsh (Fig. 2.3F). Marsh sediments in ungrazed plots contained a higher percentage of small particles.

DISCUSSION

Based on our results, we reject the first hypothesis because we did not find any effect of grazer presence on sediment deposition even though vegetation height was reduced by grazers. We accept the second hypothesis as large grazers compacted the soil, which resulted in a reduced accretion rate.

Effects of vegetation on sedimentation

Our results indicate that grazing, despite having a significant effect on vegetation height, had no effect on sediment deposition. Most previous studies showed a positive effect of vegetation on sediment deposition (Pont et al., 2002; Bouma et al., 2007; Peralta et al., 2008; Mudd et al., 2010; Suchrow et al., 2012; Baustian et al., 2012), although a few studies also reported no effect (Brown et al., 1998) or even higher sediment deposition in unvegetated marsh sites compared to vegetated ones (Silva et al., 2008). These contradictory results imply that effects may be complex and contingent on the timing of sampling as well as the location. For example, the main source of mineral sediment deposition may be from tidal inundations, storm flooding or a combination of both, depending on the site-specific tidal range and wind climate. If sediment deposition is dominated by storms and very high tides (French and Spencer, 1993; Cahoon, 2006; Neumeier and Amos, 2006b; Silva et al., 2008; Coulombier et al., 2012), vegetation structure may have limited impact because the vegetation is too deeply inundated under these circumstances to affect current velocities and thus sediment deposition. Furthermore, during the deep flooding of storms, wave energy may be too strong to be affected by the local vegetation structure. Vegetation structure may play a more important role in marshes with high sediment deposition during regular, shallower tidal inundations (Pont et al., 2002; Mudd et al., 2010). In addition, other studies have shown that spatial variations in sediment deposition are less well explained by vegetation structure than by topographic variables, such as marsh surface elevation relative to mean high tide (*e.g.* Coulombier et al., 2012, Suchrow et al., 2012) and distance from mudflat or creek edge (Temmerman et al., 2003). A study by Neumeier and Ciavola (2004) also predicted that effects of vegetation on sediment deposition could be marginal, which is in line with the results found in this study.

Previous studies estimating the effects of grazer presence on marshes have already shown that grazing can affect sediment deposition positively (Neuhaus et al., 1999) as well as negatively (Andresen et al., 1990). Suchrow et al., (2012) showed that sheep grazing in German marshes negatively affected sediment deposition in the high marsh but positively affected sediment deposition on the low marsh. Thus, effects of grazing can be location specific even within a marsh. Even though sediment deposition was not affected in this study, we did find a significant difference in particle size between the cattle-grazed and ungrazed marsh (Fig. 2.3F). However, when we expanded our focus to include all five sites in this study, we can conclude that particle size was very location specific and was unrelated to grazer presence. Several studies have shown that the main episodes of sediment deposition on many marshes occur during storms and high tides in winter (French and Spencer, 1993; Temmerman et al., 2003; Cahoon, 2006; Silva et al., 2008). As vegetation lays relatively flat on the marsh surface during winter, effects of herbivore presence on vegetation height might not translate into a significant effect on total sedimentation deposition in these marshes.

Effects of grazers on marsh accretion

In the present study, we showed that presence of large grazers (cattle) increased bulk density of the sediment (Fig. 2.3), thus reducing marsh accretion rates. In contrast to our expectations, we found a decreasing bulk density in the top as well as the deeper sediment layer with age of the marsh, which likely resulted from increasing root mass build up as vegetation develops (Van Wijnen and Bakker, 2000). However, when we focus on the marshes of 55 and 120 years old, we find an increase in bulk density again due to auto-compaction in the deeper layer. Additionally, at the 120-year-old marsh, we did not find a significant difference between the deeper sediment layers in the grazed or ungrazed sites, but only in the top layer, which is likely due to a trampling effect. This trampling effect by grazers has been largely neglected in literature so far, but could have a major impact on the long-term survival of marshes relative to sea-level rise. Back-barrier marshes generally have limited sediment deposition (van Wijnen and Bakker, 1997) and thin fine-grained sediment layers will constrain the compaction effect of large grazers. However, marshes with thicker fine-grained sediment layers could be more affected and compaction by grazers should be taken in account when predicting their ability to keep pace with sea-level rise.

Implications for management

Presence of either small or large grazers could strongly reduce vegetation height but this did not have an effect on sediment deposition in this marsh. Presence of small grazers did not affect the long-term marsh accretion rates. In contrast, compaction of the soil by large grazers and subsequent reduced rates of accretion could diminish the long-term ability of marshes to keep up with sea-level rise. Cattle and sheep grazing on European marshes is a widely used management tool to enhance local plant diversity and retard succession (Bakker, 1989; Dijkema, 1990; Kiehl et al., 1996; Bouchard et al., 2003). The practice of using cattle and sheep grazing for nature management as well as for agricultural purposes might need to be re-assessed for individual marshes in order to ensure that the ability of marshes to keep up with sea-level rise is not decreased. Such marshes might be at risk of drowning and will be lost if we keep high stocking densities of large grazers on these marshes. However, whether this happens will ultimately depend on the local supply of suspended sediments as well as the local rate of relative sea-level rise. As long as the sediment supply is high enough so that accretion rates can stay higher than the rate of sea-level rise, presence of large grazers should not pose a problem.

ACKNOWLEDGEMENTS

First of all, we would like to thank Harm van Wijnen and René van der Wal for installing the exclosures in 1994; *Natuurmonumenten* for assistance in the field and the opportunity to work on the salt marshes of Schiermonnikoog; Dick Visser for preparing graphs; Elske Koppenaal for assistance in the field; Esther Chang for editing this manuscript and Jesper Bartholdy together with an anonymous reviewer for useful comments on this manuscript. This study was funded by the NWO-ZKO project 83908320 (the Dutch Organization for Scientific Research).

3

Experimental evidence for top-down control of carbon stocks in a tidal salt marsh

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In revision for Marine Ecology Progress Series

ABSTRACT

Grazers can have a large impact on ecosystem processes and are known to exert top-down control upon vegetation composition. However, knowledge of how long-term presence of grazers affects soil carbon sequestration is limited. In this study, we estimated total accumulated organic carbon in soils of a back-barrier salt marsh, and determined how this is affected by long-term grazing by both small and large grazers in relation to age of the ecosystem. In young marshes, where small grazers predominate, hare and geese have a limited effect on total accumulated organic carbon. In older mature marshes, where large grazers predominate, cattle enhanced carbon content in the marsh soil substantially, due to soil compaction and a shift in biomass distribution in the local vegetation towards the roots. By compacting the soil, large grazers enhanced anoxic conditions thereby reducing the oxygen available for organic carbon decomposition by the local microbial community. This study showed that the indirect effects of grazing, through changing soil abiotic conditions, can significantly enhance soil carbon storage. This process should be taken into account when estimating the role of ecosystems in reducing CO_2 concentration in the atmosphere. Ultimately, we propose a testable conceptual framework that includes three pathways of how grazers can exert top-down control on carbon storage: through 1) aboveground biomass removal, 2) alteration of biomass distribution towards the roots and/or 3) by changing soil abiotic conditions that affect decomposition.

INTRODUCTION

The rapid increase in atmospheric CO2 concentration may to some extent be counteracted by carbon sequestration in natural ecosystems (Cannell et al. 1999, Janzen 2004, Le Quéré et al. 2009). Wetlands, including coastal marshes, can play an important role as carbon sinks, because of close feedbacks between vegetation, sedimentation and anoxic conditions promoting carbon storage (Valery et al. 2004, Duarte et al. 2005, Olsen et al. 2011, Kirwan and Mudd 2012). Once present in the soil, organic carbon can remain buried for a very long time (Connor et al. 2001, Chmura et al. 2003, Duarte et al. 2005, Mcleod et al. 2011). Several studies show that coastal ecosystems, such as tidal marshes, can accumulate a large amount of carbon (Chmura et al. 2003, Duarte et al. 2005, Laffoley and Grimsditch 2009, Mcleod et al. 2011). So far, studies assessing the role of marshes as carbon sinks have mainly focused on abiotic drivers, including sedimentation rate and global warming (Connor et al. 2001, Kirwan and Mudd 2012, Saintilan et al. 2013, Lovelock et al. 2013), whereas biotic drivers, such as grazer presence, have received much less attention (with exceptions of e.g., Morris & Jensen 1998, Yu & Chmura 2010, Olsen et al. 2011).

Marshes are used as feeding grounds by many different grazers ranging from large populations of migratory birds (e.g., Kerbes et al. 1990, Madsen 1991) to livestock grazing, which is used as a nature management tool in many European marshes (e.g., Bakker 1989, Kiehl et al. 1996). Grazers can have a large impact on local carbon sequestration in marshes, but results found so far have been limited and contradictory. For example, in some marshes they decreased organic carbon accumulation by removing above-ground biomass and thus reducing litter production (Morris and Jensen 1998). In other marshes they positively affected organic carbon accumulation by increasing below-ground biomass production (Yu and Chmura 2010, Olsen et al. 2011) and/or reducing turnover rates (Olsen et al. 2011). Grazing may even turn a marsh from a carbon sink into a carbon source (Taylor and Allanson 1993). These contradictory results suggest that effects of grazers on organic carbon sequestration can differ between systems and/or grazer type, and requires further study before getting to a general mechanistic understanding.

In the present study, we quantified total accumulated organic carbon during marsh development in a northwest-European back-barrier marsh (Schiermonnikoog) dominated by fine-grained sediment accretion (detailed description in methods). This back-barrier marsh gives us the unique opportunity to study processes over a long time scale due to gradual expansion of the marsh towards the east; resulting in a natural chronosequence (i.e., from 15 to 120-yrs-old marsh) ranging from east to west (Olff et al. 1997). The younger marshes are used by small grazers as feeding grounds, with highest grazing intensity at approximately 30-yrs-old marsh (Van De Koppel et al. 1996, Elschot et al. 2013). The older, most western marshes are grazed by livestock. Previous studies showed that when marshes become older, palatable plant species slowly get replaced by unpalatable ones (Leendertse et al. 1997, Veeneklaas et al. 2013) and the number of small grazers present within the ecosystem reduces (Van Der Wal et al. 2000b, Bos et al. 2004). At this stage, larger grazers become necessary to set back succession (Bos et al. 2002).

On the younger marshes of Schiermonnikoog, small grazers have been excluded from experimental plots for about 15 years, whereas on the oldest mature marsh livestock have been excluded for about 20 years from part of the marsh. The clear gradients in age and grazing type (i.e., small vs. large grazers) as well as long-term exclosure experiments present in the marsh, offer an excellent opportunity to quantify the effects of long-term grazing by both small and large grazers on carbon sequestration. Previous studies showed that grazing will not only reduce above-ground biomass but it can also increase bulk density of the soil layer by trampling (Elschot et al. 2013, Nolte et al. 2013c) thereby promoting anoxic conditions (Schrama et al. 2013a). Anoxic conditions in the soil are known to reduce the mineralization rate (Aller 1994, Sun et al. 2002, First and Hollibaugh 2010). Thus, in this study we included not only the effects of grazing on biomass of the local vegetation, but also studied the impact on local abiotic conditions due to potential soil compaction. In this study, we tested two hypotheses: 1) in young marshes, small grazers reduce carbon stocks by removing above-ground biomass of the local vegetation and 2) in older mature marshes, large grazers will increase carbon stocks due to trampling, which will enhance bulk density, promote anoxic conditions and reduce decomposition in the soil.

MATERIALS AND METHODS

Study site

This study was carried out on the back-barrier marsh of Schiermonnikoog, The Netherlands, located in the Wadden Sea (Fig. 3.1, 53°30'N, 6°10'E). 185 ha of the most western and oldest marshes are grazed by cattle in summer, with a rate of approximately 0.5 individual per ha (Bos et al. 2002). Only small grazers are present on the 1450 ha of eastern and younger marshes, which have never been grazed by cattle. They are grazed by migratory birds during winter and spring, such as Barnacle goose (*Branta leucopsis*) and Brent goose (*Branta bernicla*), and by European brown hares (*Lepus europaeus*) which are present year-round. Highest grazing intensity of geese and hare is found at marshes of intermediate age (Van De Koppel et al. 1996, Elschot et al. 2013). At these sites the biomass of nutritious palatable species is highest (Olff et al. 1997). Within our study site we observed a change in plant composition with increasing marsh age. A vegetation type dominated by *Puccinellia maritima* and *Limonium vulgare* in young marshes is replaced by a vegetation type dominated by *Festuca rubra* and *Artemisia maritima* at marshes of intermediate age (Olff et al. 1997, Bakker et al. 2005). Ultimately, a monoculture of *Elytrigia atherica* becomes dominant in mature marshes (Veeneklaas et al. 2013, Wanner et al. 2014). Large grazers reduce the cover of *Elytrigia atherica* and increase the cover of younger successional species, such as *Festuca rubra* and *Puccinellia maritima* again (Bos et al. 2002). To quantify the impact of grazing on the marsh development, a series of grazing exclosures were placed along the age gradient of the marshes in 1994 (details in next section).

Experimental set-up

Along the chronosequence, five locations were selected which differed in age and productivity (Olff et al. 1997, Kuijper and Bakker 2005). Olff et al. (1997) estimated the age of each location (i.e., the age since the marsh was formed by plant colonization on an initially bare tidal flat) using a time-series of aerial photographs. This led to approximate marsh-age estimates of 15, 30, 45, 55 and 120 years in 2010, the year we took our sediment samples (Fig. 3.1A, further details are given by Olff et al. 1997). Grazing by both hares and geese were excluded since 1994, by setting-up 6 m × 6 m grazing exclosures in the four youngest marsh ages (further details are given by Kuijper & Bakker 2005). Four exclosures in total (one exclosure per marsh age) were sampled to test the effects of small grazers. The oldest and fifth location, the 120-yrs-old marsh, was grazed by cattle until 1958, ungrazed between 1958 and 1988, and only partially grazed again after 1988. To estimate the effects of large grazers, we measured on the opposite sides of a cattle-grazed fence. Each measurement was at a distance of at least 2 m away from the fence and 2 m distance between two measurement points. Our set-up thus provided sampling of marshes of different ages and grazing types, be it in an unbalanced way: about 15 years with and without small grazers on 15, 30, 45 and 55-yrs-old marshes, vs. about 20 years with and without large grazers on 120-yrs-old marsh.

Net surface elevation change

Rates of surface elevation change (cm) were quantified by annual measurements, using duplicate Sedimentation Erosion Bars (SEB) (Boumans and Day 1993). The SEB's were established in 1994 on each of the locations, except the cattle-grazed area. Cattle are attracted by the poles and affect measurements. Each SEB consisted of three poles, which were positioned in a triangular shape with a distance of approximately 2 m between two poles. Each pole was embedded at least 1 m in the underlying sandy substrate to ensure stability over time. On top of two adjacent SEB poles, an aluminium bar could be placed which is perforated by 17 holes that were 10 cm apart. A small pin placed through each of the holes allowed estimation of the soil surface elevation to the nearest 0.1 cm. Per SEB-triangle, this resulted in 17 × 3 = 51 measurements, which were averaged to obtain the annual surface elevation change for a given SEB location per year between 1994 and 2011.

Soil sampling and lab analyses

Back-barrier marsh development starts on an initial coarse-grained (sandy) substrate: the base elevation (Olff et al. 1997). Once pioneer vegetation establishes, fine-grained sediment (silt) containing organic carbon accumulates over time on top of the coarse-grained substrate. The sharp border between both sediment types allowed us to exactly sample the total accumulated carbon that has been buried in the fine-grained sediment layer since the marsh was formed. At all five marsh ages, fine-grained sediment samples were taken inside and outside the grazing exclosure. All measurements inside the exclosures were at least 1 m from the fence to prevent edge-effects. Plots outside the exclosure were set-up at least 10 m away from the exclosure at similar base elevation of the underlying coarse-grained substrate. Having a similar base elevation enables us to identify potential effects of grazing on the thickness of the accreted fine-grained sediment layer, as the underlying coarse-grained substrate is not affected by grazing of the marsh.

Per marsh age, we sampled ten cores from the entire fine-grained sediment layer present on top of the coarse-grained substrate. We collected five cores inside and five cores outside the exclosures. The cores were taken throughout the entire exclosure to prevent any pseudo-replication effect. Total core length was compared with the depth of the hole left in the soil surface, to exclude samples that were compacted during sampling. To sample with minimal compaction we used a Tullgren soil core (10 cm in diameter and 20 cm in length) which is often used for soil fauna sampling (Van Straalen and Rijninks 1982, Schrama et al. 2012). The core was discarded and a new one taken when compaction was more than 0.5 cm. From each core two slices of 5 cm were sampled. We sampled two layers at all marsh ages, except for the 15-yrs-old marsh. The fine-grained sediment layer thickness at this site was only 7 cm, and we were forced to sample only the top layer. There was a distinct difference between the litter layer and the top of the soil layer. The first 0.5 cm of each core was discarded to avoid highest root density of the vegetation. To avoid contamination of the fine-grained sediment with coarser sediment, the bottom few cm near the underlying coarse-grained substrate were not used for analyses either. Locally occurring thin coarse-grained layers (generally of a few mm thick) within the fine-grained sediment layer (De Groot et al. 2011) were avoided as well. Although these layers might contain carbon, the number and thickness of the layers are highly variable and differ between marsh sites (De Groot et al. 2011). The coarse-grained material could increase the bulk density resulting in a biased organic carbon content found depending on number and sizes of local coarse-grained layers. Additionally, we measured the total fine-grained sediment layer thickness with a smaller corer (diameter 1.5 cm) four times in an area of one square meter surrounding each sampled core.

From each slice (of 5 cm in thick) four small sub-cores of known volume (diameter = 2.1 cm, volume: 16.7 + 1.9 cm^3) were sampled and freeze dried. After freeze drying, dry bulk density (g cm^{-3}) was estimated by weighing all four sub-cores and dividing the weight by their volume. Next, one randomly chosen sub-core was used for organic carbon analysis. All large living root fragments were removed using a 1 mm sieve. From the sieved material, we estimated percentage organic carbon. First, inorganic carbon was removed by in situ acidification with ultra-pure hydrochloric acid. Secondly, samples were combusted on a very high temperature (1010°C) with excess oxygen to make sure all carbon present was turned into CO_2 which in turn was detected with a thermal conductivity detector (further details are given by Nieuwenhuize et al. 1994).

Soil redox potential and plant biomass distribution

In November 2012, we measured the effects of grazing by small and large grazers on soil redox potential (mVolt) and plant biomass (g cm^{-2}). Due to practical constraints, we included two sites: 1) the 30-yrs-old marsh where the intensity of small grazers is highest (Van De Koppel et al. 1996, Elschot et al. 2013) and 2) the mature 120-yrs-old marsh where the large grazers were excluded. We measured redox potential at 5 cm depth using five Pt electrodes and one Hg-Cl reference electrode (replicated 15 times). All values estimated with the Hg-Cl electrode were converted with the following formulae: $y = 1.675x + 23.79$ mVolt, a formula based on calibration in the lab using a standard hydrogen electrode. Redox potential is used as a proximal measure of soil oxygen content that is potentially available for decomposition of soil organic carbon (for further information see Bochove et al. 2002).

To quantify plant biomass of the local vegetation, we collected small cores (5 cm diameter and 5 cm in length) inside and outside each exclosure (replicated ten times). We carefully placed the cores on the marsh platform to sample both above-ground as well as below-ground biomass with these cores. In the lab, all above-ground biomass was cut from the cores and sorted in dead (litter) and living plant material. The below-ground material is washed over a 1 mm sieve to remove all sediment. All samples were dried at 70°C and weighted afterwards. Additionally, based on the living roots and shoots biomass, we calculated the root:shoot ratios (defined by the below-ground living root biomass divided by the above-ground living shoot biomass (Mokany et al. 2006)).

Data analyses

Based on the weight-percentage of organic carbon together with the sediment bulk density (gr cm^{-3}), we quantified organic carbon content (g cm^{-3}) in both the upper and lower fine-grained sediment layer separately. Then we assigned the carbon content estimated in the top layer to the top 5 cm and assigned the carbon content of the deeper layer towards the rest of the fine-grained layer. Thus, if we measured on a specific site a total fine-grained sediment layer of 14 cm, we used 5 cm for the top layer and 9 cm for the bottom layer. By adding both calculated values together we estimated total accumulated

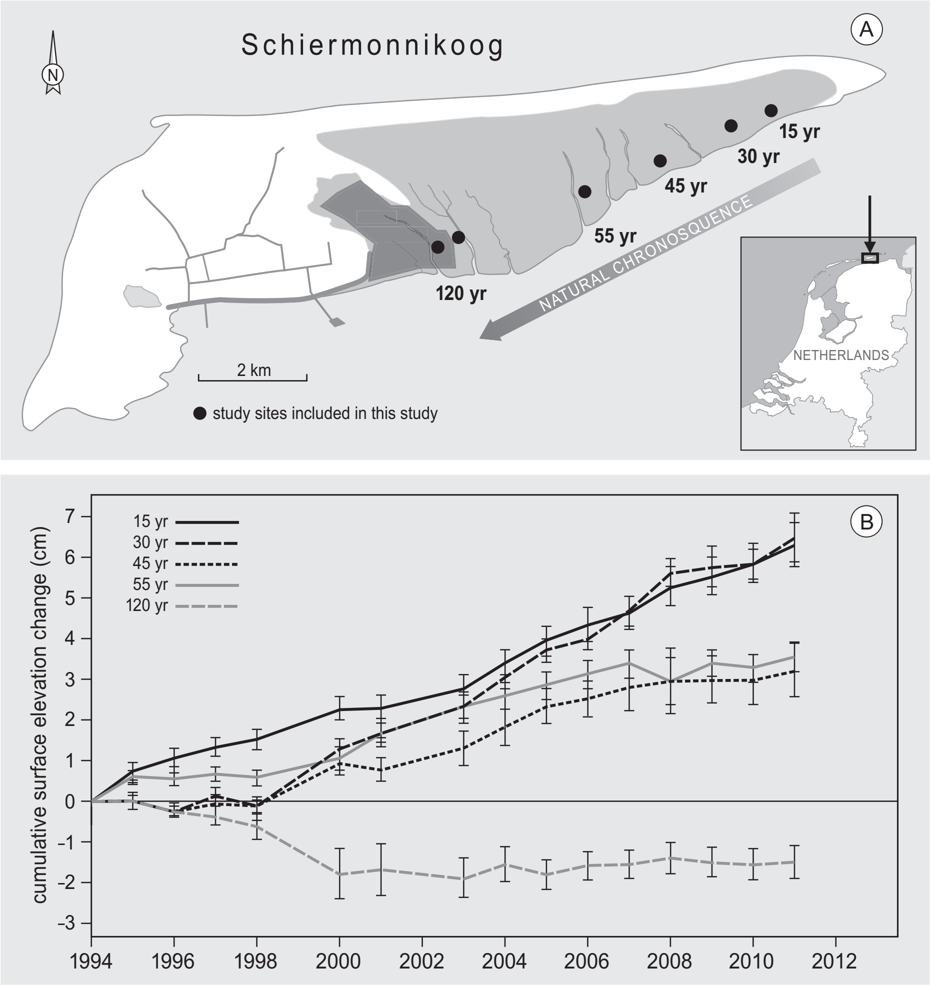

Figure 3.1. In this map the back-barrier marsh of Schiermonnikoog is indicated with the natural chronosequence. All sampled locations are indicated with black dots. For each location, the approximate age of the marsh (A) and the cumulative surface elevation change (cm) between 1994 and 2011 is given (B). The surface elevation change was not determined in the cattle-grazed marsh.

organic carbon per unit of marsh surface area (g m^{-2}). This gave us an approximate value for the total organic carbon present in the soil per soil core.

To test the effects of grazing on carbon sequestration we used two-way ANOVA's for the small grazers and t-tests for the large grazers (results in Table 3.1). Total carbon accumulated, % carbon and carbon content per layer were all analyzed separately. Due to the unbalanced design in this study, we had to analyze the small and large grazer effects separately. For the small grazers, both grazing and marsh age were used as predictor variables. If grazing had a significant effect, then we performed TukeyHSD-tests to determine for each marsh age separately, whether the small grazers had a significant effect (results in Fig. 3.2). If we found a significant effect by marsh age, then we performed a linear regression analysis with marsh age as the explanatory variable (significant correlations were plotted in Fig. 3.2).

To analyze the effects of grazing on biomass distribution and redox potential, we used two-way ANOVA's with grazing and site as predictor variables (results in Table 3.2). This was followed by TukeyHSD-tests (results given in Fig. 3.3). Root biomass and root:shoot ratios were log-transformed to account for non-normality. P-values < 0.05 were considered significant in all analyses. All data were analyzed using R, version 2.13.0 (R Development Core Team 2011).

RESULTS

Net surface elevation change

Average surface elevation change decreased with marsh age (Fig. 3.1B). Based on the sedimentation and erosion bars we found that the youngest marshes, of 15 and 30-yrs-old, both increased in surface elevation relatively fast with approximately 6 cm in seventeen years. This translates to an average increase of 3.7 ± 0.1 mm yr^{-1} for the 15 yrs-old marsh and 3.8 ± 0.1 mm yr^{-1} for the 30 yrs-old marsh, respectively (total surface elevation change divided by the number of years measured). Intermediate aged marshes, of 45 and 55-yrs-old, had a cumulative surface elevation change of approximately 3 cm. This was an increase of approximately 1.9 ± 0.1 mm yr^{-1} for the 45 yrs-old marsh and 2.1 ± 0.1 mm yr^{-1} for the 55 yrs-old marsh, respectively. The oldest location of 120-yrs showed a negative surface elevation change and decreased between 1 and 2 cm between 1994 and 2000. The elevation remained relatively stable between 2000 and 2011 (Fig. 3.1B).

Effects of age on organic carbon sequestration

Total organic carbon (g m^{-2}, organic carbon accumulated per unit soil surface), increased significantly with marsh age (Fig. 3.2A). However, the carbon accumulation stabilized at 3.300 g cm^{-2}, once the marsh was approximately 45 years old (Fig. 3.2A). The carbon accretion rate was highest at the youngest marsh, approximately 126 ± 9 g m^{-2} yr^{-1} at 15 yrs-old marsh (total accumulated carbon divided by the marsh age). This sequestration rate decreased rapidly with marsh age (Fig. 3.2A), ranging from 83 ± 4 g m^{-2} yr^{-1} at 30 yrs-old marsh, 69 ± 4 g m^{-2} yr^{-1} at 45 yrs-old marsh, 65 ± 3 g m^{-2} yr^{-1} at 55 yrs-old marsh down to 27 ± 1 g m^{-2} yr^{-1} at 120 yrs-old marsh. The percentage carbon that is present in both the top layer and the deeper layer increased with marsh age as well (Fig. 3.2B-C). In contrast, organic carbon content per soil-volume (g cm^{-3}) in both the top and the deeper layer were unaffected by marsh age (Fig. 3.2D-E).

Effects of grazing on organic carbon sequestration

The small grazers did not significantly affect total organic carbon accumulated (Fig. 3.2A) or percentage carbon (Fig. 3.2B-C). The only significant effect by the small grazers was a small increase in organic carbon content at the 30-yrs-old marsh in the top layer (Fig. 3.2D). Large grazers increased the total organic carbon accumulated in the soil substantially, increasing it from 3.197 ± 139 g m^{-2} in the ungrazed marsh to 4.408 ± 144 g m^{-2}

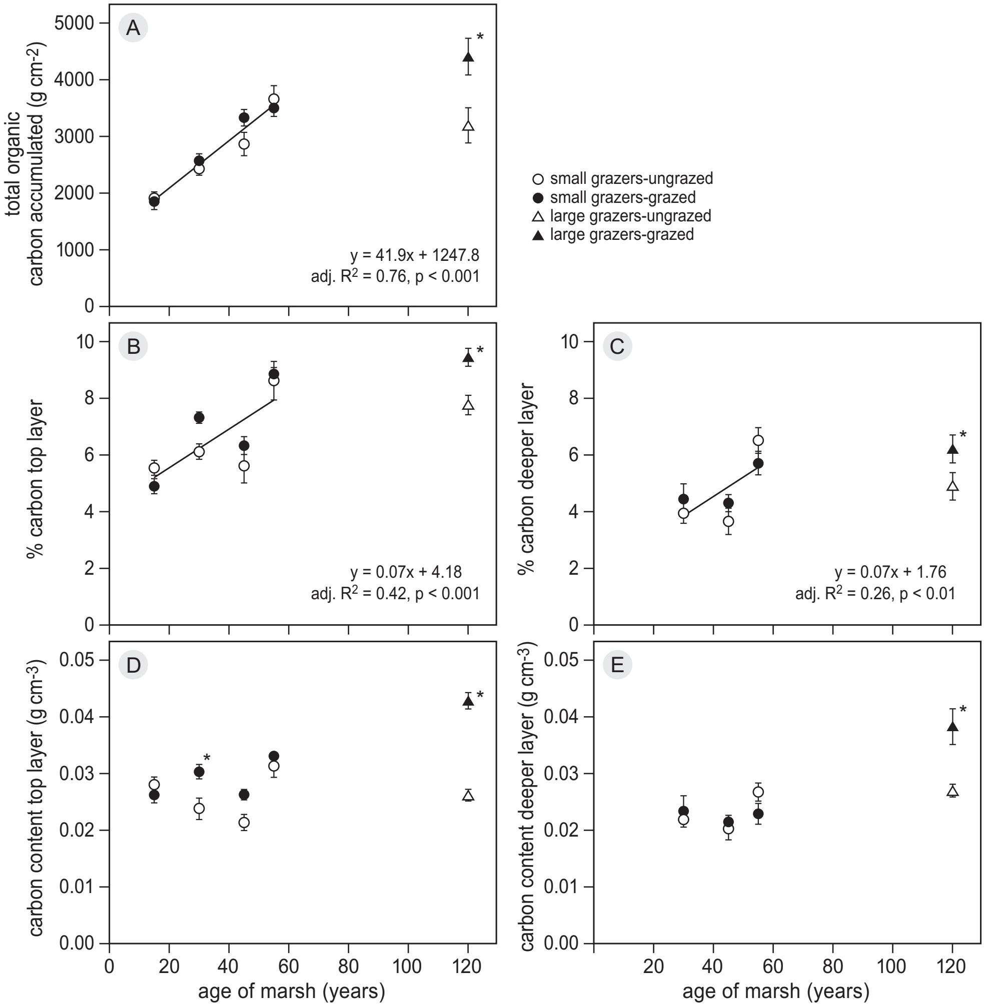

Figure 3.2. Total organic carbon accumulated (A), percentage carbon (B and C) and carbon content (D and E) in the top (left: B and D) and deeper layer (right: C and E). We compared small grazers (black circles) with ungrazed marsh (open circles) on the younger marshes, and large grazers (black triangles) with ungrazed marsh (open triangles) on the mature marsh. Significant effects due to grazing are indicated by * (p-value ≤ 0.05). Significant linear regressions are plotted to show the correlation between different organic carbon parameters and marsh age (between 15 and 55 yrs-old marsh).

in the grazed marsh, i.e., adding more than a kg of carbon in the soil per m² at 120-yrs-old marsh (Fig. 3.2A). Presence of large grazers on the 120-yrs-old marsh significantly increased percentage carbon (%) and carbon content (gr cm^{-3}) in both the top as well as the deeper fine-grained sediment layer (Fig. 3.2B-E).

Redox potential and plant biomass distribution

Both small and large grazers reduced the redox potential significantly (Fig. 3.3A, table 3.2). The significant interaction effect between grazing and age (table 3.2), implies that the effect of large grazers is much more substantial than the effect of the small grazers (Fig. 3.3A). Additionally, the redox potential was significantly lower in the mature (120-yrs-old) marsh compared to the younger (30-yrs-old) marsh site. Small grazers had no effect on the biomass distribution of the local vegetation (Fig. 3.3B-D), except for a significant reduction in litter (Fig. 3.3E). Large grazers altered the biomass allocation by reducing above-ground biomass (Fig. 3.3B), increasing below-ground biomass (Fig. 3.3C), and reducing litter (Fig. 3.3E) significantly. The total living biomass was not significantly affected by the presence of either small or large grazers and was not significantly different between both sites (Fig. 3.3D). The root:shoot ratio was unaffected by the small grazers and similar between both marsh sites, but increased significantly when large grazers were present (Fig. 3.3F).

Table 3.1. The effects of grazing on carbon sequestration. The effects of small grazers were tested with ANOVA's and the effects of large grazers with t-tests. The models were simplified when interaction effects were not significant. P ≤ 0.05 were considered significant and indicated in bold.

	Small grazers			**Large grazers**
	Age	Grazing	Age*grazing	Grazing
Total organic carbon accumulated (g m^{-2})	**$F_{1,37} = 124.7$ $p < 0.001$**	$F_{1,37} = 1.4$ $p = 0.25$	n.s.	**$t_{8.0} = 6.05$ $p < 0.001$**
% carbon top layer	**$F_{1,37} = 29.2$ $p < 0.001$**	$F_{1,37} = 0.9$ $p = 0.35$	n.s.	**$t_{7.9} = 3.62$ $p < 0.01$**
% carbon deeper layer	**$F_{1,27} = 11.0$ $p < 0.01$**	$F_{1,27} = 0.1$ $p = 0.80$	n.s.	**$t_{5.5} = 2.47$ $p < 0.05$**
Carbon content top layer (g cm^{-3})	$F_{1,37} = 2.5$ $p = 0.12$	**$F_{1,37} = 4.0$ $p = 0.05$**	n.s.	**$t_{7.1} = 9.49$ $p < 0.001$**
Carbon content deeper layer (g cm^{-3})	$F_{1,27} = 0.9$ $p = 0.34$	$F_{1,27} = 0.1$ $p = 0.80$	n.s.	**$t_{5.0} = 3.36$ $p = 0.02$**

n.s. = not significant

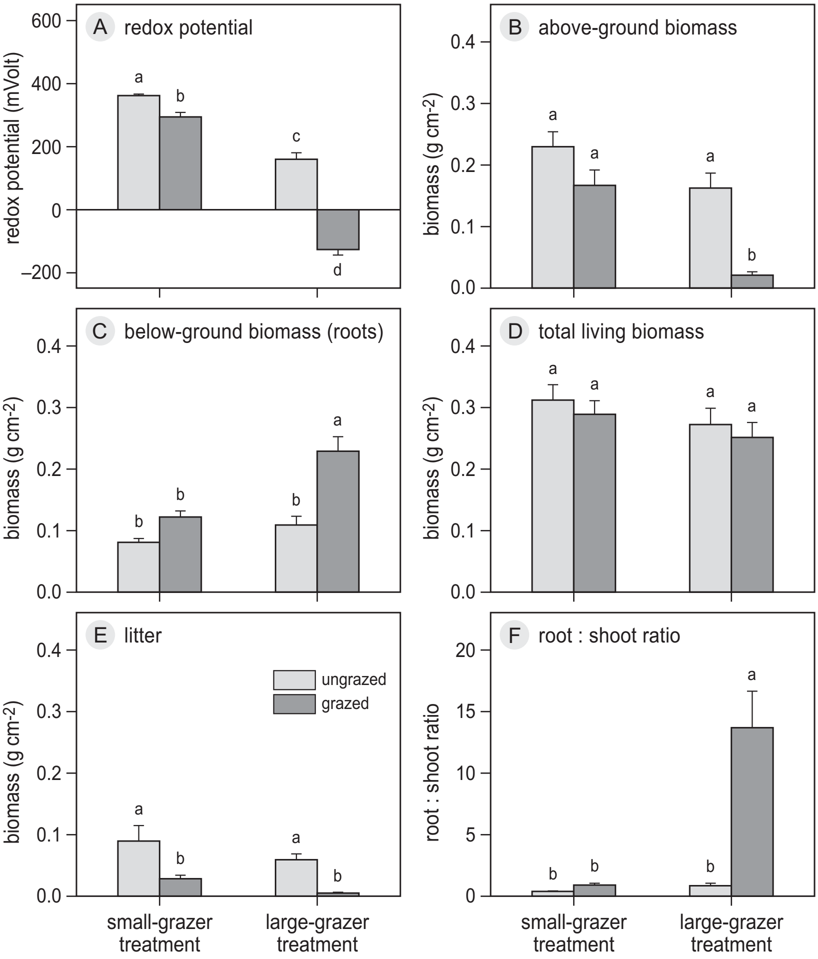

Figure 3.3. The differences in redox potential (A) and biomass distribution divided in shoots (B), roots (C), total (living) biomass (D) and litter (E), and the root:shoot ratios (F), found between grazed and ungrazed marsh for small grazers (left) and large grazers (right). Based on TukeyHSD-tests we assigned different letters when treatments were significantly different (p-value ≤ 0.05).

Table 3.2. The effects of grazing on biomass distribution and redox potential tested with ANOVA's. The models were simplified when interaction effects were not significant. P-values ≤ 0.05 were considered significant and indicated in bold.

	Grazing	Site	Grazing*site
Redox potential (mV)	**$F_{1,56}$ = 129.2** **$p < 0.001$**	**$F_{1,56}$ = 400.3** $p = 0.25$	**$F_{1,56}$ = 49.8** **$p < 0.001$**
Below-ground biomass (g cm^{-3})	**$F_{1,37}$ = 25.7** **$p < 0.001$**	**$F_{1,37}$ = 13.3** **$p < 0.001$**	n.s.
Above-ground biomass (g cm^{-3})	**$F_{1,36}$ = 24.0** **$p < 0.001$**	**$F_{1,36}$ = 24.0** **$p < 0.001$**	$F_{1,36}$ = 3.6 $p = 0.06$
Litter (g cm^{-3})	**$F_{1,37}$ = 18.3** **$p < 0.001$**	**$F_{1,37}$ = 4.0** **$p = 0.05$**	n.s.
Total living biomass (g cm^{-3})	$F_{1,37}$ = 0.8 $p = 0.37$	$F_{1,37}$ = 2.6 $p = 0.11$	n.s.
Root : shoot ratios	**$F_{1,36}$ = 80.8** **$p < 0.001$**	**$F_{1,36}$ = 70.1** **$p < 0.001$**	**$F_{1,36}$ = 3.6** **$p < 0.001$**

n.s. = not significant

DISCUSSION

Our results showed that grazers can have a large impact on carbon sequestration in a salt-marsh ecosystem. We reject the first hypothesis: that in young marshes small grazers reduce carbon stocks by removing above-ground biomass of the local vegetation, as we found no effect of small grazers on total carbon stocks. We accept the second hypothesis: that in older mature marshes large grazers increased carbon stocks due to trampling which enhanced bulk density and promoted anoxic conditions in the soil, as we found a large increase in carbon stocks and a reduction in redox potential at mature marshes. Furthermore, a previous study by Elschot et al. (2013) conducted in the same marsh showed that bulk density of the sediment (g cm^{-3}) significantly increased when large grazers were present. Previous studies assessing the effect of grazers on carbon sequestration showed they limit carbon storage by removing above-ground biomass (Morris and Jensen 1998, Sjögersten et al. 2008, Cahoon et al. 2012). However, we found that the indirect effects of grazing, for instance by altering biomass distribution of the vegetation towards the roots and through compaction of the soil thereby enhancing anoxic conditions, can outweigh the direct effects of removal of above-ground biomass (Fig. 3.4). This leads to increased carbon accumulation when large grazers were present. It is gen-

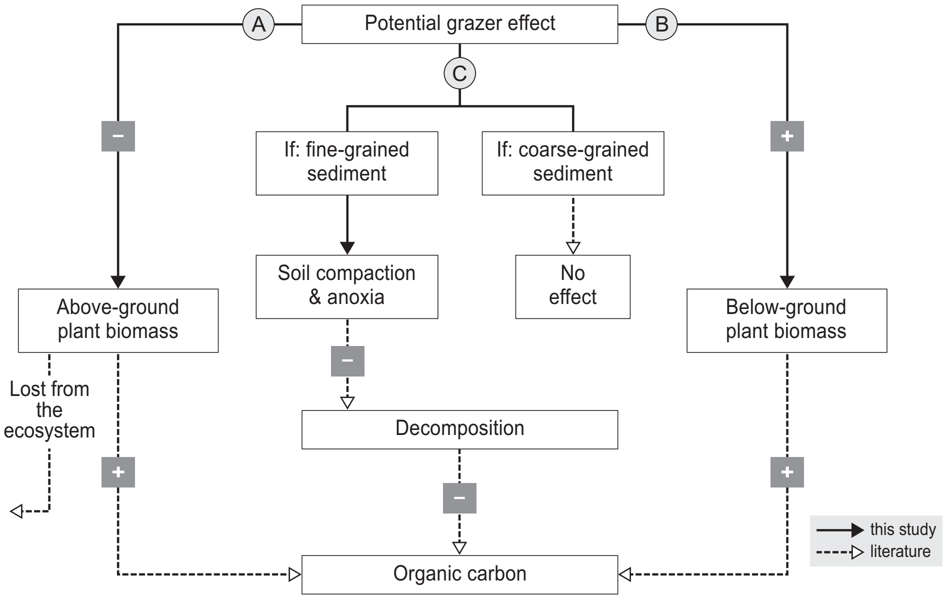

Figure 3.4. A testable conceptual framework including three pathways of how large grazers exert top-down control on carbon storage in salt marshes: through A) above-ground biomass removal, B) alteration of biomass distribution towards the roots and/or C) changing the abiotic conditions of the soil by trampling.

erally known that anoxic conditions in the soil will limit mineralization rates by the microbial community (Aller 1994, Sun et al. 2002, First and Hollibaugh 2010). Therefore, next to above-ground biomass removal and altering biomass distribution in the vegetation towards the roots, we propose that grazers exert top-down control on carbon storage via a third important pathway: by compacting the soil thereby reducing mineralization rate and enhancing carbon storage (Fig. 3.4).

Effects of large grazers on soil carbon stocks

This study showed that large grazers had a strong positive effect on carbon accumulation. So far, contradicting results have been reported for the effect of large grazers on carbon sequestration in coastal marshes (Taylor and Allanson 1993, Morris and Jensen 1998, Yu and Chmura 2010, Olsen et al. 2011). An empirical study in 2009 based on sheep grazing showed a local increase in both bulk density and organic carbon (Yu and Chmura 2010). This is in line with the results found in the present study. In contrast, cattle grazing on Danish marshes negatively affected organic carbon content (Morris and Jensen 1998), which was attributed to a direct result of above-ground biomass removal by large grazers. The results of our study reveal that large grazers can have an important positive effect on carbon accumulation in marshes.

When negative direct effects by above-ground biomass removal are less substantial than positive indirect effects caused by *i*) altered plant biomass distribution towards below-ground root biomass (Zimmerman et al. 1996, Knapp et al. 2008, Cahoon et al. 2012), and *ii*) changing local soil conditions that reduce carbon decomposition, grazers will enhance carbon sequestration in ecosystems. We propose that soil texture is an important determinant for which effect grazers have within an ecosystem (Fig. 3.4). Compaction of the soil and subsequent changing soil abiotic conditions will be more substantial in ecosystems with fine-grained (clay and silt) and/or organic-rich (peat) soils and is less likely to occur in ecosystems with more coarse-grained, sandy soils (Fig. 3.4, Schrama et al. 2013).

Above-ground biomass and litter were lower, but below-ground biomass was higher when large grazers were present (Fig. 3.3B-C). That grazing tolerant species invest more energy in their root system compared to above-ground plant parts has been shown in other ecosystems as well (McNaughton et al. 1998, Yu and Chmura 2010, Olsen et al. 2011, Sjögersten et al. 2012). In coastal marshes, below-ground biomass is likely more important as organic carbon source than above-ground biomass or litter. Most above-ground material will be easily exported as litter towards coastal waters during high tides and storms (Boschker et al. 1999). Additionally, a large part of the organic carbon input is supplied by the inundating water (Boschker et al. 1999), that contains suspended organic matter from non-local macrophytes, benthic microalgae and phytoplankton (Middelburg and Nieuwenhuize 1998). Ultimately, we conclude that grazing increased organic carbon input by increased below-ground biomass production and by reduced decomposition as a consequence of trampling, soil compaction and resulting increased anoxic conditions in the soil (Fig. 3.4).

Effects of small grazers on soil carbon stocks

In contrast to other studies showing negative effects of small grazers on carbon stocks (Van Der Wal et al. 2007, Sjögersten et al. 2012), we found no significant effect, except for a small increase in organic carbon content (g cm^{-3}) at the 30-yrs-old marsh in the top layer (Fig. 3.2D). According to Van de Koppel et al. (1996) and Elschot et al. (2013) grazing densities of hare and geese were highest at marshes of intermediate age, namely, at the 30-yrs-old marsh. This could explain why we only found significant effects by small grazers at this marsh age. Based on an average surface elevation change of 3.8 mm yr^{-1} (Fig. 3.1B), only the top layer of the soil contains sediment accreted since the exclosures were placed on the marsh. Therefore, the largest effect of grazer presence should be found in the top layer. Bulk densities of the soil (g cm^{-3}) in both the top and deeper layer were unaffected by long-term presence of small grazers (Elschot et al. 2013), hence the small increase in carbon content is not explained by compaction of the soil layer. We found a small significant reduction in redox potential (Fig. 3.3A) and a (non-significant) increase in below-ground root biomass (Fig. 3.3C). Together, they could explain the small increase found in the organic carbon content in the top layer of the fine-grained sediment layer due to the small grazers. Overall, the small increase found was not substantial enough to affect the total carbon stocks quantified in this study.

Effects of age on carbon sequestration

Carbon storage in the marsh soil is strongly related to marsh age (Fig. 3.2A). At the youngest marshes, both surface elevation change (Fig. 3.1B) and the increase in per m² organic carbon accumulation (Fig. 3.2A) were highest. A large part of the carbon that accumulates in mineral-based marshes is deposited together with the incoming fine-grained sediment (Boschker et al. 1999). In young marshes, the sediment input is highest (Van Wijnen & Bakker 2001) and high saline, anoxic conditions will limit organic carbon decomposition (Hemminga et al. 1991, Aller 1994). With increasing marsh age, the marsh platform increases in elevation (Van Wijnen and Bakker 2001), resulting in a reduced sediment deposition rate (Allen 2000) and alleviation of the stress-full environmental conditions (Bakker et al. 2005, Davy et al. 2011). At the oldest marsh, the marsh platform did not increase in elevation anymore (a negative surface elevation change is even shown), and organic carbon content per m² was no longer increasing. The negative surface elevation change found at the 120-yrs-old marsh is likely the result of auto-compaction, a natural process that occurs in older mature marshes, especially after long-term periods of drought (Allen 2000, Bartholdy et al. 2010, Cahoon et al. 2011). At the mature marsh, the total carbon stocks no longer increased. Therefore, we can conclude that the organic matter input from the inundating water together with the local vegetation vs. the output through decomposition has stabilized. Introducing large grazers at this point will increase carbon stocks.

Another potential explanation is a change in vegetation composition with marsh age (Olff et al. 1997, Davy et al. 2011). A study by Jobbágy and Jackson (2000) showed that vegetation type can have a large impact on the soil organic carbon through different biomass allocation patterns. This could explain the difference in carbon stocks found in this study. However, biomass allocation of the local vegetation was not significantly different between young marsh and mature marsh (Fig. 3.4). The positive correlation we found between carbon stock and marsh age is most likely due to continuous burial of organic carbon that is deposited on the marsh surface during high tides, together with root material of the local vegetation, and not due a change in vegetation composition.

We found that the carbon sequestration rate (g m^{-2} yr^{-1}) reduces with age of the marsh and carbon stocks stabilized when marshes reached 55 years of age. Most studies estimating organic carbon sequestration in coastal wetlands generally do not take age of the ecosystem in account (e.g., Connor et al. 2001, Chmura et al. 2003, Mcleod et al. 2011). In line with our results, a study in riverine floodplains showed that soil organic carbon accumulated rapidly at young successional stages, but sequestration rate reduced with increasing age and it stabilized after approximately 100 years (Zehetner et al. 2009). They found sequestration rates of 180 g m^{-2} yr^{-1} over the first 25 years and 100 g m^{-2} yr^{-1} over 100 years. In comparison, we found a rate of 126 g m^{-2} yr^{-1} over 15 years and 27 g m^{-2} yr^{-1} over 120 years. Which is lower than the average rate of 210 g m^{-2} yr^{-1} as was estimated for salt marshes in general (Chmura et al. 2003). Our accretion rates are lower, which could be explained by the low sedimentation rates found on European back-barrier marshes (Van Wijnen and Bakker 1997) compared to mainland marshes (Nolte et al. 2013c). Other studies that estimated carbon sequestration rates along a natural chronosequence in wetlands found that the percentage carbon in the soil increased with age of the ecosystem (Cornell et al. 2007, Osland et al. 2012, Lunstrum and Chen 2014). However, most of these studies had limited chronosequences of approximately 30 years and the ecosystems might not have reached a stable state yet (e.g., Craft et al. 2003, Cornell et al. 2007, Osland et al. 2012). Coastal wetlands are now recognized as ecosystems that can store large amounts of carbon (Chmura et al. 2003), therefore it is important to understand which factors control carbon accumulation in these ecosystems. Further studies that include long-term chronosequences, ranging over centuries, will be necessary to determine whether carbon accumulation changes with age.

Pseudo replication

This experiment gave us the unique opportunity to study long-term effects of grazing on carbon sequestration. However, we do need to address the potential problem of pseudo replication. As only one exclosure per site was sampled, this could result in samples not being completely independent from one another. The exclosures were however of a relative large size (6 m × 6 m), which allowed us to take the samples spatially spread throughout each exclosure in order to minimize any pseudo replication effect due to samples taken too closely together. The effects of large grazers on carbon sequestration, the redox potential as well as the biomass distribution were so profound that we consider the results to be robust. However, as we only tested the effects of large grazers on one marsh site, this study should be replicated in more marshes to determine whether this is in fact a general mechanism. The minimal effect we found on the 30-yrs-old marsh by the small grazers on carbon content, redox potential as well biomass distribution needs further investigation. We consider the effects of small grazers on total carbon accumulated to be robust, as all four sites showed the same result: namely, that small grazers had no significant effect on the total carbon accumulated.

Implications for management

Our results imply that, as we can manage livestock grazing in many ecosystems and it is a well-used management tool in European marshes (Dijkema 1990, Esselink et al. 2009), we can manage and enhance carbon stocks in mature marshes and potentially other terrestrial ecosystems (Sjögersten et al. 2012). However, the balance between indirect and direct effects due to grazers needs to be determined in each individual ecosystem independently. Due to current anthropogenic disturbances, natural grazers – especially the large ones – are reduced in numbers in many ecosystems (e.g., de Visser et al. 2011) and climate change is expected to further increase species loss (Thomas et al. 2004, Bellard et al. 2012). When direct effects of biomass removal is the predominant grazing effect, increased grazing intensity in well-drained sandy grassland systems such as savannas, could decrease carbon sequestration. On the other hand, trampling by large grazers will most likely increase local carbon sequestration, and this may be the predominant effect in wetland ecosystems such as marshes with fine-grained soils. Although our results are limited to a single barrier island, the mechanisms are potentially general and justify testing in other ecosystems with different grazer species and soil types (Fig. 3.4). Improving our understanding of the effect of grazers on carbon sequestration, may allow us not only to control but also to enhance the ability of ecosystems to act as carbon sinks.

ACKNOWLEDGEMENTS

First of all, we would like to thank Harm van Wijnen and René van der Wal for installing these exclosures in 1994. We acknowledge Natuurmonumenten and Elske Koppenaal for assistance in the field. We thank Maarten Schrama and two anonymous reviewers for useful comments on this manuscript, Josephine Cleyndert for assistance in the lab and Dick Visser for preparing graphs. This study was made possible with funding from the NWO-ZKO, project 83908320, the Dutch organization for scientific research.

BOX 1

Small-scale topographic heterogeneity in European sandy salt marshes

Kelly Elschot & Jan P. Bakker

ABSTRACT

Heterogeneity in an ecosystem can strongly boost biodiversity. In many European sandy tidal marshes, we find a small-scale topographic heterogeneity (of a few m^2). It is a repetitive pattern of higher elevated hummocks surrounded by lower elevated depressions. It has been mentioned in literature before, however, it remains relatively unclear how and when these patterns are formed. The marsh soil consists of a coarse-grained sediment layer formed before marsh started to develop. On top we find a layer of fine-grained sediment, which formed during marsh development. To gain insight in their formation, we measured this soil topography underlying the heterogeneous patterns. For generality, we compared these patterns between four European sandy salt marshes. Our results showed that the largest elevational difference is caused by heterogeneity of the underlying coarse-grained substratum. We concluded that the patterns in all four marshes were formed before marsh development started on the coarse-grained intertidal flat. Additionally, a smaller part of the elevational difference is explained by differences in the top fine-grained sediment layer. During early marsh development, higher elevated hummocks accumulated more fine-grained sediment, thereby enhancing the elevational differences that were already present. However, when marsh development continued, we found similar marsh accretion rates on hummocks and in depressions. Thus, in chronological order, these patterns in soil morphology were formed in pioneer stage, they got enhanced in early ecosystem development, but then they stabilized and are able to remain for 120 years.

INTRODUCTION

Salt-marsh development starts when pioneer vegetation establishes on an coarse-grained (sandy) bare intertidal flat and fine-grained sediment (silt) deposition will start accumulating (Olff et al. 1997). Vegetation is known to increase the sediment deposition rate, while it reduces the erosion rate by stabilization of the soil (Peralta et al. 2008, Mudd et al. 2010, Day et al. 2011). To summarize, the soil profile of a European sandy marsh generally consists of an underlying coarse-grained sediment layer with on top a thin layer of fine-grained sediment (Olff et al. 1997). Tidally introduced fine-grained sediment together with the local vegetation ultimately determine the morphology of the marsh platform (Temmerman et al. 2007, Fagherazzi et al. 2012, Vandenbruwaene et al. 2013). On several sandy salt marshes in Europe we observed small-scale patterns of a few m^2 in the marsh morphology. They consisted of a repetitive pattern of higher elevated hummocks (up to a few meter in diameter), surrounded by lower elevated depressions. Elevational differences between these hummocks and depressions can be up to 30 cm. Generally, we found a completely different plant community on top of these hummocks compared to the adjacent depressions. These patterns have been mentioned in several studies before (Gray and Bunce 1972, Langlois et al. 2003, Stribling et al. 2007, Balke et al. 2012), but it remains unclear how these patterns are formed and whether they are similar in different marsh types in Europe.

To gain more insight into the formation of these small-scale topographic patterns, we studied them on four different sandy marshes in Europe. Topographic patterns can be present due to heterogeneity of the underlying coarse-grained substratum and/or due to differences in local fine-grained sediment deposition. Thus, we want to test the following two hypotheses: 1) the patterns are already formed in the pioneer stage before marshes develop and fine-grained sediment is deposited on the marsh platform. Or: 2) the patterns are formed after the marsh started to develop and local patches accumulate more fine-grained sediment. To test these two hypotheses, we measured the soil profile underlying homogeneous and heterogeneous marsh. Additionally, we determined how much sediment is deposited on hummocks compared to adjacent depressions throughout ecosystem development, ranging from 15 to 120 yrs-old marsh.

METHODS

Study sites

We included four European sandy marshes in this study: Schiermonnikoog (The Netherlands, 53 30’N, 6 10’E), Terschelling (The Netherlands, 53°26’N, 5°28’E), Skallingen (Denmark, 55°30’N, 8°20’E) and the Cefni Marsh (United Kingdom, 53°10’N, 4°23’W).

Schiermonnikoog and Terschelling are back-barrier marshes on islands, Skallingen on a peninsula and the Cefni marsh is located within the Cefni Bay (Fig. 1.2). On Schiermonnikoog we studied the development of these patterns along a natural chronosequence. Olff et al. (1997) used aerial photographs to identify marshes of different ages leading to the identification of approximately 15, 30, 45, 55 and 120 yr-old marshes in 2010 (when we took most of our measurements). All marsh sites included in this study were not grazed by livestock.

Patterns in soil morphology

To determine whether the underlying coarse-grained sediment layer differed between heterogeneous and homogeneous marsh (marsh without small-scale topographic heterogeneity), we made several cross-sections from middle to low marsh on Schiermonnikoog (May 2009) as well as on the Cefni marsh (August 2011). We estimated the surface elevation and fine-grained sediment layer thickness every 50 cm, unless we were near a transition between hummock and depression, where we took measurements every 25 cm. The surface elevation was measured using an optical levelling instrument (Spectra Precision® Laser LL500 and Spectra Precision® Laser HR500 laser receiver by Trimble) with an accuracy of about 0.5 cm. The fine-grained sediment layer thickness was measured using a small soil corer (diameter = 1 cm) with an accuracy of 0.5 cm.

On the Cefni marsh, we compared two transects in heterogeneous marsh (transect 1 and 2) with one transect in homogeneous marsh (transect 3). All transects were located approximately 200 m apart from each other. On Schiermonnikoog, we compared one transect in heterogeneous marsh with one transect in homogeneous marsh. Both transects were measured on the 30 yr-old-marsh and approximately 100 m apart from each other. Both transects were located within the marsh zone.

Table B1.1. Sample size and tidal amplitude given per sampled marsh site.

Site	Sample size pair wise measurements	Tidal range (m)
Cefni marsh	55, 50 and 30 (transects 1, 2 and 3, respectively)	4.7*
Schiermonnikoog	76, 57, 63, 49 and 72 (15, 30, 45, 55 and 120 yrs-old marsh, respectively)	2.3
Terschelling	40	2.0
Skallingen	41	1.3

*The Cefni marsh is located inside the Cefni Bay and tidal range was measured outside the Bay. Dampening of the amplitude can be expected when the distance to the mouth of the Bay increases.

Coarse-grained vs. fine-grained heterogeneity in four sandy marshes

To study the generality of the patterns we compared the soil topography on four European tidal marshes. We included Schiermonnikoog (May 2009), Skallingen (September 2009), Terschelling (October 2010) and the Cefni marsh (August 2011). We pair-wise measured the absolute height of hummocks with neighbouring depressions (sample sizes and tidal range are given in table B1.1). We randomly selected hummocks that were increased in elevation. The patches ranged from a few centimetres up to a few metres in diameter. We paired each elevated hummock with a lower elevated depression within a distance of 0.5 m from the patch. For each of these paired measurements, we estimated surface elevation according to Mean High Tide (MHT) and measured fine-grained sediment layer thickness. The fine-grained sediment layer thickness was subtracted from the absolute height to determine the elevation of the underlying coarse-grained sediment layer. On the Cefni marsh we included three transects ranging from pioneer stage on the intertidal flat up to marsh. These transects were located at least 100 m away from each other. On Schiermonnikoog we included five marsh sites of different ages: 15, 30, 45, 55 and 120 yrs-old marsh.

Marsh accretion rates during marsh development

To test whether hummocks or depressions accumulate more fine-grained sediment at long term of decades, we placed Sediment and Erosions Bars (SEBs, see also (Boumans and Day 1993, Nolte et al. 2013b)) along the natural chronosequence on Schiermonnikoog. We included 15, 30, 45, 55 and 120 yr-old marsh. Each SEB consist of two poles that were placed 2 m apart within the marsh platform, with one pole located on top of a hummock and one pole located within a depression. This set-up was duplicated three times per site. For stabilization, each pole was inserted at least 1.0 m into the underlying coarse-grained sediment layer. Between 2001 and 2012, we estimated marsh accretion rates on a yearly interval. We found inconsistencies in the data of 2003, which were in such a nature, that we decided to remove them from further analyses.

Data analyses

To analyze the SEB data, we assigned each individual measurement in the field to hummock, depression or transition state (in between hummock or depression). We only included the measurements assigned to the hummocks and within the depressions in the following analyses. We calculated the average annual marsh accretion rate per marsh site, after which we tested for any significant effects between treatments using an ANOVA with marsh age and treatment (hummock or depression) as categorical predictors.

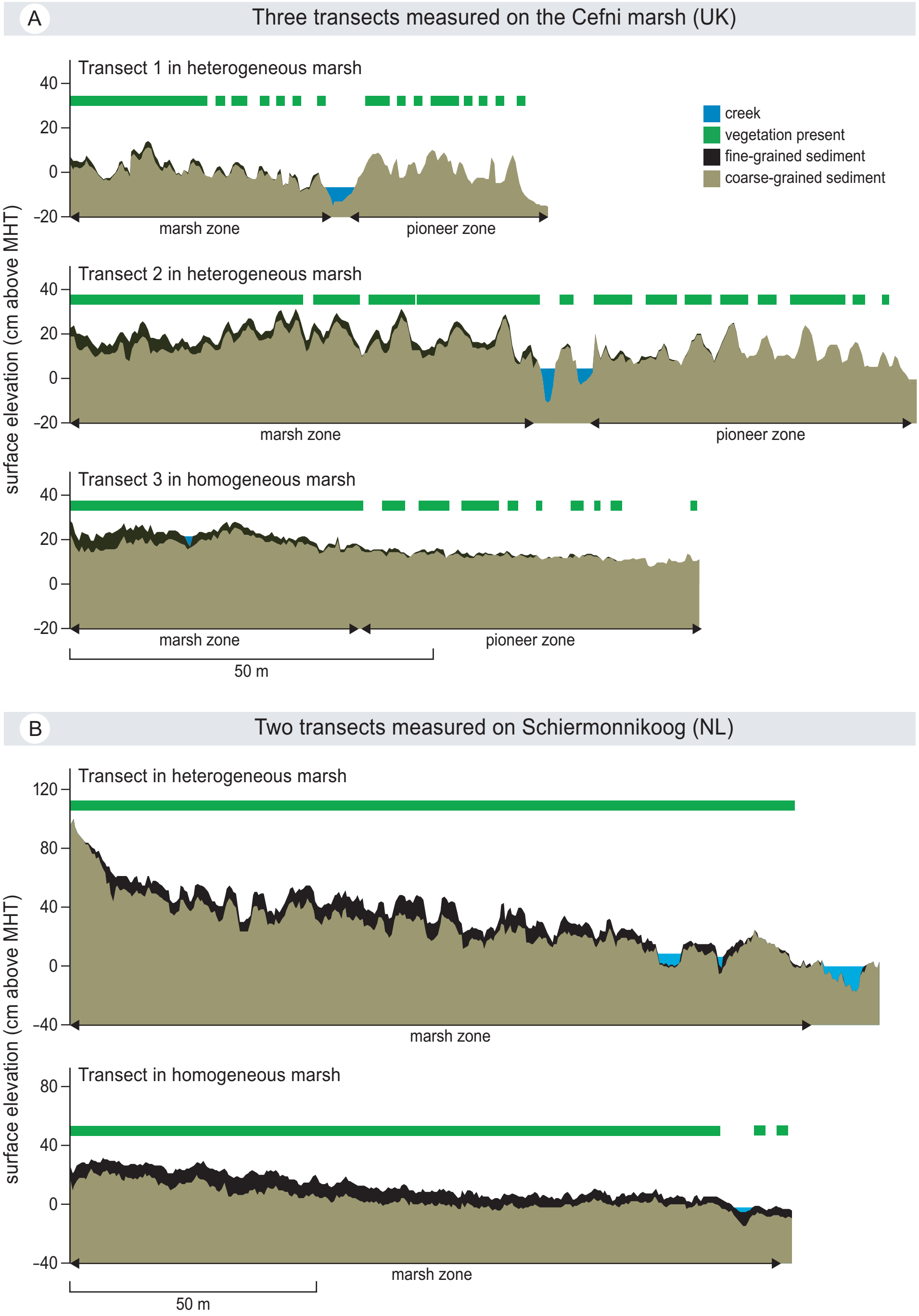

Figure B1.1. Transects on the Cefni marsh (A) and Schiermonnikoog (B). The light brown colour represents the coarse-grained sediment layer and the dark brown colour represents the fine-grained sediment layer. Only when both hummocks and depressions had accumulated fine-grained sediment we refer to it as the marsh zone, otherwise we consider it as the pioneer zone.

RESULTS

All transects showed that the top fine-grained sediment layer is following the underlying coarse-grained sediment layer (Fig. B1.1). Underlying a homogeneous marsh we found a relatively homogeneous coarse-grained sediment layer, while underlying a heterogeneous marsh we found a heterogeneous coarse-grained sediment layer. In all four marshes the topographic heterogeneity is mostly explained by the underlying coarse-grained (sand) sediment layer (Fig. B1.2). Patterns in the Cefni marsh are even for 92% explained by the coarse-grained sediment layer. However, the data collected on this site was for a large part collected in the pioneer zone where fine-grained sediment only recently started to accumulate. The marsh accretion rate (Fig. B1.3) did not differ significantly between the different marsh ages ($F_{(4,84)} = 0.33$, $p = 0.72$) or between hummocks and depressions ($F_{(1,84)} = 0.11$, $p=0.41$).

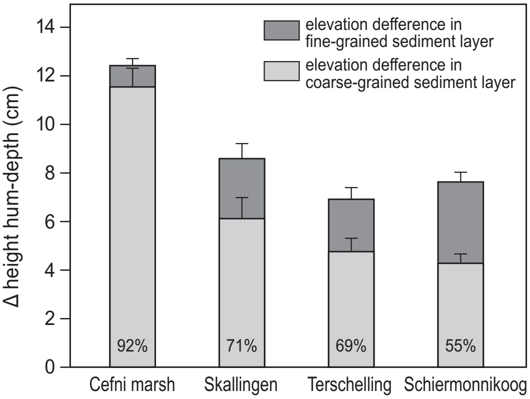

Figure B1.2. Elevational differences between hummocks and depressions estimated on four European sandy salt marshes. The elevational difference found between hummocks and depressions can be attributed to the underlying coarse-grained sediment layer (light grey) and/or the top fine-grained sediment layer (dark grey). Within each bar we have indicated (in %) how much of the elevational difference, on average, is explained by the coarse-grained sediment layer.

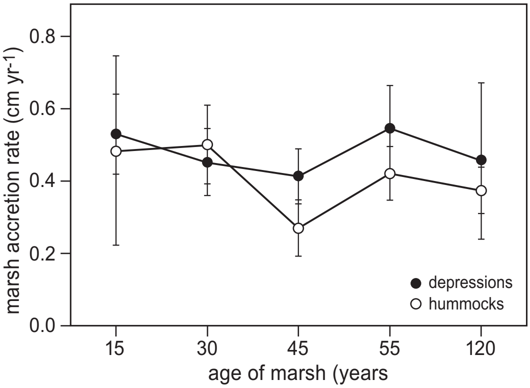

Figure B1.3. The marsh accretion rates measured between 2001-2012 (cm yr^{-1}) on hummocks and depressions along the natural chronosequence of Schiermonnikoog.

DISCUSSION

Our results are in line with our first hypothesis that the patterns are primarily formed due to a heterogeneous coarse-grained substratum that is formed before fine-grained sediment starts accumulating. Based on the cross-sections made in the Cefni marsh as well as on Schiermonnikoog, the marsh platform follows the topography of the underlying coarse-grained substrate (Fig. B1.1). In all four salt marshes, more than 50% of the heterogeneity is explained by the coarse-grained sediment, however, in three out of four considerable part of the elevational difference is also explained by the fine-grained sediment layer (Fig. B1.2). These findings are in line with our second hypothesis, that hummocks have a higher accretion rate during marsh development than the depressions. Elevation determines for a large part whether salt-marsh plant species can successfully establish (Davy et al. 2011) and we found vegetation on top of hummocks in the pioneer zone while the depressions were still bare (see Fig. B1.1, transects 1 and 2). As vegetation can increase sediment deposition (Mudd et al. 2010, Day et al. 2011) this would explain a higher salt-marsh accretion rate on top of the hummocks. On the 15 yr-old mars up to the 120 yr-old-marsh, we did not find a significant difference in marsh accretion rate between hummocks and depressions (Fig. B1.3). All these results lead us to conclude that: 1) heterogeneity in marsh topology is formed in pioneer stage before fine-grained sediment starts accumulating, 2) vegetation establishment on top of hummocks will increase sediment deposition or reduce erosion rate for a short amount of time thereby enhancing the elevational heterogeneity, and 3) once present in the salt-marsh platform, the patterns will persist as marsh accretion rates will remain similar between the hummocks and the depressions.

We have found topographic heterogeneity in four different European marshes. However, the marshes included in this study were all sandy marshes, with a thin fine-grained sediment layer on top of coarse-grained sediment. Additionally, they all have relatively low marsh accretion rates of ~3 mm yr^{-1} (Packham and Liddle 1970, Van Wijnen and Bakker 1997). Mainland and estuarine marshes generally have much higher accretion rates up to 40 mm yr^{-1} (Oenema and Delaune 1988, Dijkema et al. 2010, Suchrow et al. 2012). We found a few studies that investigated hummock formation, which used estuarine marshes (Van Wesenbeeck et al. 2008, Balke et al. 2012) or marshes within a bay (Langlois et al. 2001, 2003) as their study system. These were all marshes with relatively high sedimentation rates. In these studies, hummock formation was linked to either *Puccinellia maritima* (Langlois et al. 2001, 2003) or *Spartina anglica* (Van Wesenbeeck et al. 2008, Balke et al. 2012). According to Scholten and Rozema (1990), *Puccinellia maritima* and *Spartina anglica* will outcompete each other for space and light within the pioneer zone, and they conclude that *Puccinellia maritima* will prevail in more sandy marshes, while *Spartina anglica* will prevail in more clayish marshes. Apparently, hummock formation in the pioneer zone can occur in both sandy marshes with low accretion rates as well as in more clayish marshes with high accretion rates and, depending on soil type, either *Puccinellia maritima* or *Spartina anglica* can cause hummocks to form in the pioneer zone. However, with increasing time, *Spartina anglica* tends to form large monospecific stands on the clayish marshes, while on the more sandy marshes smaller scattered hummocks dominated by *Puccinellia maritima* remain present (Scholten and Rozema 1990). This is in line with our own observations that the small-scale topographic heterogeneity studied in this thesis is mainly present on sandy marshes with *Puccinellia maritima* as one of the dominant plant species in the pioneer zone.

Future research

Environmental heterogeneity within ecosystems can be important to boost biodiversity which is one of the key objectives in conservation ecology (Ricklefs 1977, Stein et al. 2014). Understanding how environmental heterogeneity is formed and what their impact is on primary (plant diversity) and secondary diversity (e.g. grazers) is important. In chapter 4 of this thesis we will investigate how these patterns affect both plant diversity and presence of grazers throughout salt-marsh development. We found evidence that the topographic heterogeneity is formed in the pioneer stage and the patterns remained present throughout ecosystem development. Determining the processes during the formation of these patterns and their impact in different types of salt marsh on biodiversity will be a next step.

ACKNOWLEDGEMENTS

We would like to acknowledge Harm Albers, Jan-Eise Wieringa, Elske Koppenaal, the Coastal Ecology Expedition for help with fieldwork and Dick Visser for help preparing the graphs. This study was funded by the ZKO-NWO, project number 83908320, the Dutch organization for scientific research as well as the Schure-Beijerinck-Popping Fund.

4

Positive effects of small-scale topographic heterogeneity on plant diversity and grazers throughout marsh development

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ABSTRACT Heterogeneity in ecosystems can strongly enhance plant diversity as it can increase the number of niches allowing more species to co-exist on a smaller scale. However, it remains relatively unknown how heterogeneity affects plant diversity as well as grazers and how this changes throughout long-term ecosystem development. At coastal foreshores, small-scale (few m^2) topographic heterogeneity in marsh morphology is observed consisting of higher elevated hummocks alternating with lower elevated depressions. In this study we *i*) estimated the effects of this topographic heterogeneity on plant diversity and grazers, such as hare and geese, and *ii*) how persistent these effects are during ecosystem development by comparing marshes of different ages along a 120-year chronosequence. In the pioneer stage, we found higher elevated hummocks on the intertidal flat. These patterns of hummocks and depressions enhanced plant diversity (number of species, equitability and Shannon diversity index) throughout ecosystem development, ranging from pioneer stage up to 120 year old marsh. Once hummocks were present in the marsh morphology they provided an additional niche facilitating the establishment of plant communities of later successional stages, thus enhancing not only plant diversity but also the suitability of early successional stages of marshes for small grazers.

INTRODUCTION

Ecological theory predicts that environmental heterogeneity within an ecosystem can boost local plant diversity (Ricklefs 1977, Costanza et al. 2011). When resources are distributed unevenly throughout an ecosystem, inter-specific competition is reduced, allowing more species to co-occur on a smaller scale (Ricklefs 1977, Snyder and Chesson 2004). In turn, plant diversity can have a major impact on the functioning of the ecosystem, affecting e.g. primary production and ecosystem resilience (e.g. Chapin et al. 2000; Wacker et al. 2008; Cardinale 2012). Even small-scale environmental heterogeneity can increase the resilience of ecosystems, enabling them to better cope with changing environmental conditions and extreme events such as long-term drought (Hopkins and Del Prado 2007, Godfree et al. 2011). When environmental conditions change rapidly, a wide range of species responding differently can stabilize important ecosystem processes (Hooper et al. 2005). This increased resilience will be of growing importance as rapid climate-driven changes pose a major threat to many ecosystems worldwide, and in particular those in areas where global change impacts may be expected to be the largest (Thomas et al. 2004). There is thus need for understanding the nature of heterogeneity, and how this affects diversity, especially in vulnerable ecosystems.

An important example of environmental heterogeneity is heterogeneity in soil morphology. This topographic heterogeneity can be the result of geological processes e.g. rock outcrops (Wohlgemuth 1998) or it can be biotically induced, e.g. mounds created by badgers in steppe-ecosystems or burrowing by prairie dogs in temperate grasslands (Davidson and Lightfoot 2006, Baker et al. 2013). The heterogeneity may also result from bio-geomorphic interactions between organisms and physical processes (Langlois et al. 2003, Mclaren and Jefferies 2004, Balke et al. 2012). For example, in dune ecosystems the presence of local vegetation patches catching wind-transported sand, results in the formation of large dunes alternating with dune slacks (Baas and Nield 2007). In most of these biotic and bio-geomorphic examples one or a few keystone species induce the topographic heterogeneity. Studies investigating the effect of topographic heterogeneity on diversity have mostly been short-term and limited to one trophic level (e.g. Davidson and Lightfoot 2006, Costanza et al. 2011, Baker et al. 2013) but see for example Van der Heide et al. (2012). However, especially in bio-geomorphic ecosystems, heterogeneity may evolve over time due to the interactions between organisms and physical processes. Thus, there is a strong need for studies focused on the effects of spatial heterogeneity on diversity in developing ecosystems where trophic interactions are expanding (Hooper et al. 2005, Peh and Lewis 2012 and references therein).

In this study we focus on salt marshes, which are bio-geomorphic ecosystems where the interplay of tidally introduced sediment and vegetation growth for a large part determine the long-term development of the marsh platform (Temmerman et al. 2007, Fagherazzi et al. 2012). Many European marshes contain areas with strong topographic heterogeneity, consisting of higher elevated “hummocks” surrounded by lower elevated “depressions” (Gray and Bunce 1972, Balke et al. 2012). This heterogeneity in the marsh platform can be found in marshes of different ages. The diameter of hummocks can range between 1 m and 10 m and elevational differences between hummocks and adjacent depressions can be up to 20 cm. Elevation of the marsh platform determines for a large part the distribution of plant species on the marsh (Olff et al. 1997, Davy et al. 2011) and presence of topographic heterogeneity could strongly boost plant diversity. We investigated how presence of topographic heterogeneity affects i) local plant diversity (number of species, equitability and Shannon diversity index), ii) grazers (abundance and impact), and iii) how both parameters change over time from pioneer stage to mature marshes of 120 years old.

METHODS

Study sites

To cover the entire age span, ranging from pioneer to mature marshes, we used two study sites (Fig. 4.1), a back-barrier marsh located on Schiermonnikoog (53 30’N, 6 10’E, The Netherlands) and the Cefni marsh (53°10’N, 4°23’W, United Kingdom). Schiermonnikoog has a unique natural chronosequence (Van de Koppel et al. 1996, Olff et al. 1997). Due to gradual expansion towards the east, an age and productivity gradient exists ranging from 15 to 120 yrs-old marsh (Fig. 4.1). The pioneer stage is currently lacking on Schiermonnikoog so we included the Cefni marsh which has a large pioneer zone located in front of the marsh. Both marshes are mineral based marshes where fine-grained sediment (silt) is accumulating on top of an underlying coarse-grained (sandy) substrate. Increasing fine-grained sediment layer thickness results in an increasing local productivity and this process determines for a large part the change in vegetation composition during succession (Olff et al. 1997). The marsh of Schiermonnikoog is located on a barrier island and the Cefni marsh is located in an Estuary. Schiermonnikoog is a mesotidal marsh with tidal amplitude of 2.3 m, while the Cefni marsh is a macrotidal marsh with tidal amplitude of 4.7 m. Both marshes show similar heterogeneity in soil morphology (Fig. 4.2). No livestock was present on the marsh areas we used for this study.

SCHIERMONNIKOOG

Along the chronosequence, marsh age was estimated by Olff et al. (1997) using a time-series of aerial photographs. Marsh age was based on the first establishment of vegetation. We selected five marsh ages including: 15, 30, 45, 55 and 120 years old marshes.

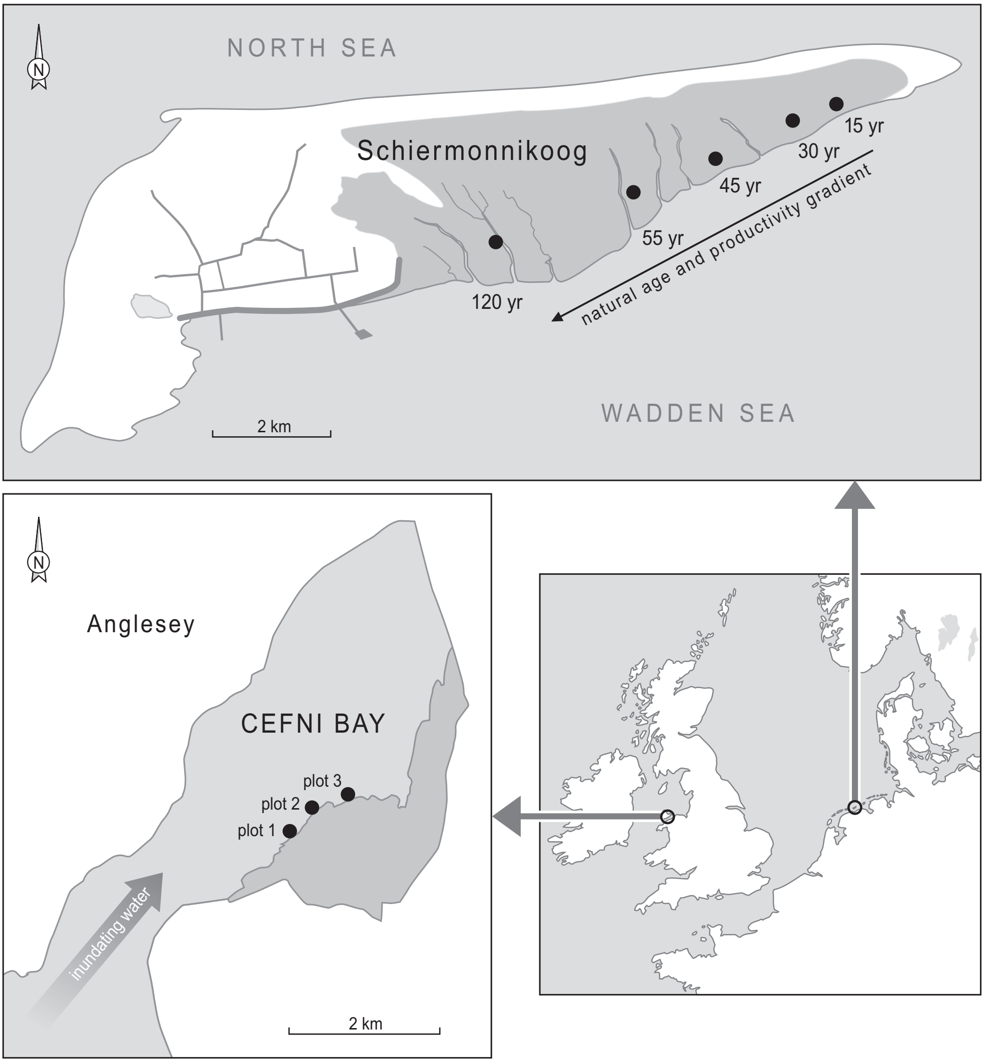

Figure 4.1. A map showing the back-barrier marsh of Schiermonnikoog (The Netherlands) and the Cefni marsh in Northern Wales (United Kingdom). The marsh area is shown in dark grey and water is shown in light grey. All plots included in this study are indicated with black dots. On Schiermonnikoog approximate age (in years) since the start of salt marsh development is given for each site.

Within each of the marsh ages, we compared zones with topographic heterogeneity present to zones without any topographic heterogeneity present, hereafter referred to as the homogeneous marsh. All were located on approximately the same marsh elevation. Several different migratory birds such as Barnacle goose, *Branta leucopsis*, and Brent goose, *Branta bernicla*, are present on the marsh during winter. Additionally, the European brown hare, *Lepus europaeus*, is present on the marsh throughout the year.

CEFNI MARSH

The Cefni marsh was included to study the formation of topographic heterogeneity in the pioneer stage. Due to continuous marsh expansion, a large pioneer zone is present in front of the marsh (Fig. 4.1). Salt-marsh development only started since the 1960s (Packham and Liddle 1970). In the pioneer zone we found elevated pioneer hummocks of varying sizes and heights, which had similar morphological characteristics as the topographic heterogeneity on Schiermonnikoog (Fig. 4.2). The main pioneer species present on the pioneer hummocks was *Puccinellia maritima*, which is an important pioneer plant species recorded on the Cefni marsh (Packham and Liddle 1970) and on Schiermonnikoog (Olff et al. 1997).

For classification purposes we refer to the sites as pioneer zone consisting of pioneer hummocks alternating with bare intertidal flat, as long as no fine-grained sediment is accumulated on top of the coarse-grained substrate of the intertidal flat. Once fine-grained sediment started accumulating on the coarse-grained substrate, and morphology of the marsh platform is conserved, we refer to these sites as marsh. From this point on the topographic heterogeneity is referred to as hummocks alternating with lower elevated depressions. When no elevated hummocks alternating with depressions were found, we refer to it as homogeneous marsh.

Figure 4.2. Topographic heterogeneity observed in pioneer stage on the Cefni marsh (left) and at 30 yrs-old-marsh on Schiermonnikoog (right). The left picture shows higher elevated pioneer hummocks alternating with the lower elevated bare intertidal flat. The right picture shows topographic heterogeneity consisting of higher elevated hummocks alternating with lower elevated depressions.

Effects of topographic heterogeneity in the pioneer stage (Cefni marsh)

In August 2011, we selected three plots on the Cefni marsh within the pioneer zone. These were 50 m × 50 m and at least 200 m apart from each other (Fig. 4.1). The three plots were all located on the bare intertidal flat, starting within 10 m of the salt marsh edge. They were present on different elevations of the underlying coarse-grained substrate: plot 1: 4.5 ± 0.5 cm, plot 2: 5.7 ± 0.4 cm and plot 3: 12.0 ± 0.2 cm above Mean High Tide (MHT). Plot 1 was located closest to the Bay mouth, while plot 3 was located furthest away (Fig. 4.1). Per plot we randomly selected about 30 hummocks of pioneer hummocks and paired each of them with controls taken on the adjacent bare intertidal flat. Controls were of similar size as the adjacent pioneer hummock, which ranges from a few cm up to 200 cm in diameter. To prevent any bias in choosing the location of the control plots, we assigned them consistently 0.5 m on the eastside of each hummock. Per paired measurement we estimated vegetation composition using a decimal scale (Londo 1976), fine-grained sediment layer thickness and surface elevation (cm above MHT). Fine-grained sediment layer thickness was measured using a small corer (1 cm in diameter), which allowed us to estimate it to an accuracy of 0.5 cm. The surface elevation was estimated using an optical levelling instrument (Spectra Precision® Laser LL500 and Spectra Precision® Laser HR500 laser receiver by Trimble), with an accuracy of 0.5 cm.

Development of topographic heterogeneity (Schiermonnikoog)

TOPOGRAPHIC HETEROGENEITY DEVELOPMENT BETWEEN 4 AND 15 YEAR OLD MARSH

In 2000, one plot of 7 m × 7 m was set up on the youngest marsh age of Schiermonnikoog (4 yrs old). The plot included both elevated hummocks and depressions. The plot was divided in smaller subplots of 0.25 m × 0.25 m. And for each subplot we estimated the fine-grained sediment layer thickness and the three most dominant plant species. In 2011, we repeated these measurements for 100 of these subplots: 50 on hummocks and 50 within depressions. This allowed us to determine changes in vegetation and fine-grained sediment layer thickness after eleven years of succession.

TOPOGRAPHIC HETEROGENEITY DEVELOPMENT BETWEEN 15 AND 120 YEAR OLD MARSH

In June 2011, we estimated the effects of topographic heterogeneity on the number of plant species, equitability and Shannon diversity index along the chronosequence on Schiermonnikoog. Equitability is used to indicate the evenness in distribution of the species present, (see for example Tuomisto 2012). We included five marsh ages: 15, 30, 45, 55 and 120 yrs-old-marsh. We chose ten random plots per site, five in marsh zones with topographic heterogeneity present and five in homogeneous marshes. The plots were chosen at approximately the same elevations. To prevent any bias from choosing a scale, we mapped at an increasing logarithmic scale: 0.5, 1, 2, 4, 8 and 16 m^2 of surface area. We randomly threw sticks on the marsh. In the zone with topographic heterogeneity present we started mapping from the centre of the nearest hummock. In the homogeneous marsh we started where the stick had landed. We estimated vegetation composition using a decimal scale (Londo 1976).

Effects of topographic heterogeneity on grazer abundance and impact throughout ecosystem development (Schiermonnikoog)

Dropping counts are a good estimate for grazing pressure for both hare (Langbein et al. 1999) and geese (Owen 1971). Hence, we estimated in June 2011 the hare and goose presence by counting number of droppings per 4 m^2 on three different marsh types: on hummocks, in adjacent depressions and in homogeneous marsh. We included all five marsh ages (i.e., 15, 30, 45, 55 and 120 yrs-old) and replicated each measurement ten times. We marked each plot with a stick and removed all 'old' droppings approximately two weeks prior to counting day. To calculate the number of droppings per day, we divided total number of droppings by the number of days between removal date and counting date.

To determine impact by the grazers on the topographic heterogeneity, we set-up 20 exclosures (6 m × 12 m) divided between the 15, 30, 45 and 55 yrs-old-marsh (n = 5 per marsh age). These exclosures were set-up in 2009 and located on top of the topographic heterogeneity including both hummocks and depressions within each treatment. Per exclosure we included three treatments: 1) no grazing, 2) only hare grazing present by goose exclusion and 3) both hare and goose grazing present. Geese were excluded using ropes at 25 and 50 cm above the ground, while both hare and geese were excluded using wire mesh. This set-up was used successfully before (Kuijper & Bakker 2005). In June 2011, we selected 0.25 m^2 plots within each treatment. We removed all biomass 1 cm above the marsh surface, sorted the samples per plant species, dried them at 70°C and weighted them afterwards. This resulted in six biomass samples per exclosure and 120 samples in total (n = 5 per treatment). To compare marsh with topographic heterogeneity present to homogeneous marsh, we included data derived from literature that had been collected on the homogeneous marsh areas of Schiermonnikoog at an earlier year (Van Wijnen and Bakker 2000).

Data analyses

To compare vegetation composition between pioneer marshes (measured at Cefni in 2011), 4 yrs-old-marsh (measured at Schiermonnikoog in 2000) and 15 yrs-old-marsh (measured at Schiermonnikoog in 2011) we had to transform the data of the pioneer marsh from the decimal scale to the three dominant plant species (Table 4.1). Based on the vegetation composition, including marshes between 15 and 120 yrs-old marsh (using the decimal scale), we calculated number of species (s), equitability (Eh) and the

Shannon diversity index (H). This enabled us to characterize the effects of topographic heterogeneity presence on plant diversity throughout long-term ecosystem development.

The Shannon diversity index (H):

$$H' = - \Sigma\, p_i \ln (p_i) \tag{1}$$

P_i = being the proportion of each species present within the plot

Equitability (Eh) was calculated as follows:

$$Eh = H' / \ln (s) \tag{2}$$

Statistical analyses

In the pioneer stage we analyzed the relation between surface elevation change and diameter of the pioneer hummocks with a general linear model, using diameter and plot as predictor variables. Differences in number of species between the three plots were analyzed with a generalized linear model (Poisson distribution), using hummock size and plot as predictor variables. Differences in total biomass on hummocks and depressions between 15 and 120 yrs-old-marshes were analyzed with an ANOVA, using marsh age and type (hummock or depression) as categorical predictors. Number of species was analyzed with a generalized linear model using a Poisson distribution. Diversity characteristics were analyzed using ANCOVA for Equitability and the Shannon diversity index. Numbers of droppings were analyzed with Tukey-tests for each marsh age separately, using type (hummock, depression or control) as categorical predictor. The effect of 1.5 years of grazer exclusion on biomass production was analyzed with a Mixed Effect Model, using grazing treatment and marsh age as fixed factors and exclosure as random factor. Values of $p < 0.05$ were considered significantly different. All analyses were performed using R, version 2.13.0 (R Development Core Team 2011).

RESULTS

Effects of topographic heterogeneity in the pioneer stage (Cefni marsh)

In the pioneer zone all hummocks were covered pre-dominantly by *Puccinellia maritima* and no fine-grained sediment had accumulated yet (Table 4.1). On the adjacent intertidal flat the main species present was *Salicornia europaea* (Table 4.1). The difference in surface elevation between hummocks and the adjacent intertidal flat significantly increased with diameter of the hummock ($t = 11.7$, $p < 0.001$). This relationship was only found in two of the three plots (plot 1 and 2, Fig. 4.3A), where hummocks increased in surface elevation up to 15 cm. Plot 3 diverged from this relationship as hummocks did not significantly increase in height with increasing size (Fig. 4.3A, significant interaction effect between plot and diameter (t = -6.7, $p < 0.001$)). Difference in surface elevation in plot 3 was limited to 3 cm. When we focus on the numbers of species found on the hummocks, all three plots showed the same relation: numbers of species increased significantly with diameter of the hummocks (Fig. 4.3B, z = 10.9, $p < 0.001$). Up to twelve species were present at a hummock size of 2 m in diameter, whereas on the adjacent bare intertidal flat a maximum of three species was found. The three plots did not differ significantly from each other (z = 1.56, p = 0.12).

Development of topographic heterogeneity (Schiermonnikoog)

TOPOGRAPHIC HETEROGENEITY DEVELOPMENT BETWEEN 4 AND 15 YEAR OLD MARSH

Pioneer hummocks present on the bare intertidal flat in the Cefni marsh (pioneer) and hummocks on Schiermonnikoog at 4 yrs-old-marsh had in common that *Puccinellia maritima* is one of the dominant plant species (Table 4.1). There were differences in vege-

Table 4.1. The difference in vegetation composition found at pioneer stage (Cefni marsh, UK) compared to 4 and 15 yrs-old-marsh (Schiermonnikoog, NL). The numbers represent the percentage of all plots where that specific plant species is ranked as one of the three most dominant present. This leads to a total of 300% per column, with the exception of the depressions in the pioneer stage as there were not always three species present. Bare soil was included as a "species" during measurements. The three most dominant plant species per age class are shown in bold.

	Hummocks			**Depressions**		
Marsh age (years)	**pioneer***	**4****	**15**	**pioneer***	**4****	**15**
Fine-grained sediment layer thickness (cm)	0	4 ± 1	6 ± 1	0	3 ± 1	7 ± 1
Bare soil	96	99	0	100	100	100
Armeria maritima	**11**	0	0	0	0	0
Artemisia maritima	0	4	**100**	0	0	**22**
Aster tripolium	7	3	4	0	0	0
Atriplex portulacoides	0	12	4	0	1	**58**
Festuca rubra	0	0	**100**	0	0	0
Glaux maritima	0	0	2	0	0	0
Limonium vulgare	0	**97**	**46**	**4**	18	**100**
Plantago maritima	0	8	40	0	0	0
Puccinellia maritima	**100**	**27**	4	0	**51**	2
Salicornia europaea	**78**	9	0	**93**	**59**	0
Spartina anglica	4	0	0	**33**	23	0
Spergularia media	4	**29**	0	0	3	6
Suaeda maritima	0	12	0	**4**	**45**	12

*Measurements taken on the Cefni marsh (UK), measurements on 4 and 15 yrs-old-marsh were taken on Schiermonnikoog (NL). **Measurements taken in 2000, at pioneer stage and 15 yrs-old-marsh were taken in 2011.

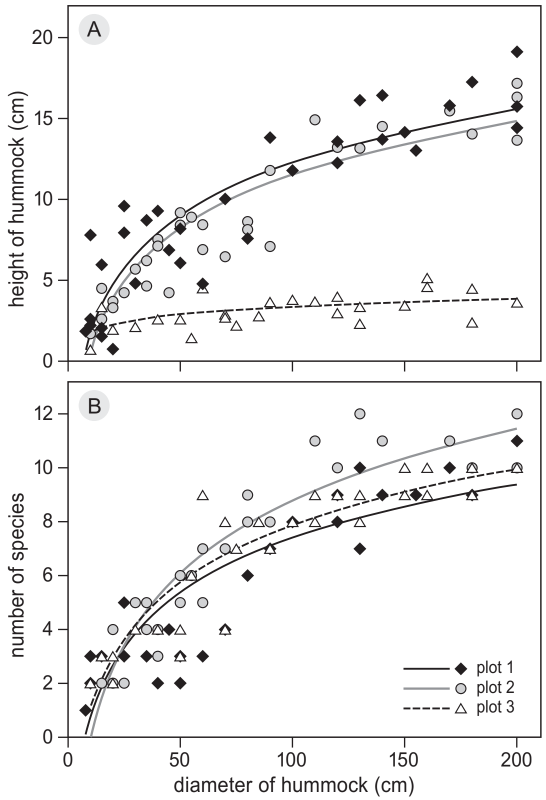

Figure 4.3. Differences in height between hummock and depression (A) and number of species (B) with increasing hummock size of the pioneer vegetation (Cefni marsh). Three plots were established on the intertidal flat located at least 200 m apart from each other. Per plot 30 pioneer hummocks were randomly selected ranging in diameter from a few cm up to 2 m. Each hummock was measured pair wise with an adjacent control plot on the bare intertidal flat. The diameter of the control plot was equal to the diameter of the hummock. Height of the hummock was measured in the centre of each hummock and indicated relative to the control plot. Numbers of species were estimated on the entire hummock.

tation dominance, for example: *Limonium vulgare* was more dominant on the hummocks at 4 yrs-old marsh. Plant succession continued between 4 and 15 years of marsh development. A clear difference in successional stages was found on top of higher elevated hummocks compared to the adjacent lower elevated depressions (Table 4.1 and Table 4.2), implying that two alternative successions had taken place on a small scale of only a few m^2.

TOPOGRAPHIC HETEROGENEITY DEVELOPMENT BETWEEN 15 AND 120 YEAR OLD MARSH

When topographic heterogeneity was present, the number of species (Fig. 4.4A-B), the equitability (4.4C-D) as well as the Shannon diversity index (4.4E-F) increased compared to the homogeneous marsh. These effects generally increased with surface area

(4A-C-E), but did not change with age of the marsh (Fig. 4.4B-D-F). The significant interaction effects found for equitability and the diversity index (Fig. 4.4C-E) showed that they only increased when topographic heterogeneity was present. Total biomass (g m^{-2}) on the hummocks was higher compared to the depressions and the homogeneous marsh (Fig. 4.5). As we derived the biomass estimates for the homogeneous marsh from literature, we could not perform any statistics comparing homogeneous vs. marsh with topographic heterogeneity present. However, based on the trend we concluded that both depressions and homogeneous marsh had approximately similar biomass estimates, whereas hummocks had more biomass, especially in the youngest and at the older sites (Fig. 4.5). The hummocks had significantly more biomass than depressions ($F_{1,95} = 59.7$, $p < 0.001$). Total biomass was also significantly different per marsh age ($F_{3,95} = 3.5$, $p = 0.02$) while no significant interaction effect was found ($F_{3,95} = 1.2$, $p = 0.31$).

Table 4.2. Change in vegetation composition on marshes with topographic heterogeneity present compared to homogeneous marsh along the chronosequence (15 to 120 yrs-old-marsh). All vegetation compositions were mapped on 16 m^2 plots ($n = 5$). Vegetation cover was estimated using a decimal scale (Londo 1976). All measurements were taken in 2011 on Schiermonnikoog. The dominant plant species are indicated in bold.

	Topographic heterogeneity present					**Homogeneous marsh**				
	15	**30**	**45**	**55**	**120**	**15**	**30**	**45**	**55**	**120**
Bare	20	1	0	6	15	30	3	6	10	18
Armeria maritima	0	0	0	0	0	0	0	0	0	0
Artemisia maritima	**15**	**16**	**15**	3	10	**4**	**13**	10	**8**	1
Aster tripolium	2	4	2	2	2	**4**	0	0	0	0
Atriplex portulac.	2	4	6	7	12	**24**	4	0	**12**	1
Atriplex prostrata	0	0	1	0	0	0	1	2	1	**5**
Cochlearia sp.	1	1	0	0	0	1	0	0	0	4
Elytrigia atherica	0	0	0	**11**	4	0	**40**	**44**	**56**	**66**
Festuca rubra	**28**	**32**	**32**	**23**	**26**	1	4	**21**	7	**5**
Glaux maritima	3	3	3	**11**	8	1	1	1	0	0
Juncus gerardii	0	6	0	9	**17**	0	4	**15**	1	**12**
Limonium vulgare	**32**	**32**	**38**	**32**	**16**	**42**	**24**	6	1	0
Plantago maritima	10	3	0	0	1	1	0	0	0	0
Puccinellia maritima	6	5	5	5	0	1	10	0	1	0
Salicornia europaea	1	3	2	1	0	1	1	0	2	0
Spartina anglica	0	1	0	0	0	1	0	0	0	0
Spergularia media	1	1	0	0	1	1	0	0	0	0
Suaeda maritima	2	2	1	1	0	**4**	1	0	0	0
Triglochin maritima	0	4	2	1	1	0	1	0	3	0
Nr. of species	**12**	**15**	**11**	**12**	**11**	**13**	**12**	**7**	**10**	**7**

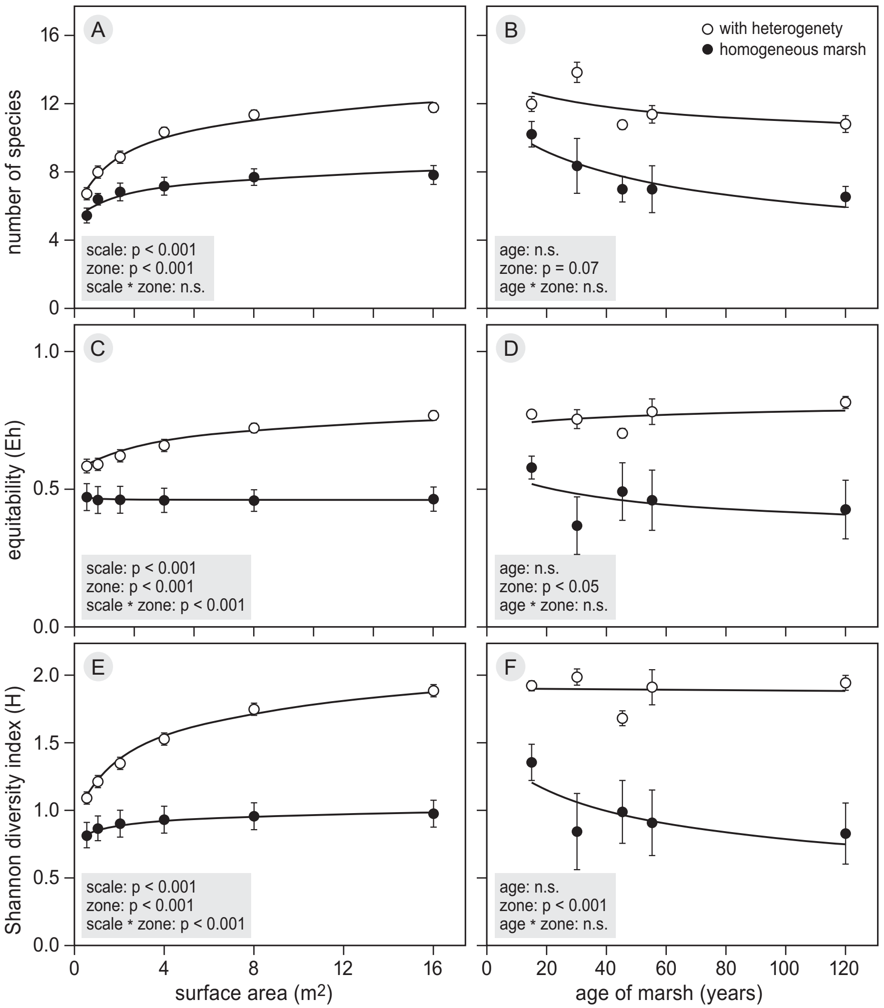

Figure 4.4. Number of plant species (A-B), equitability (C-D) and Shannon diversity index (E-F) determined on plots with increasing surface area (A, C, E) and along the chronosequence (B, D, F) ranging between 15 and 120 yrs-old-marsh on Schiermonnikoog. Open circles indicate heterogeneous marsh with topographic heterogeneity present and closed circles indicate homogeneous marsh. Data shown along an increasing surface area (A-C-E) were averaged over all marsh ages. Along the chronosequence only data measured on 16 m² are shown (B-D-F). Zone represents the differences between the two marsh zones: homogeneous or heterogeneous marsh zone.

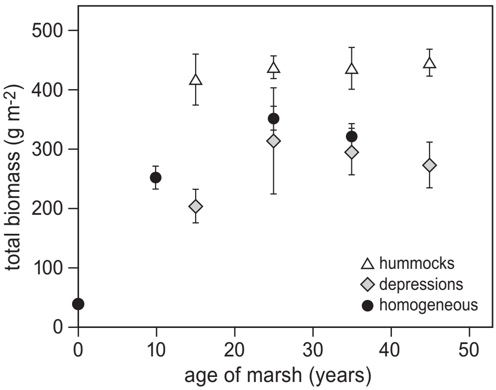

Figure 4.5. Total biomass (g m^{-2}) estimated in homogeneous marsh, on depressions ($n = 5$) and on hummocks ($n = 5$) along the chronosequence (up to 55 yrs-old-marsh). Biomass estimates on the homogeneous marsh ($n = 3$) were derived from literature (Van Wijnen & Bakker 2000). All data were collected with hare and geese grazing present.

Effects of topographic heterogeneity presence on grazer abundance and impact throughout ecosystem development (Schiermonnikoog)

In homogeneous marsh the hare abundance increased with age and productivity to a maximum value at medium-aged-marsh of 45 years old, after which the hare abundance again decreased (Fig. 4.6A). When topographic heterogeneity was present this pattern changed, with the highest hare abundance found in the youngest marshes, and hare abundance decreased with age of the marsh. Hare preferred hummocks above depressions ($p < 0.01$, $p < 0.01$) or homogeneous marsh ($p < 0.01$, $p < 0.01$) at 15 and 30 yrs-old-marsh. At 45 yrs-old-marsh, however, they had a strong preference for homogeneous marsh compared to hummocks ($p < 0.001$) or depressions ($p < 0.01$). Geese seemed to prefer the youngest site and mainly the zone where no topographic heterogeneity was found though these differences were not significant (Fig. 4.6B).

Impact of the small grazers on vegetation characteristics was highest on hummocks (Fig. 4.7). In ungrazed marsh, i.e. where both hare and geese were excluded, total biomass increased significantly on the hummocks (Fig. 4.7A, $t = 3.8$, $p < 0.001$). Biomass on hummocks was unaffected by marsh age or when only hare grazed (Fig. 4.7A, $t = 0.29$, $p = 0.76$). Within ungrazed depressions, total biomass increased significantly (Fig. 4.7B, $t = 3.0$, $p < 0.001$). Within depressions, biomass increased significantly with age of the marsh and all older sites differed significantly from the youngest site ($t = 2.16$, $p = 0.05$, $t = 2.5$, $p = 0.03$ and $t = 2.3$, $p = 0.04$ for 30, 45 and 55 yrs-old-marsh, respectively).

When topographic heterogeneity was present, *Festuca rubra* was already present in high cover at a much earlier successional stage compared to homogeneous marsh, and cover remained relatively stable between 15 and 120 years of marsh succession (table 4.2

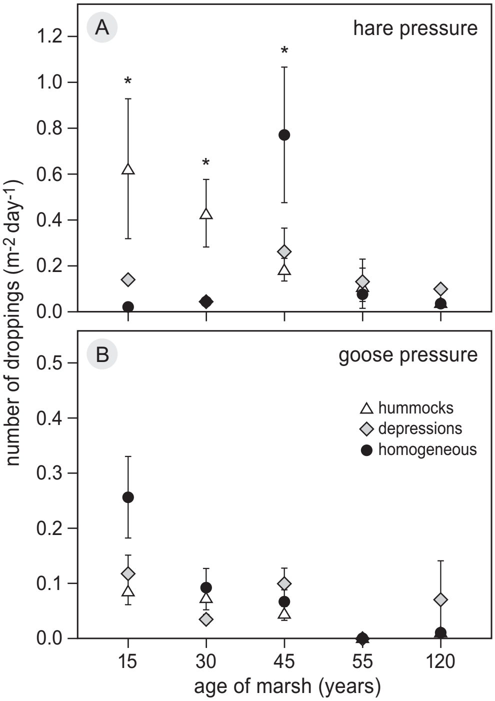

Figure 4.6. Grazer pressure of hare (A) and goose (B) estimated with number of droppings (m^{-2} day^{-1}) along the chronosequence (15 to 120 yrs-old-marsh). Data is collected per 4 m^2 plots. All droppings were removed 14 days prior to counting date.
* indicates this treatment was significantly different ($p < 0.05$) from both other treatments at that marsh age.

and fig. 4.7C). In the homogeneous marsh a clear optimum was shown at 45 year old marsh, thereafter, cover of *Festuca rubra* was quickly reduced again with increasing age (table 4.2). On ungrazed hummocks the biomass of *Festuca rubra* increased significantly (Fig. 4.7C, $t = 5.2$, $p < 0.001$). Hare grazing, i.e. when only geese were excluded, did not result in significant differences ($t = -0.54$, $p = 0.59$). Biomass reduced with age, as it was significantly lower at 55 yrs-old-marsh compared to 15 yrs-old-marsh ($t = -2.55$, $p = 0.02$). *Festuca rubra* was only marginally present in depressions and biomass was not significantly affected by marsh age or grazing treatments (Fig. 4.7D). On hummocks, *Puccinellia maritima* was unaffected by grazing treatment or age of the marsh. Within depressions, the biomass of *Puccinellia maritima* increased with marsh age as both 45 and 55 yrs-old-marsh differed significantly from the 15 yrs-old-marsh ($t = 3.0$, $p < 0.01$ for both 45 and 55 yrs-old-marsh).

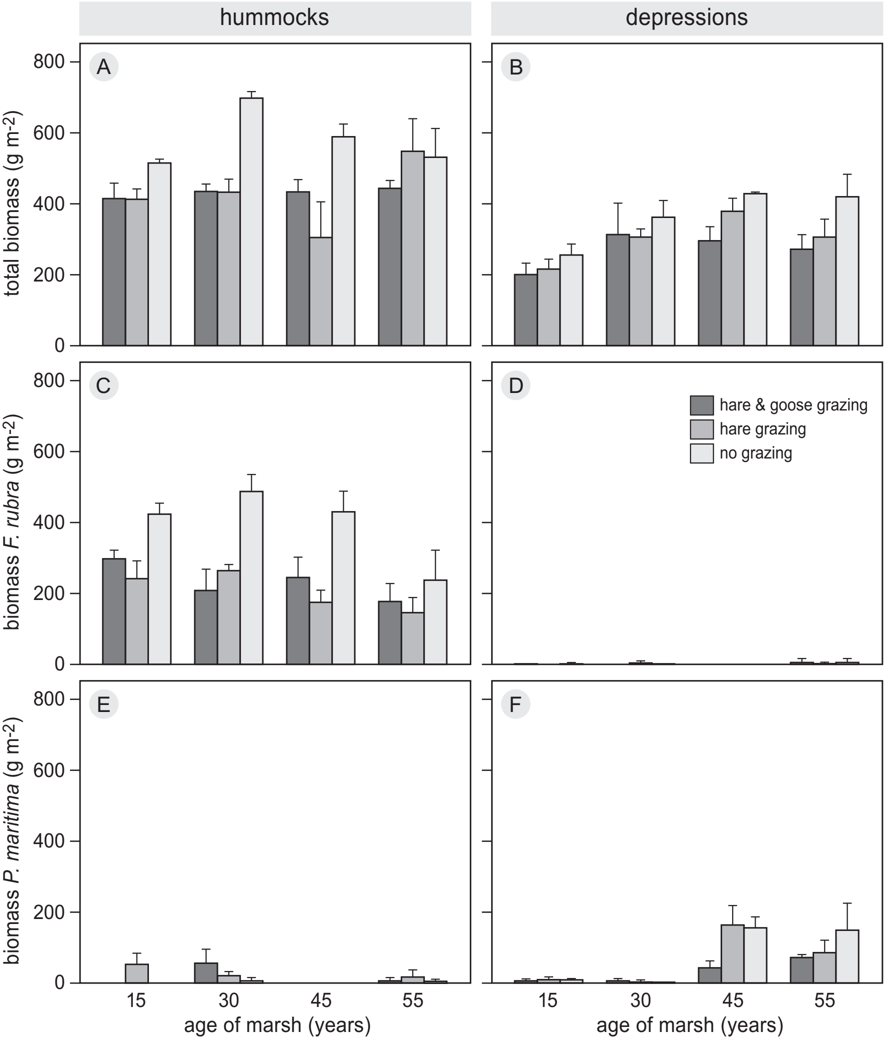

Figure 4.7. Total biomass (A, B), biomass of *Festuca rubra* (C, D) and biomass of *Puccinellia maritima* (E, F) estimated on hummocks and depressions along the chronosequence (15 to 55 yrs-old marsh). Differences are shown after small gazers (hare and geese vs. only geese) were excluded for approximately 1.5 years.

DISCUSSION

Our results clearly showed that the presence of topographic heterogeneity in the marsh soil enhanced plant diversity (number of species, equitability and Shannon diversity index) throughout long-term ecosystem development. Furthermore, it increased grazer abundance especially in early successional stages. Grazers had a large impact on the vegetation on hummocks as well as in depressions. They removed a significant proportion of the biomass present, with largest impact on hummocks in the younger marshes (Fig. 4.7). The hummocks were present already in the pioneer stage before fine-grained sediment was accumulated. The patterns got subsequently conserved under the fine-grained sediment layer in the older stages of marsh development. In young marshes the hummocks provided an additional niche, thereby facilitating the establishment of plant communities of later successional stages. As a result, the hummocks not only enhanced plant diversity, but also enhanced the suitability of marshes for small grazers, i.e. hare, early in succession.

Effects of topographic heterogeneity in the pioneer stage

In the pioneer stage we found higher elevated hummocks on the bare intertidal flat and all were dominated by *Puccinellia maritima*. Several pioneer species in marshes, e.g. *Spartina anglica* and *Puccinellia maritima*, are known to modify their environment by accumulating sediment (Figueroa et al. 2003, Van Wesenbeeck et al. 2008, Balke et al. 2012). Previous studies showed *Puccinellia maritima* can form higher elevated hummocks in the pioneer zone by decreasing erosion and increasing local sediment accumulation (Gray and Bunce 1972, Langlois et al. 2001, 2003). Repeated burial by sediment even enhanced clonal growth (Langlois et al. 2001). This would explain the strong positive correlation we found between increasing surface elevation with an increase in diameter of the hummocks. Plot 3 did not show the same correlation, but according to Langlois et al. (2003) hummock formation depends for a large part on the local hydrodynamic conditions. Limited sediment supply or too strong currents could reduce hummock formation.

Many studies in bio-geomorphic ecosystems have focused on the formation of topographic heterogeneity due to an interaction between vegetation and tidally introduced sediment (Stribling et al. 2007, Van Wesenbeeck et al. 2008, Fagherazzi et al. 2012, Balke et al. 2012). However, studies determining the effect of topographic heterogeneity on plant diversity have been limited so far (with exception of e.g. Ruifrok et al. 2014). In this study we showed that hummock presence facilitated establishment of other salt-marsh species in the pioneer zone. The number of species increased up to twelve species with increasing diameter of the patch (Fig. 4.3). Whereas, we never found more than four plant species on the adjacent bare intertidal flat. Stressful environmental conditions limit many salt marshes species from establishing in the pioneer zone (Davy et al. 2011). In harsh environments, positive interactions between plant species generally are more important in structuring local plant communities than negative interaction such as competition (Bertness and Leonard 1997, He et al. 2013). Stabilization of the soil by *Puccinellia maritima* could facilitate for the other salt-marsh plant species to successfully establish thereby enhancing plant diversity in the pioneer zone (Bertness and Leonard 1997, Langlois et al. 2003).

Development of topographic heterogeneity and the interaction with grazers throughout ecosystem development

Along the entire successional gradient the presence of topographic hummocks and depressions increased local plant diversity (enhancing number of species, equitability and Shannon diversity index, Fig. 4.5). As elevation is an important factor controlling species distribution in marshes (Olff et al. 1997, Davy et al. 2011), presence of the topographic heterogeneity resulted in multiple niches to co-occur on a small scale of a few square metres. A higher elevation generally results in a locally better drained and therefore more oxygen-rich soil (Davy et al. 2011). This will enhance the mineralization rate in the soil (Aller 1994) and hence plant production. An increase in productivity will speed up succession (Olff et al. 1997), allowing later successional species to become dominant at a much earlier stage (Table 4.1). Species such as *Puccinellia maritima* and *Limonium vulgare* first dominated on the hummocks but were found to become dominant in the depressions only in a later stage (Table 4.1 and 4.2). Thus, two co-occurring successional stages within this small-scale topographic heterogeneity of a few square metres will explain the increase in local plant diversity found throughout ecosystem development (Fig. 4.4).

Even at 120 yrs-old-marsh presence of topographic heterogeneity enhanced plant diversity. Presence of this heterogeneous pattern in soil morphology could be preventing *Elytrigia atherica* from becoming a dominant mono-culture. The high (66%) cover of *Elytrigia atherica* we found in homogeneous marsh (Table 4.2), is in line with previous studies that show that *Elytrigia atherica* becomes dominant at mature marshes (Veeneklaas et al. 2013, Wanner et al. 2014). Lower elevated areas generally have more water-logged soils, less oxygen in the soil, and hence more stressful environmental conditions (Davy et al. 2011). Depressions with these high-stress conditions surrounding the hummocks could be forming natural barriers preventing *Elytrigia atherica* from clonally expanding beyond the hummocks (Bouma et al. 2001, Scheepens et al. 2007). Based on our results we conclude that the presence of topographic heterogeneity not only boosts plant diversity in young marshes, but also maintained plant diversity in older mature successional stages.

In contrast to previous studies showing a maximum grazer abundance at marshes of intermediate ages (Van De Koppel et al. 1996, Olff et al. 1997), we found a high grazer abundance at young marshes when topographic heterogeneity was present. A high cover of *Festuca rubra* as well as an increased primary production on hummocks resulted in young marshes to become suitable for grazers at an earlier stage. *Festuca rubra* forms an important part of the diet of the grazers, i.e. hare and goose, in this ecosystem (Van Der Wal et al. 1998, Kuijper and Bakker 2005). Presence of topographic heterogeneity increased the cover of *Festuca rubra* throughout ecosystem development and this enhanced the suitability for the small grazers. On top of hummocks, we found a reduction in total biomass, ranging between 20% and 50%, when grazers were present (Fig. 4.7). This implies a very high grazing pressure on top of hummocks throughout ecosystem development.

Management implications

For conservation purposes and coastal defence many coastal ecosystems are currently being restored and created (Lithgow et al. 2013, Beauchard et al. 2013). They become increasingly important due to the effects of global climate change and the risk of flooding disasters that is increasing worldwide (Temmerman et al. 2013). With ecosystem restoration it is important to restore all ecosystem functions, which has been proven to be a difficult task (Mossman et al. 2012, Staszak and Armitage 2013). Especially a full recovery to similar biotic composition and diversity can take a very long time (over 50 years), if complete recovery is even possible (Borja et al. 2010, Mossman et al. 2012). Promoting the formation and/or actively creating small-scale topographic heterogeneity could speed-up recovery as it will positively affect plant diversity. With increasing plant diversity we could potentially increase the resilience of marshes to changing environmental conditions (Godfree et al. 2011), increasing human disturbances and loss of biodiversity (Hopkins and Del Prado 2007).

Many European marshes are grazed by livestock to increase plant species richness (Bouchard et al. 2003, Wanner et al. 2014). Previous studies showed large grazers can induce heterogeneity in the vegetation (Loucougaray et al. 2004, Nolte et al. 2013a) as well as topographic heterogeneity (Ruifrok et al. 2014) to form in marshes. This positively affects plant species richness (Loucougaray et al. 2004, Ruifrok et al. 2014) as well as invertebrate and avifauna abundance (Bakker et al. 1993). In this study we showed topographic heterogeneity is already present in (livestock-) ungrazed marshes, and that this topographic heterogeneity positively affected not only plant diversity but also grazer abundance. A next step is to study the development of the topographic heterogeneity when livestock is introduced in coastal marshes. This could impact plant diversity and grazers (vertebrate as well as invertebrate grazers) even more.

Long-term persistence of diversity in developing ecosystems

Similarly as in this study, many other studies in different ecosystems showed that environmental heterogeneity increases plant diversity (Stein et al. 2014). Additionally, it can impact other trophic levels as well: e.g. it increases insect-herbivore richness (de Araújo 2013) or alter the presence and impact of mammals within that ecosystem (Davidson and Lightfoot 2006). However, many studies do not take long-term ecosystem development into account (e.g. Wohlgemuth 1998, Davidson and Lightfoot 2006, Baker et al. 2013). In this study we found that the impact of environmental heterogeneity changed with age of the ecosystem. In young marshes, topographic heterogeneity enhanced grazer presence. In contrast, at intermediate age, grazers preferred the zones without topographic heterogeneity present. At mature marsh, the main impact of topographic heterogeneity was to maintain plant diversity and we did not find an impact on grazer presence anymore. Thus, it is important that we include long-term studies, when we want to determine the role of topographic heterogeneity in ecosystems and when we want to include multiple trophic levels.

ACKNOWLEDGEMENTS

We would like to acknowledge Esther Chang, Roel van Klink, Elske Koppenaal, Steffi Nolte, Freek Mandema and Maarten Schrama for assistence in the field and/or useful comments on this manuscript; and Dick Visser for preparing graphs. This study would not have been possible without many colleagues, bachelor students and friends assisting with fieldwork and setting-up the exclosures in 2009. This study was funded by the ZKO-NWO, project number 83908320, the Dutch organization for scientific research and the Schure-Beijerinck-Popping Fund.

5

Scale dependence of top-down vs. bottom-up control of plant composition and grazer abundance: a long-term case study on a tidal wetland ecosystem

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Henk Castelijns & Stijn Temmerman

ABSTRACT

Herbivores can exert top-down control on the vegetation composition, whereas other studies showed herbivore presence is controlled bottom-up. We hypothesize that top-down control by the vertebrate species on the primary production and bottom-up control by the primary producers on the vertebrate species within an ecosystem often co-occur, but operate on different spatial and temporal scales. Ultimately, together they will determine vegetation type and vertebrate abundances in an ecosystem. We used a highly dynamic marsh system with a large population of greylag geese (*Anser anser*), to study the importance of spatial scale in top-down vs. bottom-up control on food supply and geese abundance. No predators are present within this marsh and hunting was abandoned in 1990. The greylag geese grub for below-ground storage organs of pre-dominantly *Bolboschoenus maritimus*, thereby creating bare patches of a few square metres within the marsh vegetation. On this local patch scale, greylag geese showed top-down control by setting-back plant succession. Typical early-successional marsh species took advantage of the bare patches created by the geese. This reduced the food supply shortly, but the patches regenerated back within 12 years to a *Bolboschoenus maritimus* dominated vegetation type. On a landscape scale of square kilometres, we found an increase in marsh surface elevation that outpaced the sea-level rise. This resulted in long-term succession with a decreased cover of *Bolboschoenus maritimus*, thus imposing a bottom-up control on the food supply. Ultimately, we conclude that bottom-up control is causing the greylag geese to get evicted from the ecosystem due to a reduction in food supply in the long term of decennia. This study shows the importance of covering temporal and multiple spatial scales when studying plant-animal interactions and highlights the necessity of long-term and landscape-scale studies when estimating determining factors for species abundances.

INTRODUCTION

Grazing pressure by large populations of herbivores is increasing in many ecosystems (Van Eerden et al. 2005, Mysterud 2006, Kemp and Michalk 2007). Simultaneously, the carrying capacity of many ecosystems for herbivores is changing under the influence of global climate change (Zehnder and Hunter 2008, Madsen et al. 2011, Lohmann et al. 2012). Understanding which factors control herbivore abundances becomes increasingly important as environmental conditions will continue to change and grazing pressures could increase further (Madsen et al. 2011). Herbivore abundance is for a large part determined by the quantity and quality of the available food resources (Oene et al. 1999, White 2008). Presence of high quantity but low quality vegetation will limit the amount of herbivores able to feed successfully within an ecosystem.

The importance of top-down and bottom-up forces controlling population dynamics has been a long-standing debate in ecology (Hunter and Price 1992, Van De Koppel et al. 1996, Alberti et al. 2010). Sinclair and Krebs (2002) concluded that bottom-up control will primarily regulate population sizes of vertebrates, but this can be overruled by secondary processes such as top-down control by predators, social interactions within the species and disturbances. In this study, we will determine whether top-down control on the vegetation by the herbivores themselves, will be a key aspect that determines the food supply and grazer abundance in an ecosystem. We hypothesize that top-down control by the herbivores on the vegetation and bottom-up control through ecosystem properties, such as local productivity, often co-occur but operate on different spatial scales. Together, they will determine the food supply in an ecosystem. On the one hand, herbivores are known to affect the vegetation top-down (Olff and Ritchie 1998). They can change vegetation composition (e.g. Díaz et al. 2007), plant height (Andresen et al. 1990, Elschot et al. 2013), plant species richness (e.g. Bakker et al. 2006) as well as heterogeneity within an ecosystem (Oene et al. 1999, Adler et al. 2001). Such top-down control by grazing on the vegetation often occurs on a relatively small scale (few m^2) by impacting the vegetation locally (Olff and Ritchie 1998). Therefore, by changing the vegetation, herbivores can indirectly exert top-down control on their food resources. On the other hand, it has been shown that vegetation is controlled bottom-up, which in turn will determine the grazer abundance (Kuijper and Bakker 2005, White 2008, Center and Dray 2010). Such bottom-up control generally occurs on a landscape-scale (km^2) by large-scale external factors, e.g. natural succession (Van Der Wal et al. 2000b), available nutrients (Center and Dray 2010, Alberti et al. 2010) or other abiotic environmental factors such as weather conditions and tidal regime in wetland ecosystems (McKinney et al. 2001, White 2008, Davy et al. 2011). In these instances, large-scale bottom-up processes will primarily control grazer abundance through their food supply (Sinclair and Krebs 2002).

To test whether top-down and bottom-up controls co-occur and operate on different spatial scales, we studied plant-animal interactions both on a local (a few m²) and on a landscape scale (a few km²) throughout long-term ecosystem development. We used tidal marshes with extensive goose grazing as a model. Tidal marshes are highly dynamic ecosystems, where the marsh vegetation slows down tidal current and thereby stimulates mineral sedimentation, resulting in accretion and hence an increasing surface elevation with marsh age (e.g. Olff et al. 1997, Mudd et al. 2010, De Groot et al. 2011). If the marsh elevation rises faster than sea-level rise, this results in decreasing frequency, depth and duration of tidal inundations, and hence decreased accretion (Van Wijnen and Bakker 2001, Fagherazzi et al. 2012, Kirwan and Megonigal 2013). This dynamic character makes marshes very suitable to study ecosystem processes as strong successional differences can be shown in just a decade (Olff et al. 1997). Global increase in migrating goose populations has resulted in increasing grazing pressures on many tidal marshes (Madsen et al. 1999, Gauthier et al. 2005, Van Eerden et al. 2005, Voslamber et al. 2010). We focus on a large brackish tidal marsh in the southwest of the Netherlands (Saeftinghe), which provides feeding habitats for a large proportion of the population of greylag geese (Castelijns and Jacobusse 2010). These geese grub below-ground for storage organs of *Bolboschoenus maritimus* that are mainly present in lower elevated depressions near the creeks. By grubbing belowground, the greylag geese create bare patches (a few m²) in the marsh surface (Esselink et al. 1997, Mclaren and Jefferies 2004). Due to the abandonment of hunting, population size has strongly increased after 1990 (Castelijns et al. 1998), but reduced again in the past decade despite the absence of predators (Castelijns and Jacobusse 2010). Using the large marsh as a model, we aim at understanding the importance of top-down and bottom-up controls at various spatial scales on the long-term abundance of grubbing greylag geese in this marsh.

In this study, we specifically want to test two hypotheses that may explain the reduction in geese population size as observed in the study area: 1) local top-down control of grubbing greylag geese on the vegetation resulted in degradation of the marsh surface, a reduction in their preferred food source *Bolboschoenus maritimus*, and thus a reduction in geese abundance; 2) landscape-scale bottom-up control of sediment accretion on vegetation development resulted in a higher elevation, a reduction in the overall *Bolboschoenus maritimus* cover, and thus a reduction in geese abundance. Testing these two hypotheses will ultimately reveal to which extent herbivore abundance is controlled by local-scale (few m²) top-down control through grubbing greylag geese, or by landscape-scale (few km²) bottom-up control by sediment accretion. We tested both hypotheses by using long-term time series of goose counts (1987-2010), aerial photographs (1979-2008), vegetation maps (1979-2010) and elevation maps (1931-2010) to determine both local (m²) and landscape-scale (km²) ecosystem changes over time.

METHODS

Study site

The study area, Saeftinghe, is located in the Western Scheldt estuary in the Netherlands (Fig. 5.1, 51°21'N, 4°11'E). It is considered one of the largest brackish marshes in Western Europe, approximately 28 km² in size, and is an important feeding habitat for large populations of wintering greylag goose, *Anser anser* (Castelijns et al. 1998, Castelijns and Jacobusse 2010). A small part of the marsh is grazed by cattle. The largest part has been abandoned, but has been extensively sheep grazed up to 1993. Outside the cattle-grazed marsh the most important vegetation types are dominated by *Phragmites australis*, *Elytrigia atherica* and *Bolboschoenus maritimus*. *Phragmites australis* is mostly limited to the eastern part of Saeftinghe near the seawall, *Elytrigia atherica* is mainly dominating higher elevated creek bank levees and *Bolboschoenus maritimus* is mainly limited to the depressions between the creek bank levees. Only since the 1980s has this marsh become an important staging and wintering site for greylag geese. Till the 1990s, the greylag geese population size was limited by a high hunting pressure, but goose numbers increased rapidly when hunting was abandoned after 1990 (Fig. 5.3) (Castelijns et al. 1998). Greylag geese prefer to feed on the below-ground storage organs of *Bolboschoenus maritimus* for which they grub into the marsh soil (Amat 1986, Esselink et al. 1997). A study by Castelijns et al. (1998) showed that in the winters between 1994 and 1997, the main food sources of greylag geese in Saeftinghe consisted for 49% of tubers of *Bolboschoenus maritimus*, for 33% of above-ground plant parts of other marsh species such as *Aster tripolium* (personal observations), for 10% of agricultural plants (growing on

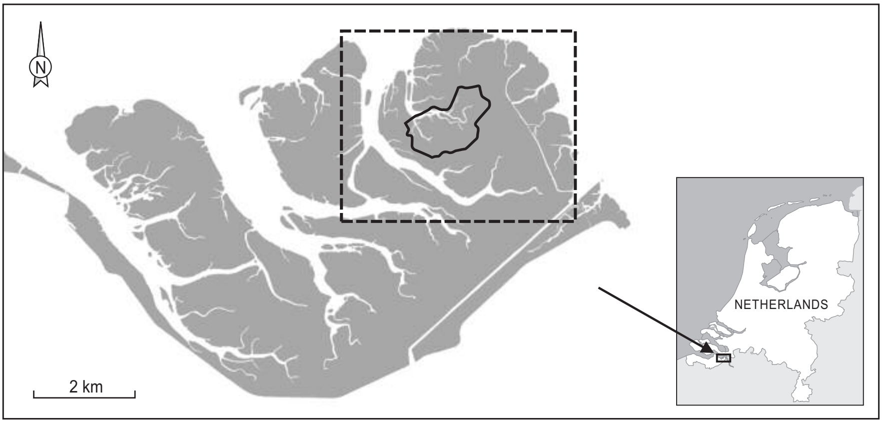

Figure 5.1. The study area located in the south of the Netherlands. It is a large brackish marsh 2800 ha in size. The greylag geese counts and vegetation covers were estimated on the entire marsh area. The black line indicates the area where we measured the marsh accretion rate (Approximately 2 km²), while, the dashed line indicates the area where we studied the regeneration of the depressions (approximately 7 km²).

arable fields adjacent to the marsh) and for 8% of seeds of *Elytrigia atherica*. They concluded this based on microscopic evidence found in fresh droppings that were collected in the field together with field observations (Castelijns et al. 1998).

Estimating the population dynamics of greylag geese

Between 1987 and 2011, numbers of greylag geese in Saeftinghe were estimated on a monthly interval from July until March the consecutive year. The majority of the geese arrive in October and all have left again by the end of February, except for a small breeding population that will remain present year round. Goose numbers were estimated on the entire marsh area (28 km^2) (data provided by Natuurbeschermingsvereniging De Steltkluut). To include estimates of the population before 1987, we included the population size estimated in literature (Castelijns and Jacobusse 2010). Between 1980 and 2011, the numbers of geese in the Netherlands were estimated based on local goose counts performed in ecosystems throughout the Netherlands in a similar manner as in Saeftinghe (data provided by Sovon).

Top-down control of grubbing geese on vegetation on a local scale

To determine the strength of the top-down control of greylag geese on the local vegetation, we studied the formation of bare patches within the vegetation by grubbing greylag geese and the subsequent re-generation of these bare patches by vegetation re-establishment. We used false-colour aerial photographs from 1979, 1990, 1998, 2004 and 2008 and analysed them in ArcGIS. We identified all bare patches in the eastern region of Saeftinghe, an area approximately 7 km^2 in size (most central point: 51°21'45N, 4°11'46E, Fig. 5.1). For each bare patch, we determined year of presence as well as absence. Once the bare patch was not visible on the aerial photograph anymore, we assumed vegetation had re-established in these bare patches (Fig. 5.2). This way, we could determine for each bare patch the minimum number of years that the vegetation had re-established in the bare patch (i.e., the minimum re-generation time). For example: when a bare patch present in the photo of 1990 had disappeared from the photo of 2004 (Fig. 5.2), we assumed this bare patch had re-generated for at least six years when we measured the vegetation composition in 2010. As we did not have aerial photographs for every year, we have five classes of 0, 2, 6 and 12 years of minimum re-generation time. After determining the coordinates from the photographs, we visited all the regenerated bare patches in the field in July and August of 2010. For each regenerated patch, we performed vegetation composition measurements in 2 m x 2 m plots using the decimal scale (Londo 1976). In order to assess the impact of greylag geese on the vegetation composition, we compared the vegetation composition in re-generated patches with the vegetation composition in depressions unaffected by the geese. As geese prefer to feed on the below-ground tubers of *Bolboschoenus maritimus*, we considered the *Bolboschoenus maritimus* dominated

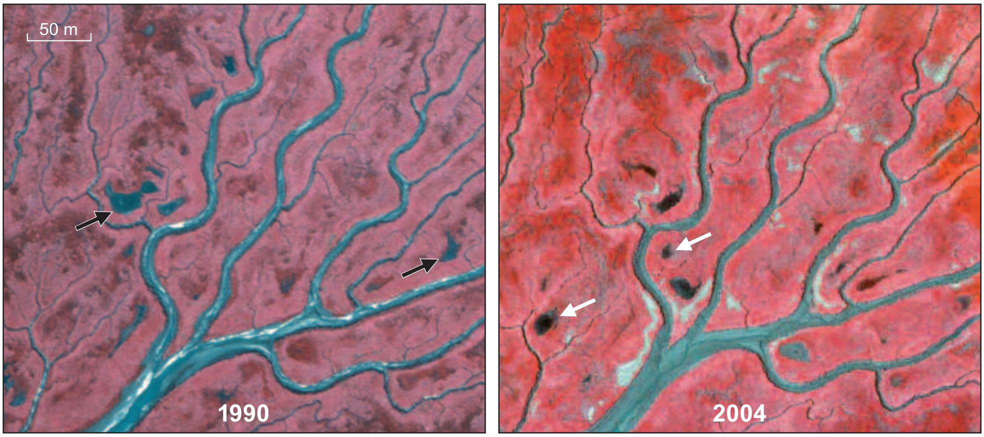

Figure 5.2. Depressions present and absent on two aerial pictures comparing 1990 with 2004. The black arrows indicate depressions present in 1990 that had disappeared in 2004 and the white arrows point to depressions present in 2004 that were not present yet in 1990.

vegetation type as the original vegetation type before geese started grubbing and created the bare patches. Hence, as a control, we measured vegetation composition in 13 plots located in *Bolboschoenus maritimus* dominated vegetation, where no visible signs of geese grubbing were present. As only three bare patches were recorded in the aerial photograph of 1979, we excluded this year from further analyses.

Bottom-up control by system development on a landscape scale

To determine the strength of bottom-up control on the marsh vegetation, i.e. the control of vertical sediment accretion on increase of marsh elevation relative to sea level and hence on succession of *Bolboschoenus maritimus* vegetation towards other vegetation types, we determined both changes in vegetation type as well as long-term surface elevation changes. To determine cover of different vegetation types we analysed aerial photographs of Saeftinghe from 1979, 1998, 2004 and 2010. Based on the false colour ranges, different vegetation types could be identified by Rijkswaterstaat. For each type, multiple vegetation composition measurements were performed in the field. Ultimately, specific vegetation types were linked with specific colour ranges in the aerial photographs, and this resulted in vegetation maps (maps and data provided by Rijkswaterstaat). This method has been intensively used and validated before, for more information see Reitsma (2006). Generally, pioneer marsh harbours a combination of *Salicornia europaea* and *Spartina anglica*, which will be replaced by secondary species such as *Puccinellia maritima*, *Aster tripolium* and *Glaux maritima* (for further details see e.g. (Olff et al. 1997). Ultimately, the lower marsh becomes dominated by a cover of *Bolboschoenus maritimus* and the higher marsh by *Elytrigia atherica* and *Phragmites australis*. In this study we focused on the total cover of three dominant vegetation types dominated by *Bolboschoenus maritimus*, *Elytrigia atherica* or *Phragmites australis*. When one of these three species was either dominant (at least 50% cover) or indicated as co-dominant, that specific vegetation type was included in the analysis. All other vegetation types were excluded from the analysis.

The distribution of marsh plant species is determined for a large part by the local marsh surface elevation (Davy et al. 2011). As marshes accumulate tidally introduced mineral sediment, the marsh surface increases in elevation as marshes become older (Lovelock et al. 2011, Suchrow et al. 2012). With ecosystem development and an increase in surface elevation, a change in vegetation composition is expected (Olff et al. 1997). An area of approximately 2 km² was used to estimate long-term marsh surface elevation change (51°21’48N, 4°11’15E). Data were available for the years 1931, 1951, 1963, 1992, 2004 and 2010. For the years 1931, 1951, 1963 and 1992 data were provided as Digital Terrain Models (DTMs) with a resolution of 20 m x 20 m. These are based on topographic and bathymetric surveys performed by the Dutch and Belgian waterway management authorities (see also Wang and Temmerman 2013; Vandenbruwaene et al. 2013). Topographic surveys were performed that resulted in elevation data points with a density of 1 point/7500 m². The elevations were mapped to 0.1 m relative to the Dutch Ordnance Level (NAP, which is close to mean sea level at the Dutch coast), resulting in a maximum vertical error of ± 0.05 m. For the more recent time steps (2004 and 2010), DTMs with a 2 m x 2 m resolution were available based on LIDAR data. These LIDAR surveys were carried out during low tide with a density ranging from 1 point/16 m² to several points/m² and a vertical accuracy of 0.2 m. The channel networks for 1931 and 2010 were merged and used as a mask to exclude grid cells located within the tidal channel network. The changes in the creek edges between the tidal channel networks of 1931 and 2010 were fairly limited (slow migration rate of the channels). We used this mask for all time steps, as the creek edges in the intervening time steps between 1931 and 2010 will be located within this mask. Besides the mean platform elevation of the selected site, additionally the standard deviation was calculated representing the spatial variation in marsh platform elevation. Historical data on mean high water level (MHWL) and mean high water level at spring tide (MHWLS) were derived from the nearby tidal gauge station at Bath. The marsh surface elevation and the levels of MHWL and MHWLS are expressed in metres above the Dutch ordnance level (NAP).

Data analyses

To link the number of bare patches to the number of geese we calculated the number of bare patches as well as number of geese per unit marsh surface area (ha). We first determined the maximum number of geese for the wintering season of each year, i.e. starting from October up until March the next year. As geese grub during winter and the number of bare patches is based on aerial photographs taken in summer, we averaged the maximum number of geese in the two years prior to the year the number of bare patches was identified. Cover of each plant species in the re-generating bare patches was tested against the cover of that same species in the control plot using two-tailed t-tests. A p-value < 0.05 was considered to indicate significant differences.

RESULTS

Estimating the population dynamics of greylag geese

After hunting was abandoned in 1990, population size of wintering greylag geese in Saeftinghe increased substantially, from approximately 5,000 in 1985 to over 50,000 geese in 1998-1999 (Fig. 5.3). Thereafter, the number of geese showed a strong decrease again. Meanwhile, the number of geese in the Netherlands was still increasing (Fig. 5.3). This implies that the decrease in Saeftinghe is only a local effect that is likely due to a decrease in food supply, given that there is a lack of predators in this ecosystem.

Top-down control of grubbing geese on a local scale

The total number of bare patches and the population size of the greylag goose showed similar trends (Fig. 5.4). That is, both increased up to 2004 and showed a similar decrease after 2004. They were strongly positively linearly related (number of bare patches = 3.3 * number of greylag geese – 7.3, $R^2 = 0.93$). On a marsh area of approximately 7 km^2 we identified in total 107 bare patches. Of these patches 9, 7, 25 and 66

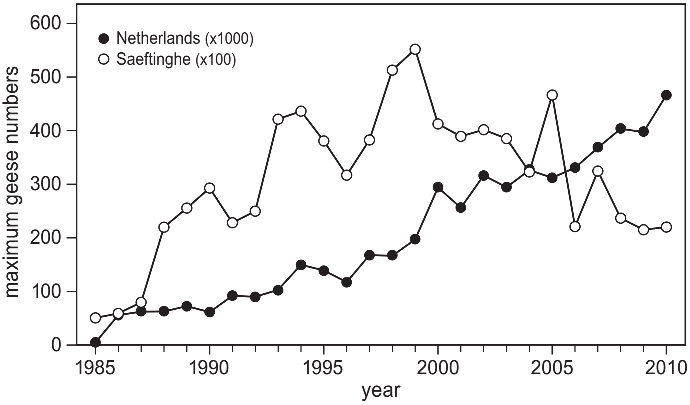

Figure 5.3. Maximum number of wintering greylag geese, estimated annually in the Netherlands (± 41.500 km2) and Saeftinghe (± 28 km^2). Maximum numbers are estimated on a monthly interval between fall and spring of the consecutive year. Goose numbers are shown x1000 for the Netherlands and x100 for Saeftinghe (data from Sovon Vogelonderzoek Nederland and Natuurberschermingsvereniging De Steltkluut). Data between 1985 and 1987 were obtained from literature (Castelijns and Jacobusse 2010).

became re-vegetated in 1990, 1998, 2004 and 2008 respectively (Table 5.1). Most of them were between 4 and 10 m in diameter, with some exceptions ranging up to 25 m in diameter. As a control, we studied 13 plots in non-disturbed *Bolboschoenus maritimus* dominated vegetation.

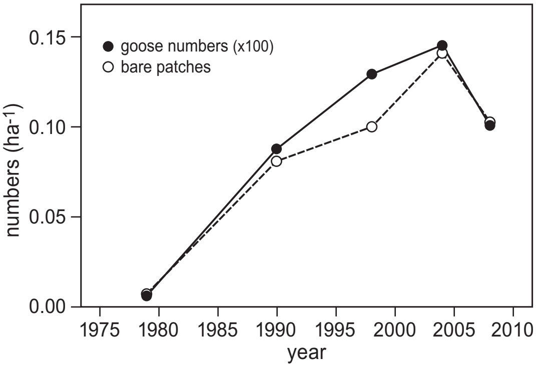

Figure 5.4. The temporal evolution of the number of bare patches and the number of greylag geese. Numbers of geese were determined by the maximum number of geese counted for the entire marsh area (28 km²) and these were averaged over the two years prior to the year the number of bare patches was determined. Number of bare patches was determined for the eastern part of the marsh (approximately 7 km²).

Table 5.1. Vegetation cover (%) estimated per 2 m x 2 m in bare patches after 0, 2, 6 and 12 years of vegetation re-establishment (average ± SE). Plots estimated in *Bolboschoenus maritimus* dominated vegetation are shown as control plots indicating the vegetation composition before greylag geese grub for below-ground tubers and hence remove the vegetation to form bare patches.

	Years after vegetation re-established				
	0	2	6	12	Control plot
Sample size (n)	66	25	7	9	13
Bare	79 ± 3	43 ± 6	21 ± 8	19 ± 7	12 ± 4
Litter	1 ± 1	6 ± 5	3 ± 5	17 ± 5	12 ± 4
Agrostis stolonifera	1 ± 1	4 ± 2	18 ± 10	6 ± 3	10 ± 5
Aster tripolium	8 ± 2	28 ± 5	13 ± 8	8 ± 5	0
Atriplex prostrata	1 ± 1	5 ± 2	3 ± 2	4 ± 2	9 ± 3
Elytrigia atherica	0	4 ± 3	13 ± 8	15 ± 6	11 ± 4
Glaux maritima	2 ± 1	0	6 ± 4	0	0
Juncus Gerardii	0	0	0	0	1 ± 1
Puccinellia maritima	1 ± 1	5 ± 2	5 ± 3	2 ± 2	0
Salicornia europaea	6 ± 2	3 ± 2	7 ± 6	0	0
Bolboschoenus maritimus	2 ± 1	2 ± 1	17 ± 8	38 ± 4	46 ± 4
Spartina anglica	0	0	0	0	3 ± 3
Total cover	20 ± 3	53 ± 6	79 ± 8	64 ± 8	76 ± 4

Several early-successional species were found in the bare patches which were not present in the control plots, implying greylag geese facilitate for these early-successional species (Table 5.1, Fig. 5.5). *Salicornia europaea* was observed as one of the first species re-establishing in the bare patches. However, cover was generally limited and therefore, it was not significantly different from the control plots where the species was never present (Fig. 5.5A). We found significantly higher cover of both *Aster tripolium* and *Puccinellia maritima* in the bare patches compared to the control plots (Fig. 5.5B and C). Both species, *Elytrigia atherica* and *Bolboschoenus maritimus*, gradually re-colonized

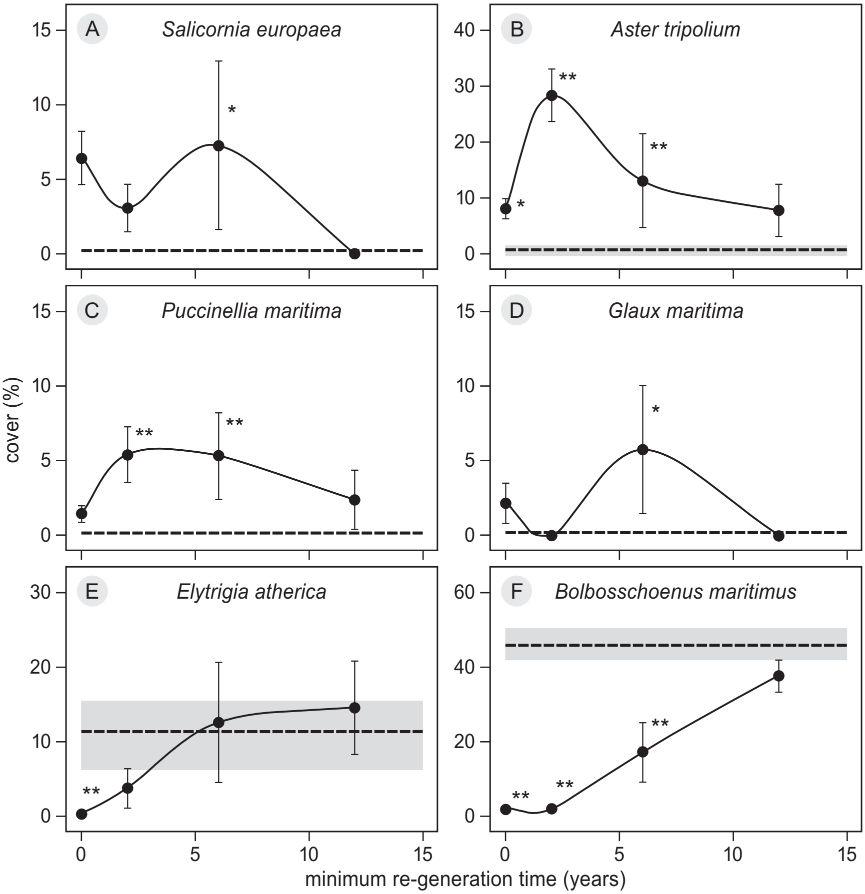

Figure 5.5. The cover of six plant species that established in the bare patches (average ± SE) showed in relation to the minimum number of years of re-generation (note: different y-axes for different species). Data are shown for different times of re-generation, after 0, 2, 6 and 12 years (with n = 66, 25, 7 and 9, respectively). Average cover of each species in control plots (in *Bolboschoenus maritimus* dominated vegetation, n = 13) is indicated with a black broken line surrounded by the standard error (grey area). For each point the significant difference between bare patch and control plot were indicated (** = $p < 0.05$, * = $p < 0.10$).

the bare patches and re-generated back to similar cover percentages as the control plots (Fig. 5.5E and F). *Elytrigia atherica* reached a similar cover of approximately 11% after six years of re-generation, and *Bolboschoenus maritimus* reached a similar cover of approximately 50% after 12 years of re-generation. Even though greylag geese did degrade the marsh locally thereby reducing their food supply, the bare patches re-generated back to a similar vegetation type as the control plots after about a decade.

Bottom-up control by system development on a landscape scale

Total cover of the three potential late successional vegetation types all clearly showed an increase from 1979 up to 2004 (Fig. 5.4). However, between 2004 and 2010 both *Phragmites australis* and *Elytrigia atherica* types continued to increase, whereas the *Bolboschoenus maritimus* vegetation type showed a decrease in cover from 8.8 km^2 in 2004 to 4.6 km^2 in 2010. Thus, the evolution of the *Bolboschoenus maritimus* vegetation cover (Fig. 5.6), the number of geese and the number of bare patches (Fig. 5.4) followed a similar temporal evolution. They increased to a maximum in 2004 and after that decreased again.

The surface elevation of the marsh platform strongly increased with time at a rate which was faster than the rise of mean high water level (MHWL) (Fig. 5.7). The rate of surface elevation change reduced from 2 cm year^{-1} towards 1 cm year^{-1} in the past few decades, but this was still higher than the average 0.4 cm year^{-1} increase in MHWL between 1930 and 2010. Hence, from 1931 to 2010 the marsh evolved from a low elevated tidal marsh (mean platform elevation 0.47 m below MHWL) towards a more high elevated tidal marsh (mean platform 0.31 m above MHWL) and through natural succession the vegetation composition is changing accordingly (increase in cover of *Elytrigia atherica* and *Phragmites australis*, whereas *Bolboschoenus maritimus* vegetation type decreased in cover).

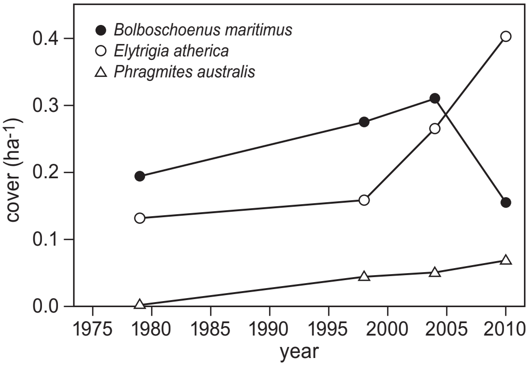

Figure 5.6. The temporal evolution of the total cover of the three dominant vegetation types (*Bolboschoenus maritimus*, *Elytrigia atherica* and *Phragmites australis*) estimated on the entire marsh area (cover of the plant species is given in ha per ha of marsh surface area).

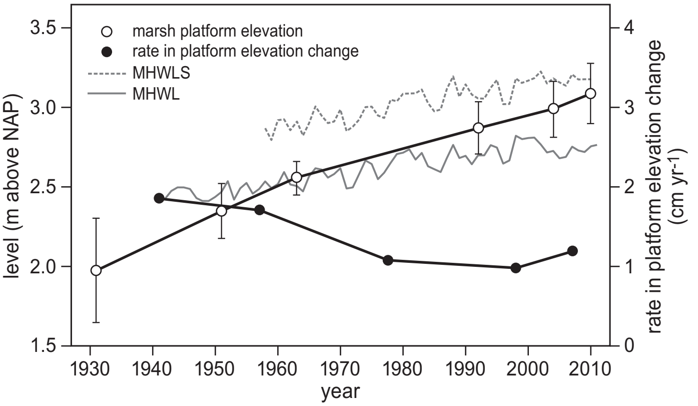

Figure 5.7. Marsh platform elevation change (m) and rate of elevation change (cm yr-1) in relation to Mean High Water Level (MHWL) and Mean High Water Level during Spring tides (MHWLS). All levels are shown relative to the Dutch ordnance level (NAP).

DISCUSSION

Our results are partially in line with our first hypothesis that top-down control of grubbing geese on the vegetation resulted in local degradation of the marsh surface, a reduction in their preferred food source *Bolboschoenus maritimus*, and this would reduce the food supply for the geese. However, these effects were limited in time, as in 12 years the patches regenerated back to a *Bolboschoenus maritimus* vegetation type. This is also in contrast to previous studies, where grubbing geese caused large-scale marsh degradation that continued even after the geese had disappeared (Jefferies et al. 2006, Peterson et al. 2013). Our results were in line with our second hypothesis that landscape-scale bottom-up control of sediment accretion on vegetation development resulted in a higher elevation, a reduction in the overall *Bolboschoenus maritimus* cover (through vegetation succession during 30 years), and thus would result in a reduction of the food supply for geese. Present results showed that bottom-up and top-down controls can co-occur, be it on different spatial as well as temporal scales. Overall, we found that in the long-term (decades) the food supply for greylag geese is controlled bottom-up by landscape-scale ecosystem development driven by sediment accretion, rather than by top-down control of the geese on the vegetation development.

Local-scale top-down control of grubbing geese

On a local patch scale of a few square metres, grubbing greylag geese showed to exert top-down control on the vegetation by creating bare patches thereby reducing their food source. This is in line with previous studies showing that grubbing geese can have strong negative effects on coastal habitats (Kerbes et al. 1990, Srivastava and Jefferies 1996, Esselink et al. 1997, Mclaren and Jefferies 2004). However, in contrast to these studies, we found regeneration of the patches to a similar vegetation type, whereas some conclude regeneration might not even be possible (Peterson et al. 2013). In the present study, we could not determine when the first pioneer species successfully established in the bare patches. However, we did find recovery of the patches towards a similar vegetation type dominated by *Bolboschoenus maritimus* (Fig. 5.5). During recovery several early successional species established in the bare patches. Therefore, presence of grubbing geese resulted in our study in a local set-back of the vegetation succession and not in the more permanent and large scale degradation as observed in previous studies (Jefferies et al. 2006, Peterson et al. 2013). It has been shown that small grazers, such as hare, can retard succession (Kuijper and Bakker 2005, Gedan et al. 2009), whereas large grazers, such as livestock, can bring back earlier-successional plant species in older marsh systems (Bos et al. 2002). Our results showed that greylag geese can temporarily bring back younger-successional plant species, be it on a much smaller scale of a few m^2 instead of the potential km^2 wide impact of cattle (Bos et al. 2002).

Landscape scale bottom-up control through marsh accretion

The marsh surface increased rapidly due to high accretion rates that outpaced local sea-level rise (Fig. 5.7). Marsh surface elevation and inundation frequency are important determinants for the distribution of plant species in marshes (Olff et al. 1997, Davy et al. 2011). *Bolboschoenus maritimus* is the preferred food choice for greylag geese (Amat 1995, Castelijns et al. 1998) and this plant species generally dominates the lower elevated depressions in between creek bank levees with high soil water availability (Dijkema 1990, Piernik 2005). *Elytrigia atherica* is generally limited to higher elevated creek bank levees without water logging conditions (Davy et al. 2011, Veeneklaas et al. 2013). An increase in marsh elevation and a reduction in water logging conditions enable *Elytrigia atherica* expansion from the higher elevated levees towards the lower elevated depressions, thereby outcompeting *Bolboschoenus maritimus* and reducing it in cover.

Herbivore presence in time

A bottom-up induced landscape-scale decrease in the main food source will reduce the food supply for the greylag geese and reduce their abundance. This is especially the case when not all *Bolboschoenus maritimus* present in the system will be accessible for the geese, as is highly likely given earlier studies. These previous studies showed that greylag geese need a local disturbance of otherwise tall and dense *Bolboschoenus maritimus* vegetation, so that they can land in the disturbed area and use such spots to get access to the *Bolboschoenus maritimus* food source (Esselink et al. 1997). Furthermore, greylag geese can only forage on small, newly developed tubers of limited sizes (Amat and Varo

2008). Moreover, greylag geese might be limited to *Bolboschoenus maritimus* in lower elevated depressions with water-logging conditions. This will soften the soil and allow the geese to easier grub into the soil (Esselink et al. 1997). A landscape-scale increase in the marsh platform elevation, as observed in Saeftinghe, generally decreases tidal inundation and increases soil drainage and soil compaction (He et al. 2011). This will reduce the number of *Bolboschoenus maritimus* patches that are accessible for the geese even further. Ultimately, we showed both top-down and bottom-up control on the vegetation occurred simultaneously but on different spatial scales and the effect changed along a temporal scale. Based on the increase in marsh surface elevation and the natural succession towards *Elytrigia atherica* on a landscape scale, we conclude that grazer abundance is pre-dominantly controlled bottom-up on a landscape-scale (km^2).

Conservation implications

Global increase in migrating goose populations has resulted in increasing grazing pressures on many tidal marshes (Gauthier et al. 2005, Van Eerden et al. 2005, Jefferies et al. 2006, Voslamber et al. 2010). The impact of such high grazing pressures differs between marshes and could depend on local abiotic stress as well as heterogeneity present within the system. Firstly, extreme abiotic conditions (Shumway and Bertness 1994, Mclaren and Jefferies 2004, Davy et al. 2011, Peterson et al. 2013) or low tidal regime (Kirwan and Guntenspergen 2010) can limit successful (re-) establishment and development of many marsh species. Our study site is a relatively high productive, brackish marsh with a high tidal regime. Re-colonization by early successional species in the bare patches will be less limited in this marsh, compared to less productive, more saline marshes with low tidal regimes. Secondly, Saeftinghe is a very heterogeneous marsh. Creeks are bordered by higher elevated levees dominated by *Elytrigia atherica*, alternating with small depressions covered by *Bolboschoenus maritimus*. When grubbing geese start feeding on below-ground tubers, they generally continue until all their preferred food choice is removed (Esselink et al. 1997, Jefferies et al. 2006). According to many studies, this foraging behaviour results in degradation of large marsh areas (Kerbes et al. 1990, Jefferies et al. 2006, Peterson et al. 2013). Due to the patchy and heterogeneous structure of Saeftinghe, *Bolboschoenus maritimus* is present in smaller patches forcing the geese to continuously move on to new unexplored patches and thereby limiting their potential detrimental impact on the marsh' vegetation. Thus, the impact of grubbing geese could be very marsh specific and may depend on many different environmental conditions such as present heterogeneity and local abiotic conditions.

This study showed the complexity of determining the factors that control grazer abundance within an ecosystem. Many studies try to determine sustainable population densities for grazers in ecosystems by monitoring the food supply, but often they focus on the top-down control by the grazers and do not include large- scale, bottom-up controls on the food supply (e.g. (Hansen et al. 2006, Perea et al. 2015), but see also (Madsen et al. 2011). Marino et al. (2014) found that the number of grazers sustainable within an ecosystem is not static but fluctuates with annual precipitation. Additionally, we showed that next to environmental conditions, such as weather, and the impact of the grazers themselves, also the natural development of an ecosystem needs to be taken in account when we want to estimate the number of grazers that can be maintained sustainable within an ecosystem.

ACKNOWLEDGEMENTS

We would like to thank Annette Wielemaker for help with arcGIS; Dick Visser for preparing graphs; and both de Natuurberschermingsvereniging De Steltkluut and Sovon for providing data on the populations of greylag geese on Saeftinghe and the Netherlands. Furthermore, we would like to thank het Zeeuwse Landschap for allowing us to work in Saeftinghe and both Rijkswaterstaat and RIKZ for providing the aerial photographs, vegetation maps and surface elevation data. This work was funded by the NWO- ZKO, project 83908320, the Dutch organization for scientific research.

6

General synthesis: vegetation patterns and grazers on tidal marshes

Kelly Elschot

INTRODUCTION

Grassland ecosystems are used for livestock grazing on a global scale, resulting in very high grazing pressures (Kemp and Michalk 2007). Additionally, due to changing environmental conditions and human impact, populations of native grazers are reducing in some ecosystems (De Visser et al. 2011), while they are increasing in other ecosystems (e.g. Fox et al. 2005). With these global changes in grazing pressures, it is important to gain understanding on how they impact vegetation characteristics, the interactions between grazers and vegetation, and the effects on important ecosystem processes. In this thesis I studied this, using tidal marshes as a model ecosystem.

Many different grazers are present on tidal marshes. Migratory birds use marshes as stop-over sites along their migration route or as staging site during winter (Madsen 1991, Van Der Graaf et al. 2007). Small grazers, such as hare and rabbits, can graze on the marshes year-round (Van Der Wal et al. 2000c). Additionally, large grazers, such as cattle, sheep or horses, are kept on the marshes for nature management or agricultural purposes (Bakker 1989, Kiehl et al. 1996, Bouchard et al. 2003, Nolte et al. 2013a). Both small and large grazers can have a strong impact on the vegetation (e.g. Andresen et al. 1990, Silliman et al. 2005, Bertness et al. 2014), compact the soil (Schrama et al. 2013, Nolte et al. 2013b) and alter accretion rates (Suchrow et al. 2012, Nolte et al. 2015). Small grazers are known to retard succession (Van Der Wal et al. 2000, Kuijper and Bakker 2005, Gedan et al. 2009), while large grazers can set back the successional clock by bringing back young-successional plant species, thereby boosting plant diversity (Bos et al. 2002). In the past few decades, populations of geese have increased substantially and this resulted in increased grazing pressures on coastal wetlands as well as agricultural fields (Kerbes et al. 1990, Madsen 1991, Gauthier et al. 2005, Van Eerden et al. 2005, Wuczyński et al. 2012). For conservation purposes, we need to increase our understanding of how grazer presence impact important marsh characteristics, and how this in turn affects grazer abundance.

THESIS OVERVIEW

In this thesis, I used long-term field-based experiments together with long-term datasets, to study the role of grazers in tidal marshes and how grazer abundance is affected by small-scale topographic heterogeneity in the marsh platform. I included different spatial scales (few square metres vs. kilometres) as well as different grazer types (small grazers like hare and geese vs. large grazers like cattle and above-ground grazing by cattle, hare, Barnacle geese and Brent geese vs. below-ground grubbing by Greylag geese). Firstly, I determined how presence of small grazers and large grazers affect important marsh characteristics: vegetation height, the marsh accretion rates (**chapter 2**) and carbon sequestration (**chapter 3**). To unravel the formation of small-scale topographic heterogeneity in tidal marshes, I compared similar topographic patterns present in four different European marshes in **box 1**. In **chapter 4** I studied how the presence of the small grazers as well as the local plant diversity is affected when this topographic heterogeneity is present within the marsh. Finally, I included small-scale topographic heterogeneity that is created by grubbing Greylag goose, *Anser anser*, and studied their impact on plant diversity as well as the abundance of Greylag geese on the marsh (**chapter 5**).

I divided this study in three main questions:

1. What is the effect of long-term, above-ground grazing on the local marsh vegetation, salt-marsh accretion rates and carbon sequestration?
2. What is the effect of topographic heterogeneity on the local marsh vegetation and grazer presence?
3. What is the long-term effect of below-ground grubbing on the marsh vegetation and how this in turn affects grazer abundance?

These questions are discussed in detail in the following sections. The main findings are summarized in table 6.1.

MAIN FINDINGS

1. What is the effect of long-term, above-ground grazing on the local marsh vegetation, salt-marsh accretion rates and carbon sequestration?

Effects of grazing on vegetation height and marsh accretion rates

Marshes need to accumulate enough sediment from the inundating water, to keep up with the accelerating sea level (FitzGerald et al. 2008, Church and White 2011). Many studies already have tried to predict this by estimating the marsh accretion rates (Van Wijnen and Bakker 2001, Kirwan and Megonigal 2013). However, the number of studies focusing on the long-term effects of herbivores on vegetation structure and subsequent effects on marsh accretion has been limited (but with exception of: e.g. Neuhaus et al. 1999, Suchrow et al. 2012, Nolte et al. 2013b, 2015). In **chapter 2**, we showed that both small grazers (hare, Barnacle goose and Brent goose) and large grazers (cattle) reduced vegetation height. However, they did not affect sediment deposition. An important result we found was that trampling by large grazers negatively affected marsh accretion rates by compacting the soil, whereas small grazers had no effect on the marsh accretion rates. Grazing by livestock is used as a tool in nature management to maintain plant diversity in many European marshes (Bakker 1989, Kiehl et al. 1996). Although we did not find that grazers significantly reduced the amount of sediment deposited on the marsh platform, we found a reduced marsh accretion rate and proposed that soil compaction by large grazers needs be taken into account when estimating the ability of coastal systems to cope with an accelerating sea-level rise.

EFFECTS OF GRAZING ON CARBON SEQUESTRATION

Another effect of grazers on marshes that has received limited attention is the impact of grazers on carbon sequestration. Tidal marshes can trap large amounts of carbon in the marsh soil (e.g., see Laffoley and Grimsditch 2009, Mcleod et al. 2011). However, knowledge of how presence of grazers affects soil carbon sequestration is limited. In **chapter 3** we estimated total accumulated organic carbon in soils of a back-barrier salt marsh, and determined how this is affected by long-term grazing by both small and large grazers. Small grazers (hare, Barnacle goose and Brent goose) had a limited effect on total accumulated organic carbon, whereas large grazers (cattle) enhanced carbon content in the marsh soil substantially, due to soil compaction and a shift in biomass distribution in the

Table 6.1. A summary of the main findings presented in this thesis. Each column represents one type of grazer included in this thesis, as well as presence of topographic heterogeneity. Each row shows a marsh characteristic that was either positively (+), negatively (−) or unaffected (0) by the grazing type or topographic heterogeneity present. Empty cells indicate that it was not estimated in this study. The corresponding chapter is given in brackets behind each effect.

Marsh characteristic	**Small above-ground grazers** (hare, Barnacle goose and Brent goose)	**Large above-ground grazers** (cattle)	**Topographic heterogeneity**	**Small below-ground grubbers** (Greylag geese)
Vegetation height	– (Ch. 2)	– (Ch. 2)		– (Ch. 5)
Sediment deposition	0 (Ch. 2)	0 (Ch. 2)		
Bulk density	0 (Ch. 2)	+ (Ch. 2)		
Salt–marsh accretion rate	0 (Ch. 2)	– (Ch. 2)	0 (Ch. 4)	
Redox potential	– (Ch. 3)	– (Ch. 3)		
Shoot biomass	0/– (Ch. 3/Ch. 4)	– (Ch. 3)	+ (Ch. 4)	– (Ch. 5)
Root biomass	0 (Ch. 3)	+ (Ch. 3)		– (Ch. 5)
Litter biomass	– (Ch. 3)	– (Ch. 3)		
Carbon sequestration	0 (Ch. 3)	+ (Ch. 3)		
Veg. succession			+ (Ch. 4)	– (Ch. 5)
Plant diversity			+ (Ch. 4)	+ (Ch. 5)
Small grazer abundance			+/0 (Ch. 5/6)*	– (Ch. 5)***

+ = positive effect, – = negative effect, 0 = no effect. * Positive effect on Hare, Brent geese and Barnacle geese; no effect on Greylag geese, ** Positive effect on hare abundance; no significant effect on abundances of Barnacle geese and Brent geese, ***Greylag geese had a short–term negative effect on their own food supply.

local vegetation towards the roots. By compacting the soil, large grazers enhanced anoxic conditions, thereby reducing the oxygen availability for organic carbon decomposition by the local microbial community. Effects of large grazers on carbon stocks likely differ between ecosystems with soils consisting of fine-grained or large- grained sediment. Independent of grain size, in many different ecosystems grazing has been shown to enhance the below-ground biomass of the local vegetation (see for example McNaughton et al. 1998, Yu and Chmura 2010, Olsen et al. 2011, Sjögersten et al. 2012). However, when the soils consist of coarse-grained sediment, trampling by large grazers will likely have a limited effect on the anoxicity of the soil (Schrama et al. 2013a). In these instances, the most dominant effect of large grazers will be above-ground biomass removal and grazing will negatively affect carbon sequestration (McNaughton et al. 1998, Sjögersten et al. 2012). When the soil consists of fine-grained sediment, then large grazers can compact the soil, reduce oxygen availability for the decomposers and thus positively affect carbon sequestration. Ultimately, we hypothesized that large grazers can increase carbon sequestration in ecosystems, when the soil consists of fine-grained sediment and soil compaction by trampling results in anoxic conditions in the soil.

2. What is the effect of topographic heterogeneity on the local vegetation and grazer presence?

At several tidal marshes we observed small-scale (i.e., a few square metres) heterogeneity in marsh morphology that consisted of higher elevated hummocks alternating with lower elevated depressions. These heterogeneities have been mentioned in literature before (e.g. Gray and Bunce 1972, Allen 2000), but it remained relatively unknown how they are formed or how they impact important marsh dynamics. In **box 1**, we determined that the largest part of the heterogeneity was explained by heterogeneity in the underlying coarse-grained sediment. Additionally, a smaller part was explained by a thicker fine-grained sediment layer on top of the hummocks compared to the depressions. Based on these results we concluded that the patterns are formed in pioneer stage before fine-grained sediment is accumulating on the vegetated marsh platform. Several studies showed that vegetation will increase sediment deposition locally and/or reduce erosions rates (e.g. Peralta et al. 2008, Mudd et al. 2010). As vegetation establishes on the hummocks first (**box 1**), they will have a higher fine-grained sediment deposition and hence accretion compared to the neighbouring depressions. When the marsh develops further and vegetation has established successfully in the depressions, marsh accretion rates become equal between hummocks and depressions (**box 1**). This resulted in the patterns to get maintained throughout ecosystem development and we found that they were still present at 120 years old marsh (**box 1**).

In **chapter 4** we studied how presence of this topographic heterogeneity altered plant diversity and grazer presence (hare, Barnacle goose and Brent goose). A general theory in ecology is that young ecosystems are unsuitable for grazers due to low primary production (Oksanen et al. 1981, Van De Koppel et al. 1996). Plant diversity is still low as well. With increasing marsh age: 1) an increase in primary production, 2) an increase in plant diversity and 3) a larger population of grazers is found (Van De Koppel et al. 1996, Olff et al. 1997). Studies on tidal marshes have shown that when succession continues even further, the palatable plant species get replaced with unpalatable ones. This results in grazers to get evicted from the ecosystem and populations of small grazers (Van Der Wal et al. 2000b) and plant diversity (Gray and Bunce 1972, Veeneklaas et al. 2013) reduce again. This thesis now showed that throughout ecosystem development (from 15 to 120 yrs-old marsh), plant diversity increased and this was maintained in time when topographic heterogeneity was present (compared with a homogeneous marsh) (**chapter 4**). Additionally, we found a high grazing pressure on top of hummocks at very young successional stage. Elevation determines for a large part the plant community in tidal marshes (Davy et al. 2011) and presence of higher elevated hummocks allowed later successional plant species to establish earlier in succession. Ultimately, we concluded that topographic heterogeneity: 1) increased plant diversity throughout ecosystem development, and 2) increased the abundance of small grazers, such as hares and geese, in young marshes.

3. What is the long-term effect of below-ground grubbing on the vegetation and how this in turn affects grazer abundance?

So far, we have focused on the effects of grazers that feed on above-ground plant parts. This type of grazing is much less detrimental for the marsh vegetation, compared to grazers that grub below ground for storage organs of the vegetation. Several migrating bird species, such as Greylag goose (Esselink et al. 1997) and Lesser Snow goose (Mclaren and Jefferies 2004), are known to create large bare patches in the marsh vegetation (Esselink et al. 1997, Mclaren and Jefferies 2004). In extreme cases, they can even degrade large marsh areas (Kerbes et al. 1990, Jefferies et al. 2006, Peterson et al. 2013). In **chapter 5**, we studied a large population of grubbing Greylag goose and estimated their top-down effect on the marsh vegetation. Additionally, we estimated large-scale bottom-up effects of marsh accretion on the cover of their preferred food source: Sea club-rush, *Bolboschoenus maritimus*.

Greylag geese grub for the below-ground storage organs, thereby creating bare patches (of a few square metres) within the marsh vegetation. We determined how these patches regenerated in time. In our study site, a reduction in population size of the Greylag goose has been observed in the past decade, despite the absence of predators (Castelijns and Jacobusse 2010). We hypothesized that this is the result of a reduction in their food source. We found that on a local patch scale, Greylag geese set back plant succession. Typical early-successional plant species established in the bare patches created by the geese. In contrast to other studies that observed negative effects of grubbing geese (e.g. Kerbes et al. 1990), we found a positive effect on plant diversity. Grubbing reduced the food resources of the marsh for Greylag geese shortly, but the patches regenerated back within 12 years to a *Bolboschoenus maritimus* dominated vegetation type. On a landscape scale of square kilometres, we found an increase in marsh surface elevation that outpaced current sea-level rise. This resulted in a strong decrease in cover of *Bolboschoenus maritimus* as part of the natural succession, which could explain the reduction in Greylag geese abundance. Ultimately, we conclude that although Greylag geese can exert a top-down control on plant diversity, on the long-term bottom-up control by marsh accretion is causing the Greylag geese to get evicted from the ecosystem and thereby plant diversity to decline.

THE IMPACT OF GRAZERS ON IMPORTANT ECOSYSTEM DYNAMICS

The results in this thesis showed that the impact of grazers on marshes depends largely on body size as well as forage mechanism. Larger-bodied grazers have been shown to have a larger impact on plant diversity (Bakker et al. 2006). Additionally, they are also more likely to change processes in an ecosystem by changing local soil properties due to their increased body weight (Olff and Ritchie 1998, Schrama et al. 2013a). We found a very limited effect by small above-ground grazers, whereas large above-ground grazers had a large impact on marsh dynamics through trampling of the soil (**chapter 2 & 3**). The largest effect is likely to occur in grasslands with fine-grained or peat-based soils (Schrama et al. 2013b). Soil compaction might not only alter the soil properties, such as aeration and water content, but will also change the vegetation composition (Van Klink et al. 2015). When we want to introduce livestock to ecosystems that have never been grazed by livestock before, we need to take into account the potential indirect effect on an ecosystem through changing soil properties.

Next to body size, we also found that the forage mechanism will determine for a large part the impact of a grazer. Grazers that remove only the above-ground plant parts of the vegetation will allow the vegetation to recover fairly quickly. However, when grazers remove both the above- and below-ground plant parts, then it will become much more difficult for the vegetation to regenerate (Peterson et al. 2013), and may even cause ecosystem collapse (Kerbes et al. 1990, Jefferies et al. 2006, Christianen et al. 2014). In marshes, grubbing geese feed on below-ground storage organs of the local vegetation. This foraging behaviour results in bare patches to occur within the marsh vegetation (Esselink et al. 1997, Mclaren and Jefferies 2004). These bare patches can have large impacts on the functioning of marshes, both negatively; by enhancing erosion of the marsh surface and deteriorating soil conditions (Mclaren and Jefferies 2004, Jefferies et al. 2006, Peterson et al. 2013), but also positively; by providing a habitat for other marsh species, such as crabs (Daleo et al. 2011), and an increase in plant diversity (**chapter 5**).

THE IMPACT OF LARGE GRAZERS AND HETEROGENEITY ON SMALL-GRAZER ABUNDANCE

The abundance of a species within an ecosystem is largely determined by the available food resources (White 2008). This in turn is largely determined by large-scale abiotic factors, such as weather conditions and available nutrients. However, interactions between grazers (both negative through competition and positive through facilitation) can also have a large impact on the abundance of a grazer (Arsenault and Owen-Smith 2002, Farnsworth et al. 2002). For example, many grassland ecosystems are grazed by multiple grazer species and may also be used for livestock grazing (Kemp and Michalk 2007). They will have to compete for the available food resources, which could lead to a reduction in grazer abundance (Farnsworth et al. 2002, Augustine and Springer 2013). In contrast, in several grassland ecosystems different grazer species were found to facilitate for each other (McNaughton 1976, Augustine and Springer 2013).

In tidal marshes, grazers have been shown that they can facilitate for each other, namely, hare facilitating for geese (Van Der Wal et al. 2000c) and cattle facilitating for geese (Bos et al. 2002, Kuijper et al. 2008). In this study, we estimated the effects of cattle grazing on 1) small grazers that graze above ground and 2) geese that grub for below-ground storage organs (Fig. 6.1 and 6.2). In line with previous studies, we found highest above-ground grazer abundance of Barnacle geese, Brent geese and hare at marshes of intermediate age, after which they reduced in abundance again (Fig. 6.1.A, chapter 2, Van De Koppel et al. 1996). The number of the small grazers increased again when cattle were introduced (Fig. 6.1A, Bos et al. 2002, Kuijper et al. 2008). Meanwhile, dropping counts estimated in Saeftinghe showed that the below-ground grubbing Greylag geese highly preferred to feed in *Bolboschoenus maritmus* vegetation and in the bare patches surrounded by *Bolboschoenus maritmus* (Fig. 6.2), whereas we found almost no droppings in the drier cattle-grazed parts. Presence of livestock can facilitate for the small above-ground grazers, but we found no facilitation for the below-ground grubbers. When grazers facilitate for each other, they generally enhance the available food resources (McNaughton 1976, Arsenault and Owen-Smith 2002). Greylag geese prefer to feed on *Bolboschoenus maritimus* (Amat 1995) that dominates in the lower elevated depressions, whereas cattle were present on the drier parts of the marsh. Similarly as in other marshes, we observed short grazing lawns with high plant species diversity in the cattle-grazed marsh (Bos et al. 2002, Wanner et al. 2014) and not an increase in *Bolboschoenus maritimus* cover (personal observations).

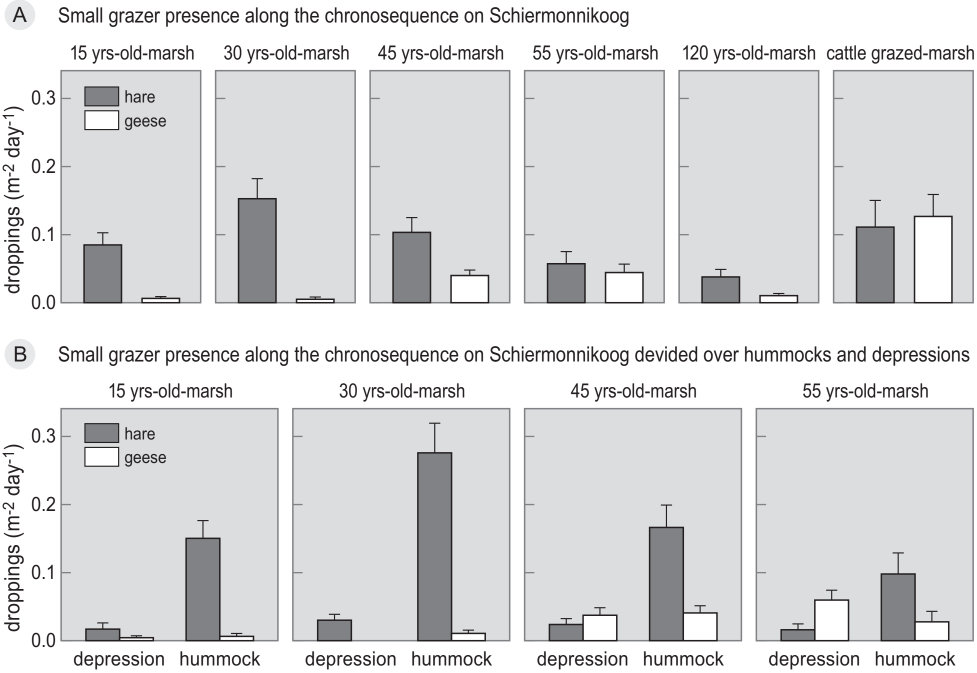

Figure 6.1. Dropping counts estimated for Barnacle geese, Brent geese and hares together, along the natural chronosequence on Schiermonnikoog in November 2010. First we show the dropping counts estimated in 15 yrs-old marsh up to 120 yrs-old marsh, and we compared them with the cattle-grazed marsh (A). Secondly, we zoom in on the young marshes (15 yrs-old marsh up to 55 yrs-old marsh) to show the effect of small-scale patterns present in marsh morphology (B).

Next to grazer presence we found that topographic heterogeneity also affected the abundance of grazers in tidal marshes (**chapter 4** and Fig. 6.1.B). Many studies estimating the impact of spatial heterogeneity in ecosystems found an increase in plant diversity (Costanza et al. 2011, Ruifrok et al. 2014, Stein et al. 2014). However, the impact of topographic heterogeneity on the presence of grazers had not received a lot of attention. Red fescue, *Festuca rubra*, is a preferred food choice of the small grazers in tidal marshes (Van Der Wal et al. 2000c, Van Der Graaf et al. 2005) and we found a very high cover on top of higher elevated hummocks, while cover was still very low when the heterogeneity was not present (**chapter 4**). In young low productive marshes, where limited biomass production limits the number of grazers, the presence of such higher elevated hummocks increased the number of grazers able to forage efficiently within the ecosystem (**chapter 4**, Fig. 6.1.B). Whether heterogeneity will increase grazer abundance in other ecosystems will likely depend on the overall level of stress. Low productivity or high stress environmental conditions, such as high temperature, drought or high salinity, that gets alleviated when heterogeneity is present, could increase the food supply and thereby grazer abundance in other ecosystems as well.

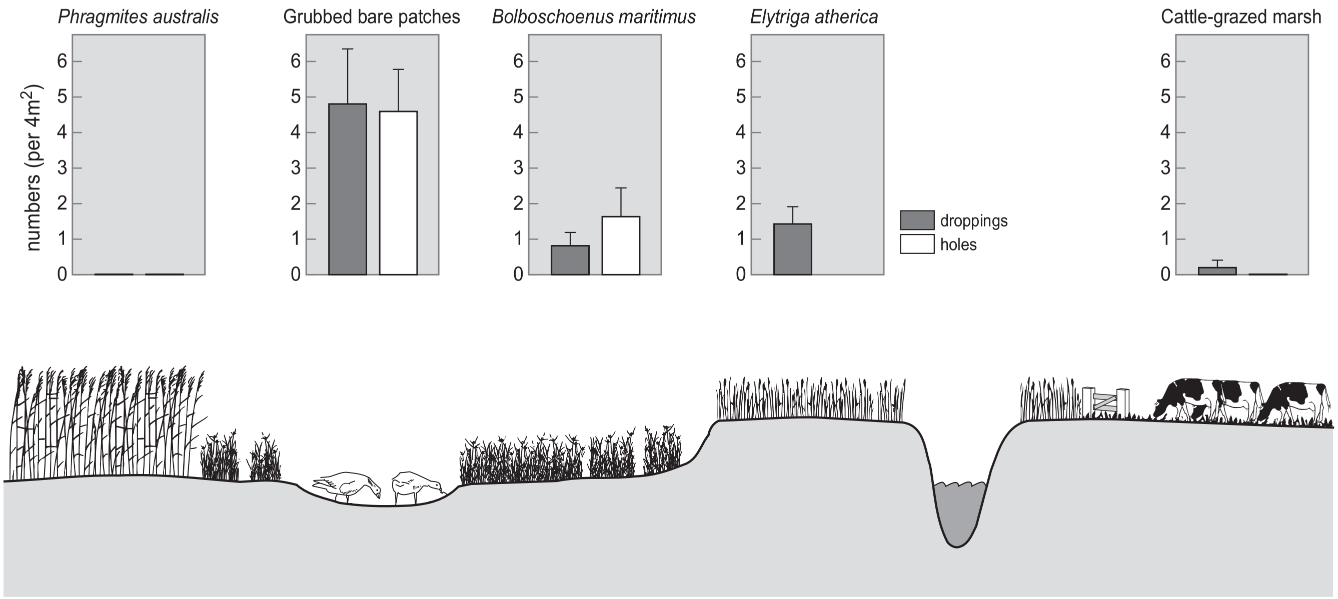

Figure 6.2. Number of droppings and grubbed holes (of a few cm wide and a few cm in depth) by Greylag geese comparing several plant communities and the cattle-grazed marsh. Droppings were estimated in February 2009 on Saeftinghe.

MANAGEMENT IMPLICATIONS

Marshes get frequently inundated and harbour many specialized plant species which can cope with these stressful environmental conditions (Więski et al. 2009). Therefore, the protection of marshes has become important in the conservation of biodiversity in Europe. Many European marshes are used for livestock grazing, which is generally used as a nature management tool (Kiehl et al. 1996, Bakker et al. 2003, Bouchard et al. 2003). Cattle grazing can bring back young-successional plant species and thus increase or maintain local plant diversity in these coastal habitats (Bos et al. 2002, Bakker et al. 2003). Next to numerous plant species, also many vertebrate species benefit from grazing (Van Wieren and Bakker 2008). For example, breeding birds prefer low to moderate grazing pressure with a high patchiness in the vegetation structure (Mandema et al. 2014b), while geese prefer marshes with high stocking densities (Mandema et al. 2014a). Many invertebrate species prefer tall vegetation, which can be found in moderately grazed or ungrazed salt marshes (Van Klink et al. 2013).

In this study, I focused on the impact of the different types of grazers on the vegetation and how this affects important marsh dynamics. Effects of small above-ground grazers were very limited. Below-ground grubbers had a large impact on the vegetation composition, but only for a limited period of time as the bare patches regenerated back in approximately 12 years. With respect to cattle, I found that these large animals had a very large effect through trampling of the soil. Trampling by livestock has been largely neglected in ecology so far (but with exceptions of e.g. (Schrama et al. 2013a, Nolte et al. 2013c, Veldhuis et al. 2014). Trampling by cattle reduced the marsh accretion rates (**chapter 2**) while, it enhanced the carbon sequestration rate in the marsh soil (**chapter 3**). Whether the positive impact of large grazers on biodiversity and carbon sequestration, outweighs the negative impact on marsh accretion rate will be very site specific, depending on the problems the marsh are facing. Marshes with high sedimentation rates will be less affected by a reduced accretion rate following cattle grazing. Hence, livestock grazing on these sites could be used to provide increased carbon sequestration rates as well as increased biodiversity. The impact of grazers on both vegetation and soil characteristics should be taken into account in future studies that use models to estimate whether coastal habitats can cope with an accelerated sea-level rise.

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Summary

INTRODUCTION

A large part of the global terrestrial area is covered by grasslands and they are being grazed by both wildlife and domestic livestock, resulting in very high grazing pressures. These grazers will have a large impact on the local vegetation and can alter important ecosystem functions. Furthermore, due to changing environmental conditions and human impact, populations of native grazers are reducing in some ecosystems, while they are increasing in others. With these global changes in grazing pressures, it is important to gain understanding on how they impact vegetation characteristics, the interactions between grazers and vegetation, and the effects on important ecosystem processes. In this thesis I studied this, using tidal marshes as a model ecosystem.

THE IMPACT OF GRAZERS ON IMPORTANT MARSH DYNAMICS

Throughout the year, many small grazers use marshes as feeding habitats. Migratory birds are present in European marshes during winter. Other small grazers, such as hare and rabbits, are present throughout the entire year. Next to these small grazers, we also find livestock on many European marshes. The effects of livestock grazing on the marsh vegetation have been studied intensively in ecology. They are known to reduce vegetation height and increase plant diversity. By bringing back younger successional plant species in mature marshes, they are known to facilitate for small grazers. However, their impact on many important ecosystem functions has not received a lot of attention so far. In this thesis, I found that the impact of a grazer within an ecosystem depends for a large part on their body size as well as forage mechanism.

In **chapters 2 and 3** we studied the impact of small grazers (Barnacle goose, Brent goose and hare) and large grazers (cattle), which graze on above-ground plant parts. We measured their effect on vegetation height, sediment deposition, marsh accretion rates and carbon accumulation in the marsh soil. We found that both small grazers and large grazers reduced the vegetation height significantly. However, this did not affect sediment deposition (**chapter 2**). Additionally, small grazers had no effect on marsh accretion rates (**chapter 2**) or carbon accumulation in the marsh soil (**chapter 3**). Based on our results, we concluded that the impact of small grazers on the functioning of tidal marshes were fairly limited. In contrast, we found that cattle had a negative impact on marsh accretion rates (**chapter 2**), while they positively affected carbon accumulation in the marsh soil (**chapter 3**). Through trampling, they increased the bulk destiny and this reduced the marsh accretion rates. Furthermore, by increasing the bulk density in the soil, they also reduced the oxygen availability and therefore the organic carbon decomposition by the microbial community. This enhanced carbon sequestration in the marsh soil. These effects of large-bodied grazers on soil properties in tidal marshes has been largely neglected so far, but need to be considered when we want to introduce livestock to ungrazed marshes.

Next to above-ground grazing, we also find small grazers that grub for below-ground storage organs in tidal marshes. This type of grazing removes the entire plant and it is therefore much more difficult for the vegetation to regenerate. This grubbing behavior generally causes bare patches to form within the marsh vegetation. In extreme cases, it can lead to large marsh areas to become degraded. We studied the regeneration of these local bare patches created by grubbing Greylag geese (**chapter 5**). Additionally, we studied ecosystem development on a landscape scale. Within our study site, a large population of Greylag geese is reducing in size and we hypothesized that geese grubbing on a local scale or ecosystem development on a landscape scale, is in fact reducing their food supply. We found that the bare patches regenerated back to a similar vegetation type within about 12 years. Therefore, the geese do reduce their food supply, but only shortly and very locally. Very interestingly, we found an increase in plant diversity as young-successional plant species established in these bare patches during regeneration. On a landscape scale, we found a very high accretion rate that outpaced the rising sea-level. Their preferred food source, *Bolboschoenus maritimus*, reduced in cover, while *Elytrigia atherica* was increasing in cover. *Bolboschoenus maritimus* is generally limited to the lower elevated depressions between the creek banks, whereas *Elytrigia atherica* dominates op top of the creek banks. An increase in elevation would allow *Elytrigia atherica* to expand towards the depressions and *Bolboschoenus maritimus* to reduce in cover. Therefore, we concluded that the natural development of the marsh on a landscape scale is causing the Greylag geese to get evicted from the ecosystem and not due to local degradation by the geese themselves. Additionally, and in contrast to other studies showing the negative effect of grubbing small grazers, we concluded that grubbing geese can positively affect plant diversity through a local set-back of the plant succession.

THE IMPACT OF LARGE GRAZERS AND HETEROGENEITY ON SMALL-GRAZER ABUNDANCE

In tidal marshes, small grazer abundance is known to change with increasing productivity. At young successional stages, where productivity is still low, limited biomass production limits the amount of small grazers that can forage within the system. As the marsh develops and productivity increases, then the abundance of small grazers increases as well. However, at mature marshes the cover of nutritious plant species get replaced by unpalatable ones and the small grazers reduce in abundance again. Large grazers are known to facilitate for small grazers by bringing back the nutritious plant species again. In line with these previous studies, we also found an increase in the abundance of small above-ground grazers when cattle were introduced in mature marshes. However, we did not find any evidence for the cattle facilitating for below-ground grubbers (**chapter 6**). As mentioned previously, we found a reducing population of Greylag geese in our study site due to natural succession. In contrast to the small above-ground grazers, we did not find an increase in the abundance of small below-ground grubbers when cattle were present.

Next to the effect of the large grazers, we also found an effect by small-scale heterogeneity in the marsh platform on small grazer presence (**chapter 4**). We studied a small-scale topographic heterogeneity (of a few square metres) that consisted of higher elevated hummocks alternating with lower elevated depressions. By comparing the soil characteristics underlying the heterogeneity in four European marshes, we concluded that this pattern is formed in the pioneer stage, before marsh formation starts and fine-grained sediment accumulates on the marsh platform (**box 1**). Throughout ecosystem development, ranging from pioneer to mature marshes, this heterogeneity increased plant diversity (**chapter 4**). Additionally, we found a very high grazing pressure by hare on top of the higher elevated hummocks, which was especially higher in the young successional stages of 15 and 30 yrs-old marsh compared to homogeneous marsh (**chapter 4**). Although limited primary production in young marshes generally limits the abundance of grazers, presence of higher elevated hummocks increased local primary production and the hare could profit from these local elevated patches.

MANAGEMENT IMPLICATIONS

Many European marshes are grazed by wildlife as well as by livestock, to maintain plant diversity. For management purposes, we need to understand the impact of these different types of grazers on the vegetation and on important marsh dynamics. The results in this thesis showed that small above-ground grazers reduced the vegetation height, but their effects on important marsh dynamics (that were studied in this thesis) were very limited (**chapters 2 and 3**). Below-ground grubbing geese had a large impact on the vegetation composition and this increased plant diversity in tidal marshes, although this effect was only present for a limited period of time until the bare patches regenerated (**chapter 5**). With respect to cattle, these large-bodied animals had a very large effect through trampling of the soil. Trampling by cattle reduced the marsh accretion rates (**chapter 2**), while it enhanced the carbon sequestration rate in the marsh soil (**chapter 3**). Whether the positive impact of large grazers on biodiversity and carbon sequestration, outweighs the negative impact on marsh accretion rate will be very site specific, depending on the problems the marsh are facing. Marshes with high sedimentation rates will be less affected by a reduced accretion rate. Hence, livestock grazing on these sites could be used to provide increased carbon sequestration rates next to an increased biodiversity. These impacts of grazers on both vegetation and soil characteristics should be taken into account in future studies that use models to estimate whether coastal habitats can cope with an accelerated sea-level rise.

Samenvatting

INTRODUCTIE

Een groot deel van het landoppervlak op aarde is bedekt met graslanden en deze worden doorgaans door zowel inheemse diersoorten als door vee begraasd. Dit leidt vaak tot een zeer hoge beweidingsdruk. Daarnaast neemt door menselijk handelen en onder invloed van de veranderingen in omgevingsfactoren, het aantal inheemse grazers in sommige graslanden af terwijl ze toenemen in andere. Al deze veranderingen in begrazingsdruk benadrukken het belang om goed te begrijpen wat de rol van een grazer is binnen een ecosysteem: hoe beïnvloeden ze de kweldervegetatie, wat zijn de interacties tussen de vegetatie en de grazers en hoe beïnvloeden ze samen belangrijke ecosysteem processen. Op deze vragen ligt de focus van mijn onderzoek, waarbij ik kwelders gebruik als mijn studie systeem.

EFFECTEN VAN GRAZERS OP BELANGRIJKE KWELDER PROCESSEN

Op Europese kwelders fourageren veel verschillende grazers. Migrerende ganzen overwinteren hier, terwijl andere grazers (zoals hazen, konijnen en slakken) er het hele jaar aanwezig zijn. Naast deze kleine grazers worden ook veel Europese kwelders begraasd door vee. De effecten van begrazing door vee op de kweldervegetatie is al behoorlijk intensief bestudeerd in de ecologie. Ze reduceren de vegetatiehoogte, verhogen de plantendiversiteit en grote grazers faciliteren vaak voor kleine grazers door planten uit jongere successie stadia weer in aantallen te laten toenemen. Maar aan de effecten van vee op belangrijke ecosysteem functies is tot dusver nog weinig aandacht geschonken. Uit de verschillende studies uitgevoerd in dit proefschrift bleek dat de effecten van verschillende grazers binnen een ecosysteem voor een groot deel afhangen van hun lichaamsgrootte en de manier van begrazing.

In **hoofdstuk 2 en 3** hebben we de effecten onderzocht van kleine grazers (hazen, brandganzen en rotganzen) en grote grazers (vee) op vegetatiehoogte, sediment invang, ophoging van het kweldermaaiveld en koolstofopslag in de bodem. Zowel de kleine als de grote grazers reduceerden de vegetatiehoogte, maar dit bleek geen effect te hebben op de hoeveelheid sediment dat werd ingevangen tijdens overstromingen. De kleine grazers hadden ook geen effect op de ophoging van het maaiveld (**hoofdstuk 2**) of op de koolstofopslag in de bodem (**hoofdstuk 3**). Hieruit concludeer ik dan ook dat de kleine grazers weinig invloed hebben op de ecosysteem processen die onderzocht zijn in dit proefschrift. In tegenstelling tot de kleine grazers, hadden de grote grazers wel een grote invloed op de ophoging van het maaiveld (**hoofdstuk 2**) en de koolstofopslag in de bodem (**hoofdstuk 3**). Door het aanstampen van de bodem reduceerden ze de hoogte van het kweldermaaiveld, terwijl de koolstofopslag in de bodem juist toenam. Dit komt doordat de toename in dichtheid van de grond de aanwezigheid van zuurstof in de bodem reduceerd, waardoor de afbraak van organisch materiaal door microben in de bodem wordt afgeremd. Deze effecten door vertrapping van grote grazers op bodemprocessen is in de ecologie tot nu toe grotendeels genegeerd, maar zijn belangrijk in de afweging of vee geïntroduceerd kan worden in natuurgebieden waar nog niet eerder vee begrazing heeft plaats gevonden.

Naast bovengrondse begrazing zijn er ook grazers op kwelders die in de kwelderbodem graven naar ondergrondse wortelstokken van de vegetatie. De hele plant wordt hierbij verwijderd en bij dit type begrazing is het veel lastiger voor de vegetatie om weer te herstellen. Dit ondergrondse grazen (of wroeten) resulteert doorgaans in open plekken in de kweldervegetatie. In extreme gevallen kan dit zelfs leiden tot volledige verwoesting van grote kwelder oppervlakten. In **hoofdstuk 5** hebben wij gekeken naar het herstel van kale plekken die gecreëerd zijn door wroetende grauwe ganzen. Daarnaast hebben we de natuurlijke successie van het volledige landschap meegenomen. In ons studie gebied bevindt zich een hele grote populatie grauwe ganzen, maar de laatste jaren neemt dit aantal af. We willen nu weten of het voedselaanbod voor de grauwe ganzen afneemt door het wroeten van de ganzen zelf of dat dit een effect is van natuurlijke successie. Uit onze studie bleek dat de kale plekken in ongeveer 12 jaar herstelden naar een vegetatie vergelijkbaar met wat er aanwezig was voor de ganzen begonnen met wroeten. De grauwe ganzen reduceerden met het wroeten dus wel degelijk hun voedselaanbod, maar dit was slechts een tijdelijk effect. Terwijl de kale plekken herstelden vestigden verschillende planten uit jongere successie stadia zich in de kale plekken. De wroetende ganzen hadden dus een positief effect of de plantendiversiteit. Op landschapsschaal vonden we een hele snelle ophoging van het maaiveld, en deze was zelfs hoger dan de gemeten zeeniveau stijging. Ook was er een sterke afname van zeebies, *Bolboschoenus maritimus*, terwijl strandkweek, *Elytrigia atherica*, sterk toenam. Zeebies domineert doorgaans de lager gelegen depressies tussen de verhoogde kreekbanken, terwijl strandkweek op deze verhoogde banken domineert. Een verhoging van het maaiveld geeft strandkweek de kans om zich uit te breiden van de banken naar de lager gelegen depressies. Hierdoor zal zeebies afnemen. Gebaseerd op deze resultaten concluderen wij dat natuurlijke successie resulteert in een afname van zowel het voedselaanbod als de grauwe ganzen en niet door het creëeren van kale plekken door de wroetende ganzen zelf. Daarnaast, en in tegenstelling tot eerdere studies die de negatieve effecten van wroetende ganzen laten zien op de kwelders, vonden wij een positief effect op de plantendiversiteit doordat de successie lokaal in de tijd terug werd gezet.

EFFECTEN VAN GROTE GRAZERS EN HETEROGENITEIT OP DE AANTALLEN KLEINE GRAZERS

De aantallen van kleine grazers die aanwezig zijn op kwelders is afhankelijk van de lokale productiviteit. Op jonge kwelders is de lokale productiviteit nog erg laag, gelimiteerde biomassa productie van de lokale vegetatie limiteert het aantal kleine grazers dat effectief kan fourageren in het gebied. Met toenemende successie neemt de productiviteit en het aantal kleine grazers toe. Als de successie verder gaat, neemt het voedselaanbod weer af doordat het aantal planten met hoge voedingswaarde afneemt in het systeem en het aantal planten met lage voedingswaarde toeneemt. Hierdoor nemen de aantallen kleine grazers weer af in het gebied. Op dat moment kan de introductie van vee voor de kleine grazers facciliteren, doordat het aantal planten met hoge voedingswaarde weer toeneemt in de aanwezigheid van vee. In lijn met andere studies, vonden we ook een groter aantal kleine grazers (brandganzen, rotganzen en hazen) in het vee begraasde gebied. Maar toen we focusten op de aantallen grauwe ganzen, was er geen enkele aanwijzing dat vee voor de grauwe gans faciliteert (**hoofdstuk 6**). Zoals eerder vermeld neemt het aantal grauwe ganzen af in ons studie gebied. Maar in tegenstelling tot de kleine bovengrondse grazers, vonden we geen facilitatie van ondergronds wroetende grazers in de aanwezigheid van vee.

Naast de effecten van grote grazers, vonden wij ook een effect van kleinschalige heterogeniteit in kwelder topografie dat de aantallen kleine grazers beïnvloedde (**hoofdstuk 4**). Deze patronen in kwelder topografie bestaat uit een mozaïk van hoger gelegen “hummocks” en lager gelegen “depressies” (samen ongeveer een paar vierkante meter in grootte). In vier verschillende Europese kwelders hebben we de grondprofielen onder deze patronen met grond boringen in kaart gebracht. Hieruit bleek dat de patronen al gevormd zijn in de pionier fase, voordat er kwelder gevormd wordt en fijn sediment neerslaat op de grove onderliggende zandlaag (**box 1**). Ook bleek dat onafhankelijk van de kwelder leeftijd (van pionier fase tot en met 120 jaar oude kwelder), de aanwezigheid van deze patronen de plantendiversiteit verhoogde (**hoofdstuk 4**). Als laatste vonden we een hele hoge begrazingsdruk van hazen op de hoger gelegen hummocks, wat vooral in jonge (15 en 30 jaar oude) successiestadia sterk verhoogd was in vergelijking tot relatief homogene kwelder. Ondanks studies die laten zien dat een te lage primaire productie in jonge kwelders het aantal grazers limiteert, vinden wij in jonge kwelders een verhoogde primaire productie op de hoger gelegen hummocks waar de hazen van profiteren.

IMPLICATIES VOOR MANAGEMENT

Veel Europese kwelders worden begraasd door zowel inheemse grazers als door vee. Vanuit een management perspectief is het dan ook zeer belangrijk om te begrijpen wat de effecten van deze verschillende grazers zijn op de vegetatie en belangrijke ecosysteem processen. Gebaseerd op de resultaten in dit proefschrift concludeer ik dat de kleine bovengrondse grazers weliswaar de vegetatiehoogte reduceren, maar dat ze vrijwel geen invloed op belangrijke ecosysteem processen hadden (die zijn onderzocht in dit proefschrift, **hoofdstukken 2 en 3**). Wroetende grazers hadden een groot effect op de samenstelling van de vegetatie en verhoogden de plant diversiteit, maar dit effect was tijdelijk, want de kale plekken herstelden uiteindelijk weer naar een vergelijkbare vegetatie samenstelling als voorheen (**hoofdstuk 5**). Begrazing door vee had een enorm effect door het aanstampen van de bodem. Dit reduceerde de ophoging van het kweldermaaiveld (**hoofdstuk 2**), terwijl de koolstofopslag in de bodem toenam (**hoofdstuk 3**). Of de positieve effecten van veebegrazing (verhoging van koolstofopslag en planten diversiteit) opwegen tegen de negatieve effecten (verlaging van het maaiveld), zal per kweldergebied verschillen. Kwelders met een hoge sediment depositie zullen minder problemen ondervinden met veebegrazing en de resulterende verminderde ophoging van het kwelder oppervlakte. In deze gebieden zou veebegrazing dus actief de koolstofopslag kunnen verhogen naast het in stand houden van de biodiversiteit. De effecten van de verschillende grazers op de kweldervegetatie en de bodem eigenschappen moeten in toekomstige studies wel meegenomen worden, waarbij vaak met behulp van theoretische modellen wordt bepaald of kwelders kunnen meekomen met het versneld stijgend zeeniveau.


SCHIERMONNIKOGER VISHANDEL
STEEDS HET BESTE

Dankwoord

Na vele jaren, die enerzijds voorbij zijn gevlogen maar anderzijds wel een eeuwigheid hebben geduurd, is dan toch dit boekje tot stand gekomen.

Het begon allemaal in mijn masterfase waarin ik al snel ontdekte dat onderzoek wel mijn ding was. Vooral gedurende mijn eerste onderzoek bij Mariska te Beest, maanden plantjes kweken en meten in de kassen van het biologisch Centrum. Daarna wilde ik toch wel graag het veld in en liep ik binnen bij Patrick Jansen, waarna ik binnen een maand op een vliegtuig zat richting Panama. Drie fantastische maanden heb ik samen met Laura Vonk rondgerend in het regenwoud. Gedurende mijn gehele masterfase heeft Han Olff mij begeleid en gemotiveerd. Han, ontzettend bedankt voor alle steun! Toen kwam al snel een PhD positie beschikbaar bij Jan Bakker en deze heb ik met beide handen aangegrepen…

Samen met Tjeerd Bouma heeft Jan een project aangevraagd bij het NWO-ZKO voor twee PhD studenten: eentje voor Groningen en eentje voor Yerseke. Uiteindelijk ben ik aangenomen voor het veldwerk-deel en mijn collega Qi hui voor het modelleer-deel van dit project. Met een grote groep begeleiders achter me ben ik enthousiast van start gegaan, eerst op Schiermonnikoog en Saeftinghe en na een bezoekje tijdens de Coastal Ecology Workshop in Wales hebben we de Cefni marsh ook maar als veldsite toegevoegd. Omdat dit niet in het budget zat heb ik hiervoor wat extra subsidie gekregen van het Schure-Beijerinck-Popping fonds. Gedurende mijn hele PhD heb ik veel steun gekregen van mijn begeleiders en ik wil ze dan ook allemaal ontzettend bedanken. Jan, voor je niet aflatende steun en vertrouwen, je passie voor kwelders en natuurbehoud zijn een inspiratie. En vooral je nuchtere opmerkingen zo af en toe hebben mij geholpen om op het juiste pad te blijven en de druk te verlichten. Tjeerd, bedankt voor je enthousiasme, steun en ideeën gedurende dit project. Af en toe dat mailtje hoe het allemaal ging heeft me erg gesteund en je positieve feedback op alle lappen tekst die ik naar je stuurde heeft heel veel bijgedragen aan het tot stand komen van dit boekje. Stijn Temmerman, Johan van de Koppel en Julia Stahl hebben veel bijgedragen door mee te denken tijdens onze meetings in Utrecht, gedurende het opzetten van de experimenten en later door feedback te geven op manuscripten. Ook Han Olff bleef op de achtergrond een rol spelen gedurende dit hele project, met meedenken over experimenten en manuscripten. Bedankt dat ik nog altijd bij je mag aankloppen!

Natuurlijk hebben vele anderen bijgedragen aan het tot stand komen van dit boekje. Al mijn collega's bij COCON: Ciska, Mariska, Joris, Grant, Nina, Alejandro, Francisco, Sanne, Bernd, Jan, Cleo, Erustus, Irma, Thijs, Ellen van V, Ellen W, Tjisse, Chris, Rampal, Jasper, Ruth, Wimke, Fons, Michiel, Marjolijn en Marlies. Vooral de kweldergroep wil ik bedanken: Steffi, Roel, Freek, Ruth, Alma, Roos, Maarten en natuurlijk Elske. Elske en

Maarten hebben veel geholpen in het veld en meegedacht. Simpelweg bedankt voor het biertjes drinken op de herdershut. Elske, tijdens de jaarlijkse SEB metingen op Terschelling hebben we de nodige pittige dagen, avonturen en gezelligheid meegemaakt! Neem een wandeling in dichte mist op het wad op Terschelling als voorbeeld, die dag vergeet ik in ieder geval niet gauw... Ruth and Nina, thank you very much for all the help with GIS and the statistics. Hiernaast wil ik vele anderen bedanken voor de gezelligheid op Schier: Serena, Els, Ellen W, Kees, Siemen, Jim en alle master- en bachelor studenten voor de gezelligheid en vele avondjes uit eten bij van der Werff.

Ook moet natuurlijk nog even de Coastal Ecology Expeditie genoemd worden! Jan Bakker, allereerst bedankt voor de organisatie en samen met alle mede-kustecologen die erbij waren voor de gezelligheid! Steffi, Elske en Wimke, ik zal de memorabele 24 uur die we onbedoeld op Langli hebben doorgebracht nooit meer vergeten...er zijn er niet veel die kunnen vertellen dat ze op een onbewoond eiland zijn gestrand (en overleven)! Jouke Franke, Dick Visser, Jan van de Burg, Jacob Hogendorf, Yzaak de Vries, Nelly Eck en Ingeborg Jansen wil ik allemaal ontzettend bedanken voor alle hulp gedurende mijn PhD! Zonder jullie zou menig onderzoeker met zijn handen in het haar zitten... Vooral Dick voor de fantastische lay-out van dit boekje! Ook voor het verzamelen van de data heb ik de nodige hulp gehad: Jan-Eise, Harm, Mark, Judith, Nathalie en Hetty, bedankt voor jullie inzet tijdens de bachelor cursussen en theses. Vooral Anke Vermeulen wil ik bedanken voor het prachtige master project dat we hebben gedaan in Saeftinghe. Zelfs om 4 uur opstaan kon je pret en motivatie niet drukken!

I would like to thank Martin Skov and Angus Garbutt for helping me set up my fieldwork in Wales, for welcoming me in your groups as well as introducing me to so many people! Special thanks for Marc, Hillary and Rachel for adopting me and giving me a social life in Bangor! You all made my stay in Bangor very memorable. Wouter, thanks for the help with the aerial photographs of Saeftinghe. Finally, I still need to thank all the people at NIOZ in Yerseke: especially Lennart IJzerloo, Bas Koutstaal, Paul Klaassen, Jim van Belzen and Jan Megens for all the help with my work in Saefinghe, Anette Wielemaker and Daphne van der Wal for help with ArcGIS and Francesco and Lucy for all the nice evenings while staying at the Keete. A special thanks also for all the participants of the Coastal Ecology Workshop for the nice days/evenings sharing ideas, drinks and diners. Frauke, we had a lot of fun on the CEW's as well as on our roadtrip to Föhr with Steffi!!

Natuurmonumenten, Zeeuwselandschap, Rijkswaterstaat, Sovon en de Steltkluut vereniging wil ik van harte bedanken voor alle hulp in het veld en voor het gebruik van jullie foto's, data en expertise. Vooral Henk Castelijns wil ik nog even persoonlijk bedanken voor de rondleidingen en goede gesprekken over de grauwe ganzen in Saeftinghe.

Nu wil ik nog graag al mijn vrienden en familie bedanken! Niet alleen voor alle steun maar zeker ook dat jullie me steeds weer hebben vergeven dat ik niet altijd op verjaardagen en feestjes aanwezig was, doordat ik weer eens op een veldstation zat in de middle of nowhere... Joris, ontzettend bedankt voor alle steun, geduld en zeker ook voor het functioneren als uitlaatklep als het allemaal wat minder ging tijdens de afronding... Margien, die er altijd was wanneer ik weer terug in Groningen kwam, de schrijfweekjes aan de Moesel en nu weer voor alle hulp bij de allerlaatste loodjes als mijn paranimf. Ook Heleen wil ik van harte bedanken voor alle steun en hulp gedurende het project en als mijn paranimf! En dan nog Joris, Remko, Stefan, Jeffrey, Freek, Marieke, David, Margien, Maurits, Maarten en Irene, ontzettend bedankt voor jullie hulp met het opzetten van de exclosures en allerlei metingen in het veld! Als laatste motivator moet ik mijn jochie bedanken.. die zelfs al in de buik wonderen verricht... hij heeft zijn mama zover gekregen om haar proefschrift af te ronden...

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