Effects of vegetation patterns and grazers on tidal marshes
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Effects of long-term grazing on sediment deposition and salt-marsh accretion rates

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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 focusing 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](image_url)
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 grazer-
s 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 verti-
cal 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 \(4\text{m}^2\) 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; Rodríguez 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 1 mm 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).

![Graph showing herbivore activity (droppings day\(^{-1}\) m\(^{-2}\)) estimated in November 2010. Activity of both geese and hares is shown along the natural age gradient.]

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

<table>
<thead>
<tr>
<th>Vegetation height</th>
<th>Small grazers</th>
<th>Large grazers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>Grazing</td>
<td>Age*grazing</td>
</tr>
<tr>
<td>F(3,72) = 7.78</td>
<td>p &lt; 0.001</td>
<td>F(1,72) = 7.39</td>
</tr>
<tr>
<td>Total sediment</td>
<td></td>
<td></td>
</tr>
<tr>
<td>accumulated</td>
<td>F(3,35) = 53.07</td>
<td>F(1,35) = 0.30</td>
</tr>
<tr>
<td></td>
<td>p &lt; 0.001</td>
<td>p = 0.87</td>
</tr>
<tr>
<td>Fine-grained</td>
<td>F(3,35) = 105.80</td>
<td>F(1,35) = 0.08</td>
</tr>
<tr>
<td>sediment layer</td>
<td></td>
<td></td>
</tr>
<tr>
<td>thickness</td>
<td>p &lt; 0.001</td>
<td>p = 0.78</td>
</tr>
<tr>
<td>Bulk density layer</td>
<td>F(3,35) = 23.94</td>
<td>F(1,35) = 3.00</td>
</tr>
<tr>
<td>0.5-5.5 cm</td>
<td>p &lt; 0.001</td>
<td>p = 0.09</td>
</tr>
<tr>
<td>Bulk density layer</td>
<td>F(2,26) = 26.67</td>
<td>F(1,26) = 2.62</td>
</tr>
<tr>
<td>5.5-10.5 cm</td>
<td>p &lt; 0.001</td>
<td>p = 0.12</td>
</tr>
<tr>
<td>Percentage particles</td>
<td>F(3,32) = 6.28</td>
<td>F(1,32) = 1.07</td>
</tr>
<tr>
<td>&lt;63µm</td>
<td>p &lt; 0.01</td>
<td>p = 0.31</td>
</tr>
</tbody>
</table>

*n.s. = not significant

**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.
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 struc-
ture 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.

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