Effects of vegetation patterns and grazers on tidal marshes

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1 General introduction

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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

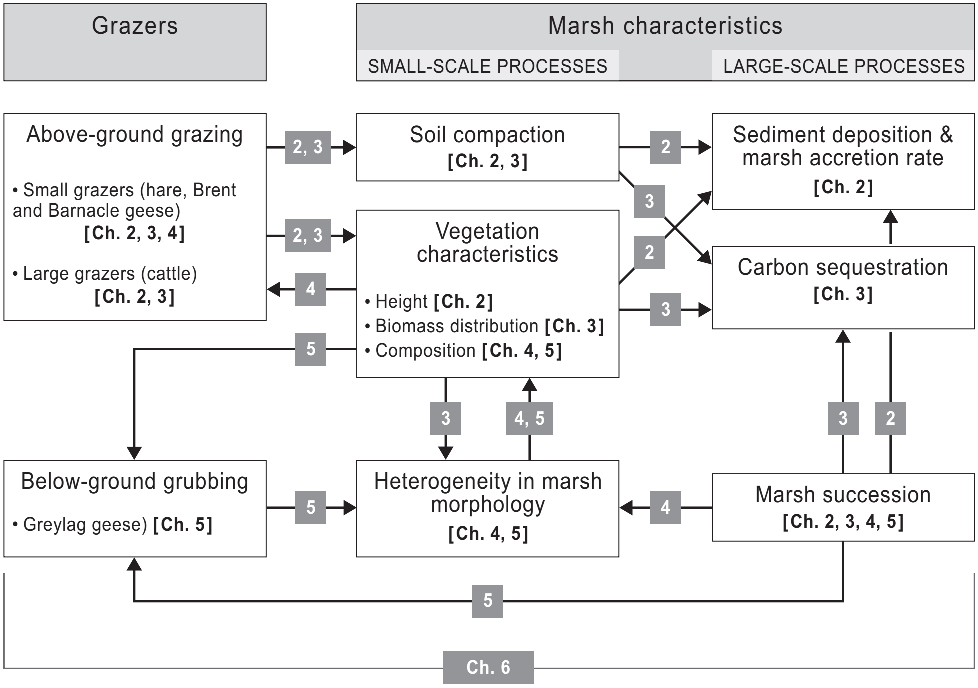

Figure 1.1. A schematic overview of the different interactions studied in this thesis. Numbers in the scheme represent the different chapters

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

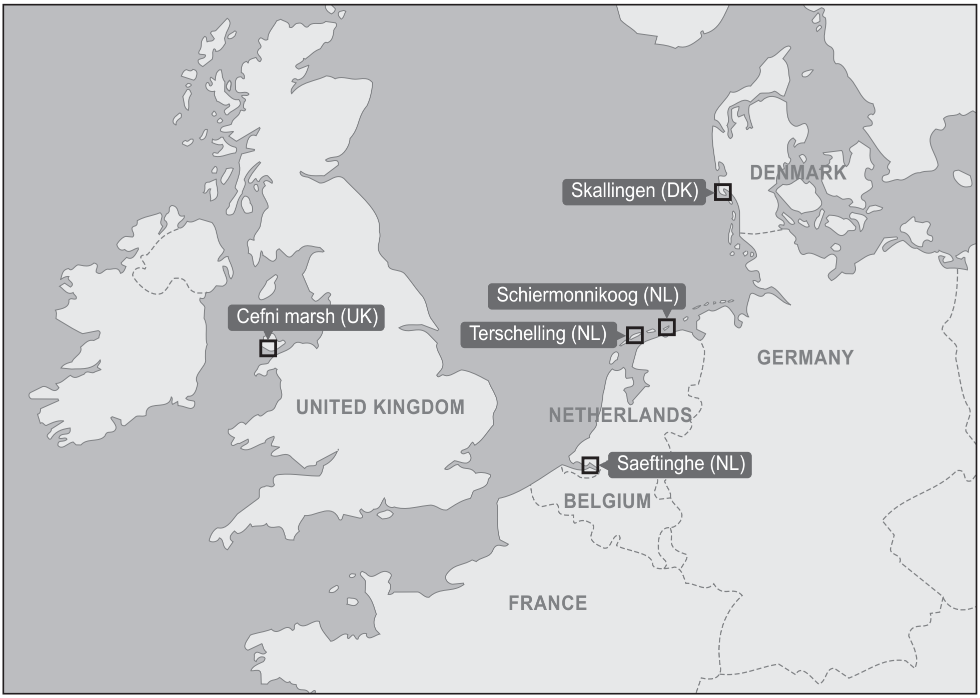

Figure 1.2. Five European tidal marshes (black squares) that were included in this thesis.

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 cord-grass *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).