

Chapter 4 Short-term impact of sheep grazing on salt-marsh vegetation succession in a newly created salt-marsh site³

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4.1 Abstract

In this paper, the effect of three winter seasons of sheep grazing on cover, composition and species richness of vegetation, *Elymus athericus* expansion and forage quality of salt-marsh species were studied. Four zones were selected: three in real salt-marsh habitat (low, intermediate and high levels) and the fourth in the transition between salt-marsh and sand dune habitat. In each of the three salt-marsh zones, one site was selected and two sites were designated in the transitional zone. Half of each site was excluded from grazing (so-called enclosures) all year round, while the other half was accessible to sheep from mid-August until mid-June (enclosure areas). At each zone, 10 plots (2m × 2m) were established: five within enclosure and five within enclosure sites. In all plots, the cover of all species was estimated in the growing season in 2005 (initial state) and 2007 (state after two years of grazing). In addition, a total of 1516 quadrates (50cm × 50cm) were used to harvest the biomass of species to estimate the forage quality variation during the grazing period inside the plots. The forage quality variables were the percentages of crude protein, acid detergent fibre and neutral detergent fibre. The data of the cover of dominant salt-marsh species, species richness, total cover, plant composition and forage quality parameters are compared between enclosure and enclosure plots and between two sampling years (2005 and 2007) using repeated measurements (general linear model) separately for each zone. The results showed that after three years of plant succession, sheep grazing had a positive influence on plant richness on the high part of the salt-marsh, a negative effect in the transitional zone and no effect in the other zones. Grazing had no effect on cover and plant composition. Forage quality parameters were affected by sheep grazing only in the low salt-marsh zone. *Limonium vulgare* had the highest forage quality and *Elymus athericus* had the lowest. It would appear that grazing with the current intensity and number of grazers would fail to hamper the expansion of *Elymus*

athericus. A higher intensity of mixed sheep-cattle or cattle grazing would be needed to better control this highly prolific species.

Key words: Succession, Management, Intertidal habitats, Forage quality, *Elymus athericus*

4.2 Introduction

Salt-marshes are important intertidal ecosystems. Many salt-marsh plant species and their associated communities are rare (Doody et al. 1993) and vulnerable to extinction (Westhoff et al. 1993). These areas are also important refuges for many animal species and play a great role for the conservation of biodiversity in general (Lefeuvre et al. 2000). The salt-marsh vegetation itself supports a wide variety of animals (Heydemann 1960; 1962; Adam 1990), many of which are restricted to saline habitats (e.g. Doody 1992; Pétilion et al. 2008). Salt-marshes are considered particularly important for migratory birds and waterfowl, which depend on these habitats for food and roosting sites (see e.g. Rowcliffe et al. 1995; Zedler & Callaway 1999; van der Wal et al. 2000; Dierschke & Bairlein 2004).

Natural succession in salt-marshes tends to lead to a monospecific vegetation, dominated by late-successional plant species (e.g. Adam 2002), such as *Elymus athericus* which is spreading all over European salt-marshes (van Wijnen et al. 1997). Moreover, *Elymus* species have invaded lower salt-marsh communities at several sites (Bakker et al. 1997a). At some of these sites (e.g. Schiermonnikoog, the Netherlands) they even occur below the mean high water (MHW) level. Expansion of *Elymus athericus* leads to a decrease of the diversity and richness of both vegetation (Roozen & Westhoff 1985; Bakker 1989; Andresen et al. 1990; Leendertse 1995; Bakker 1998; Bos et al. 2002; Kleyer et al. 2003; Bouchard et al. 2003) and fauna (Pétilion et al. 2005). It has been shown that following abandonment *Elymus athericus* build up dense stands with low plant species diversity (e.g. Bakker et al. 1997a). The expansion of *Elymus* leads to a decrease in plant (and animal) diversity in the absence of grazing (Kleyer et al. 2003). These invasions may also reduce salt-marsh functions, such as the export of organic matter towards marine systems (Valéry et al. 2004) and their role as a fish nursery ground (Laffaille et al. 2005).

In this context, the use of management practices for maintaining young salt-marsh stages and reducing late-successional stages have been recommended and are being applied in many sites. It has been shown that cattle grazing could hamper the expansion of *Elymus athericus* consequently increasing the species diversity (e.g. Olff et al. 1997; Kleyer et al. 2003). Moreover, higher stocking rates were shown to be better suited to conserve plant diversity and richness in areas in which *Elymus athericus* was dominant (Bakker et al. 2003; Kleyer et al. 2003). In contrast, high intensity grazing is known for its deleterious effects for both animal (Laffaille et al. 2000; Pétilion et al. 2007) and plant conservation (Bouchard et al. 2003). Forage quality is also important as it has been reported that high quality patches attract more birds (Olff et al. 1997; Piedboeuf & Gauthier 1999; Bos et al. 2005) increasing the importance of such salt-marsh vegetations as a feeding ground for migratory birds (cf. Laffaille et al. 2000). For example, wild-ranging Brent Geese preferred the plots with the highest nitrogen content, and declining forage quality due to changing vegetation composition and structure during succession decreased the number of birds present (Olff et al. 1997). Moreover, difference in nutritional quality of forage between marshes is likely to have had consequences for goose fitness, and may have contributed to the reported declines in gosling survivorship and size (Ngai & Jefferies 2004). Forage quality of salt-marsh species could be influenced by grazing of large herbivores (cattle or sheep). Indeed, the effect of large herbivore grazing on forage quality in terrestrial habitats has been proven (e.g. Pavlů et al. 2006). Nevertheless, until now no study directly targeting the effect of large herbivore grazing on forage quality in salt-marsh habitat has been identified. All studies were related to the influence of forage quality on herbivore behaviour, particularly geese (e.g. Olff et al. 1997).

Previous studies on grazing of salt-marshes mainly dealt with the impact of cattle grazing on the composition, structure and the productivity of salt-marsh vegetation (e.g. Bakker 1989; Andresen et al. 1990; Esselink et al. 2002). Therefore, little information is

available on the influence of sheep grazing (e.g. Tessier et al. 2003). Here, we explore the impacts of low-stock sheep grazing on salt-marsh vegetation, by considering two main target variables: species richness (as an index of conservation value) and total and individual species cover (as an indicator of successional state). As herbivores impact plant species differently, according to their quality and availability, we also considered the effect of grazing on both plant biomass and forage quality. We hypothesized that sheep grazing should enhance species richness and decrease the cover of late-successional species (mainly *Elymus athericus*), and that these patterns can be explained by changes in biomass and forage quality. In order to encompass salt-marsh heterogeneity, this hypothesis was tested in three salt-marsh zones, as well as in a transitional zone between salt-marsh and Marram sand dune (hereafter called floodmark zone), all within the same study area.

4.3 Material and methods

4.3.1 Study area

The study area, which corresponds to the grazed part of the nature reserve the IJzermonding, consists of 16ha of tidal marsh. On the right bank of the IJzer (a Flemish nature reserve owned and managed by the Agency of Nature and Forest of the Flemish Community), large-scale restoration initiatives were taken to create or restore ecological gradients in a contact zone between an estuary and coastal dunes. Restoration works took place during a five-year period from 1999 to 2003. A dike was constructed in 2001 and *Ammophila arenaria* was planted in 2002. Since the early nineties, a small herd of sheep has been grazing part of the dune area with the general aim to maintain a low grassland sward, and to avoid ruderalisation of dune grassland. From 2005 onwards, sheep have also been grazing the tidal marshes and the rest of the dune area, to maintain a pioneer stage and a species rich saline grassland through selective grazing on more competitive species, such as *Elymus athericus*

and *Phragmites australis*, and to maintain species rich, low sward dune grassland (Hoffmann et al. 2006c). The developing salt-marsh vegetation has a high potential as a feeding area for overwintering birds (Hoffmann et al. 2005), which is one of the reasons for investigating the forage quality of its vegetation.

4.3.2 Methods

Five sites (in four zones) were selected in 2004 before the start of the growing season, three in salt-marsh habitat in three different elevational zones (low, intermediate and high) and two in the floodmark zone with respect to dominant plant species. Each site was 27m × 12m large, half of which (27m × 6m) was excluded from grazing (hereafter referred to as enclosures), while the other half was accessible to sheep (hereafter referred to as exclosures). In this way, we were able to follow vegetation succession with and without grazing during three consecutive years (2005-2007). The study area is grazed with a flock density of *ca.* 1 sheep/ha salt-marsh from mid-August to mid-June. Salt-marsh sites were dominated by *Salicornia europaea* and *Suaeda maritima* in the low zone, by *Elymus athericus* in the high zone and by *Limonium vulgare* and *Puccinellia maritima* in the intermediate zone. In the transitional zone, site vegetation was dominated in one site by *Calamagrostis epigejos*, *Agrostis stolonifera* and *Erigeron canadensis*, and *Trifolium* spp. *Erigeron canadensis* and *Sedum acre* dominated the other site. In each zone in salt-marsh habitats 10 plots (2m × 2m) were established: 5 in exclosures and 5 in enclosures. In addition, 10 plots were established in the two transitional sites. In all plots, the Londo-scale was used to estimate cover data at the end of the growing season (mid-August) in 2005 and 2007.

4.3.3 Forage quality

During 2005, the biomasses of the four zones were sampled on a monthly basis in both exclosures and enclosures. Since these data did not show much variation between 2

consecutive months, sampling efforts were lowered and in the period of 2007 the same sites were sampled on a two-monthly basis up to the beginning of winter 2007. Vegetation sampling started in May 2005, while grazing started in mid-August 2005. The data collected during May, June and July was used to compare enclosure and exclosure plots before the beginning of grazing.

In each biomass sampling session, every exclosure and enclosure area was sampled, taking 5 replicas in each zone. In doing so, for 5 exclosures and 5 enclosures in four zones, a total of 40 plots were taken per sampling session in the whole area. To avoid sampling the same plots in consecutive sampling sessions, a systematic sampling technique, was used where the sampling positions are selected at regular intervals along parallel transects at equal distances ('t Mannetje 2000; Fig. 4.1). Finally the wet biomass in each plot per year (in exclosure and enclosure) was calculated by a summation of all biomass divided by the number taken in sessions.

In every plot all available above-ground biomass within a 50cm × 50cm quadrat was cut off using a pair of garden shears (making a total of 1516 quadrats from 2005 until 2007). The gathered material was packed in labelled paper bags and transported to the lab where every sample was divided into several subsamples at species level. Afterwards the subsamples were dried at 65°C during a 48 hour period, making them ready to estimate forage quality parameters.

The subsamples with a dry mass of at least 5gr were ground through a 0.8mm screen. Afterwards the following forage quality parameters were determined using a Near- Infrared Spectroscopy procedure (NIRS) (cf. Birth & Hecht 1987): percentage of Crude Protein (CP), Neutral Detergent Fibre (NDF) and Acid Detergent Fibre (ADF). A calibration line to interpret the NIRS results was constructed, using wet analyses of 10% of the samples; CP% of the samples was determined using the Kjeldahl technique (AOAC 1990), NDF% was

determined based on the van Soest and Wine (1968) procedure. Cell walls were analysed using an ANKOM-220 fibre analyzer (ANKOM Technol. Crop. Fairport, NY) apparatus using the method described by van Soest et al. (1991; 1994) by sequentially adding neutral detergent (for NDF) and acid detergent (for ADF).

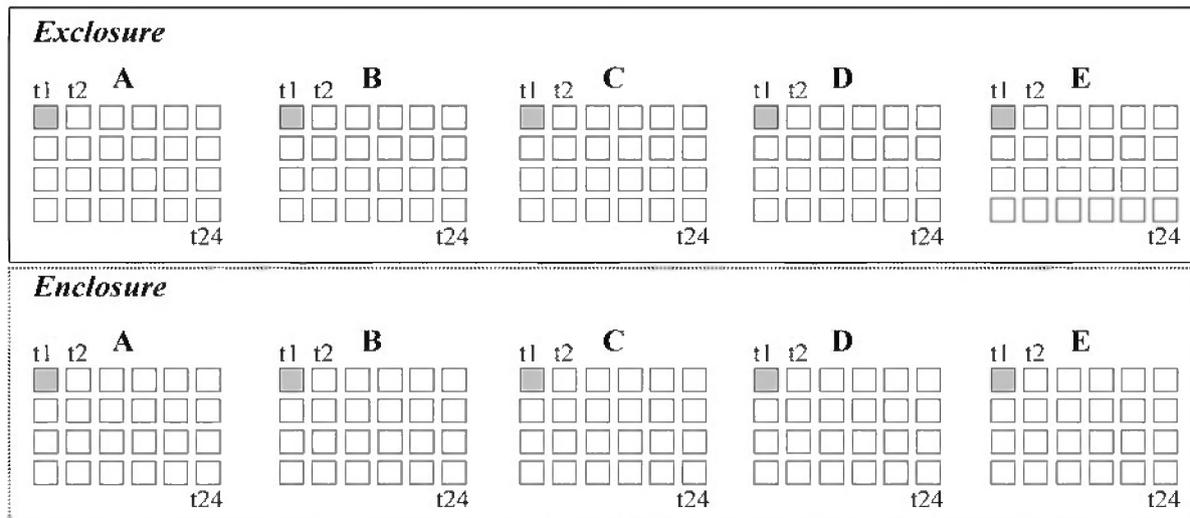


Fig. 4.1. Sampling method of the exclosures and enclosures: letters A, B, C, D and E indicate the location of the replicas; boxes represent the cut 50cm × 50cm quadrates and the labels t1, t2... indicate the sampling session (e.g. every quadrate with label t1 was cut in the first session).

4.3.4 Data analysis

Community composition was assessed by a detrended correspondence analysis (DCA), using CANOCO for windows 4.5 (Lepš & Šmilauer 2005). Since axes 1 (eigenvalue = 0.98) and 2 (eigenvalue = 0.58) explained a large proportion of the variation, only scores on the first two axes were used as a measure for plant community species composition. The scores on DCA-1, DCA-2, total cover, species richness and the cover of dominant salt-marsh species were transformed into $\log_{10}(x+1)$ to meet the normal distribution. Consecutively, the scores on DCA-1, DCA-2, total cover, species richness and the cover of dominant salt-marsh species were compared between grazed and ungrazed plots using repeated measurements General Linear Models (GLM) with grazing as a between-subject factor and year as a within-subject

factor was applied. In case of significant interaction between grazing and year, parameters were tested year by year using the t-test. The impact of grazing is expected to be put into evidence by a significant interaction between year and grazing factor, i.e. no impact of grazing at the beginning of experiment in 2005, and significant impact two years later (2007).

Biomass and forage quality parameters collected in May, June and July 2005 were compared by t-tests between exclosure and enclosure areas as a basal point (in case no significant difference was shown between exclosure and enclosure areas, grazed and ungrazed sampling started at the same plots, half of them with grazing and half of them without grazing).

The data collected from August 2005 until November 2007 was used to detect the influence of sheep grazing on biomass and forage quality parameters. Repeated measurement GLM was used to compare the biomass and forage quality parameters between grazed and ungrazed plots with grazing as the between-subject factor and year as the within-subject factor. The impact of grazing is expected to have a non significant effect of both the interaction between year and the year factor combined with a significant effect on the grazing factor, i.e. significant impact of grazing at the end of 2005 as well as two years later.

In all cases, the data were transformed into $\log_{10}(x+1)$. Finally, GLM and LSD were also used to compare the forage quality parameters among different salt-marsh species.

4.4 Results

4.4.1 The effect of grazing on species richness, total cover and plant community composition

Grazing had a positive influence on species richness in the high zone (Table 4.1, Fig. 4.1A). Species richness did not show a significant difference in 2005 between grazed and ungrazed areas while a significant difference was detected in 2007 ($t= 8.99$, $df= 4$ and

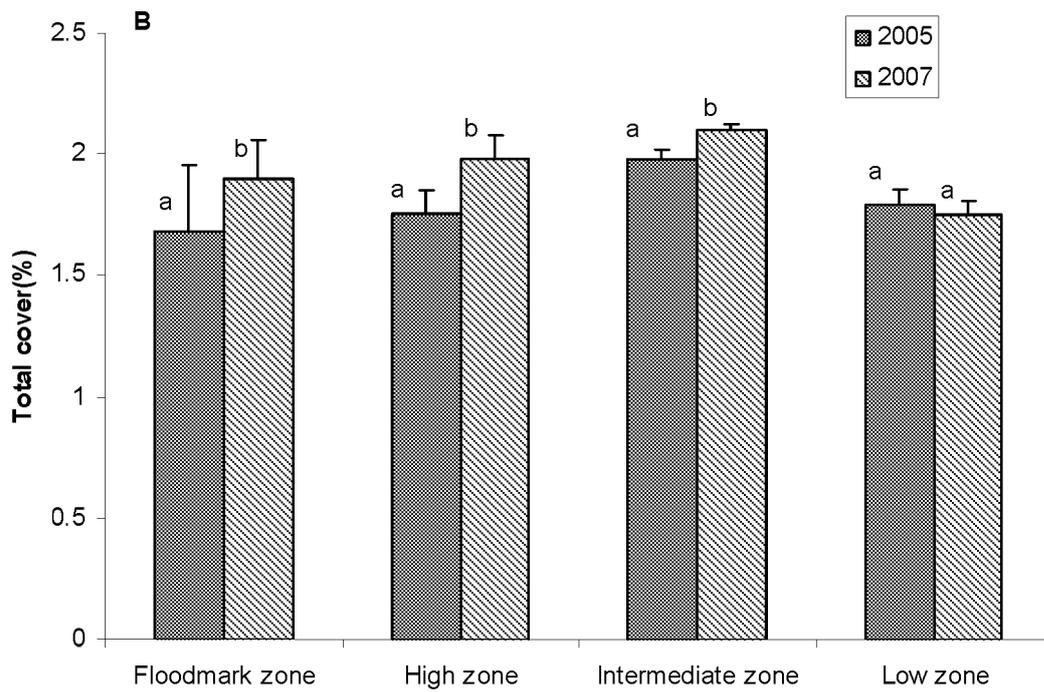
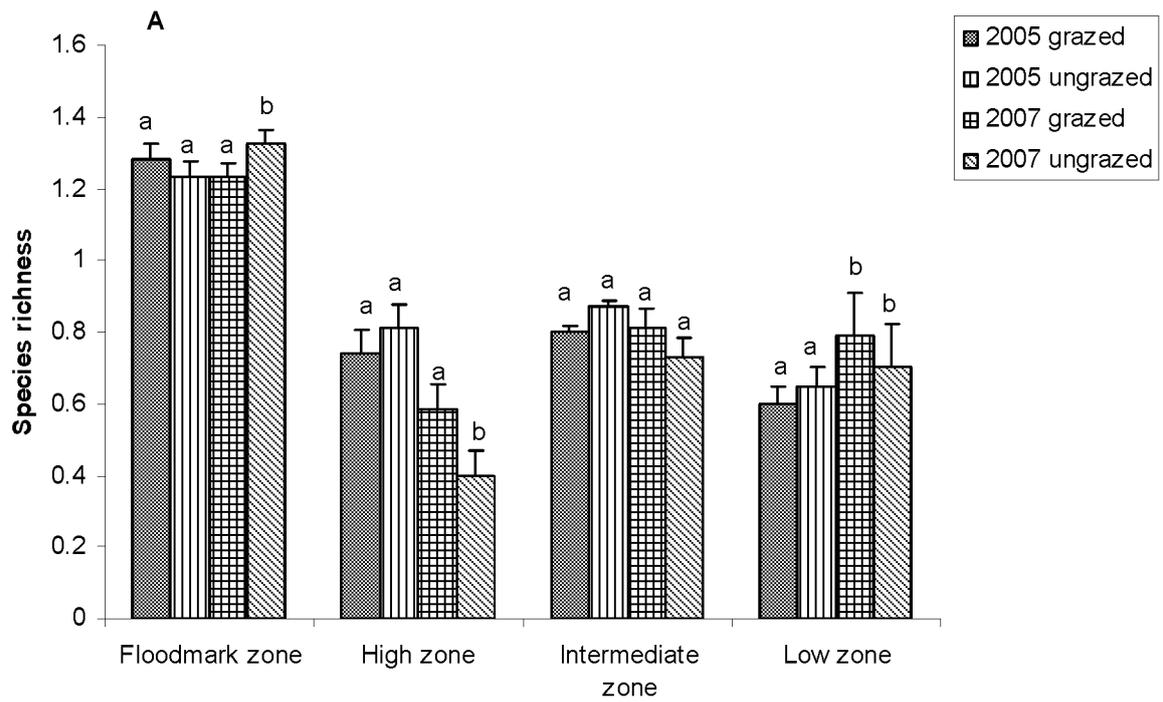
$p < 0.01$). In addition, there was no significant difference between 2005 and 2007 in grazed plots while in ungrazed plots species richness decreased ($t = 7.45$, $df = 4$ and $p < 0.01$).

Grazing had a significant influence on species richness in the floodmark zone (Table 4.1, Fig. 4.1A). Species richness had no significant difference in 2005 between grazed and ungrazed areas while a significant difference was detected in 2007 ($t = -3.466$, $df = 4$ and $p = 0.03$). In addition, there was no significant difference between 2005 and 2007 in grazed plots while in ungrazed plots, species richness increased with natural succession ($t = -2.29$, $df = 4$ and $p = 0.04$).

Sheep grazing had no significant influence on species richness in the intermediate and low zones. Species richness increased in the low zone over time ($t = -2.29$, $df = 4$ and $p = 0.05$). Vegetation composition and total cover changed over time but no significant effect of grazing was detected on vegetation composition and total cover in any zone (Table 4.1, Fig. 4.1B). Although grazing had no significant influence on percentage cover of dominant species, the percentage cover of *Elymus athericus* ($t = -1.92$, $df = 9$ and $p = 0.05$) increased and the percentage cover of *Salicornia europaea* ($t = 3.84$, $df = 9$ and $p < 0.01$) decreased over time (Fig. 4.1C).

Table 4.1. The result of repeated measurements to study the effect of grazing on species richness, total cover, composition and dominant individual species cover.

| Vegetation parameter | Zone | Year | | | Grazing | | | Grazing × Year | | |
|--|--------------|------|--------|-----------------|---------|------|-----------------|----------------|-------|-----------------|
| | | df | F | <i>p</i> -value | df | F | <i>p</i> -value | df | F | <i>p</i> -value |
| Species richness (per 4m ²) | Floodmark | 1 | 0.77 | 0.40 | 1 | 0.08 | 0.78 | 1 | 12.55 | 0.00 |
| | High | 1 | 38.54 | 0.00 | 1 | 0.43 | 0.53 | 1 | 7.43 | 0.02 |
| | Intermediate | 1 | 1.67 | 0.23 | 1 | 0.03 | 0.87 | 1 | 0.66 | 0.43 |
| | Low | 1 | 4.08 | 0.05 | 1 | 0.17 | 0.67 | 1 | 0.81 | 0.37 |
| Total cover (%) | Floodmark | 1 | 13.77 | 0.00 | 1 | 0.01 | 0.95 | 1 | 0.52 | 0.48 |
| | High | 1 | 10.46 | 0.01 | 1 | 1.79 | 0.22 | 1 | 0.83 | 0.38 |
| | Intermediate | 1 | 22.67 | 0.00 | 1 | 2.09 | 0.19 | 1 | 1.25 | 0.29 |
| | Low | 1 | 0.04 | 0.85 | 1 | 0.96 | 0.35 | 1 | 0.54 | 0.48 |
| DCA1 | Floodmark | 1 | 5.29 | 0.05 | 1 | 0.15 | 0.70 | 1 | 0.73 | 0.41 |
| | High | 1 | 7.33 | 0.40 | 1 | 1.04 | 0.33 | 1 | 0.40 | 0.54 |
| | Intermediate | 1 | 0.18 | 0.67 | 1 | 1.62 | 0.23 | 1 | 2.11 | 0.18 |
| | Low | 1 | 164.90 | 0.00 | 1 | 1.69 | 0.22 | 1 | 0.48 | 0.50 |
| DCA2 | Floodmark | 1 | 0.14 | 0.71 | 1 | 1.32 | 0.28 | 1 | 0.48 | 0.50 |
| | High | 1 | 3.42 | 0.10 | 1 | 0.33 | 0.57 | 1 | 0.81 | 0.39 |
| | Intermediate | 1 | 7.24 | 0.02 | 1 | 0.02 | 0.88 | 1 | 11.62 | 0.00 |
| | Low | 1 | 21.25 | 0.00 | 1 | 1.26 | 0.29 | 1 | 1.19 | 0.31 |
| <i>Elymus athericus</i> | High | 1 | 3.60 | 0.05 | 1 | 0.11 | 0.75 | 1 | 0.81 | 0.39 |
| <i>Limonium vulgare</i> | Intermediate | 1 | 1.01 | 0.34 | 1 | 1.20 | 0.30 | 1 | 1.64 | 0.23 |
| <i>Salicornia europaea</i> | Low | 1 | 13.14 | 0.00 | 1 | 0.92 | 0.36 | 1 | 0.01 | 0.91 |



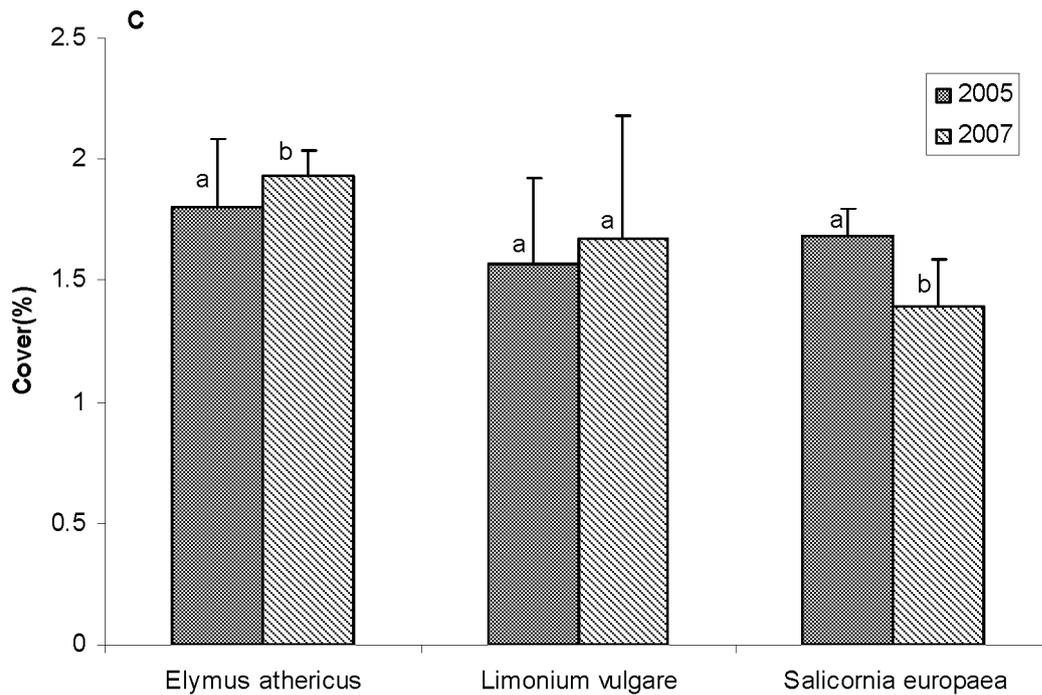


Fig. 4.1. Changes in species richness (A), total cover (B) and dominant species cover (C) by sheep grazing and time at different zones. Different successive letters indicate significant differences (at $p < 0.05$) between plots within a zone (A) and between years (B and C); Species richness is the number of species per 4m²; see Table 1 for details on GLM.

4.4.2 The effect of grazing on biomass and forage quality parameters

There was no significant difference between enclosure and enclosure plots for biomass and forage quality parameters at the beginning of the study (May, June and July 2005) (Table 4.2). Therefore, detecting the significant differences between grazed and ungrazed plots in later analyses could be considered to be a product of grazing.

Grazing had a significant effect on biomass, %ADF and %CP in low zone (Table 4.3). Biomass ($t = -4.04$, $df = 18$ and $p < 0.01$) and %CP ($t = -11.82$, $df = 18$ and $p < 0.01$) was decreased by grazing, while %ADF ($t = 9.63$, $df = 18$ and $p < 0.01$) was increased by grazing (Fig. 4.2). Grazing had no significant effect on biomass and quality parameters in high, intermediate and floodmark zones (Table 4.3).

Table 4.2. Comparisons between enclosure and enclosure areas at the beginning of the study for biomass and forage quality parameters (the data collected during May, June and July 2005 were used).

| Biomass and quality parameters | Zone | df | t | p-value |
|--------------------------------|--------------|----|-------|---------|
| Biomass (gr) | Floodmark | 8 | 1.46 | 0.65 |
| | High | 8 | -2.02 | 0.08 |
| | Intermediate | 8 | -0.45 | 0.66 |
| | Low | 8 | 1.27 | 0.23 |
| CP (%) | Floodmark | 8 | 1.63 | 0.16 |
| | High | 8 | 1.78 | 0.13 |
| | Intermediate | 8 | 1.45 | 0.20 |
| | Low | 8 | -0.25 | 0.81 |
| NDF (%) | Floodmark | 8 | -0.16 | 0.87 |
| | High | 8 | -1.40 | 0.22 |
| | Intermediate | 8 | -0.89 | 0.40 |
| | Low | 8 | 0.78 | 0.45 |
| ADF (%) | Floodmark | 8 | -0.52 | 0.62 |
| | High | 8 | -1.42 | 0.21 |
| | Intermediate | 8 | -1.74 | 0.14 |
| | Low | 8 | 1.99 | 0.10 |

Table 4.3. The results of repeated measurements on the effect of sheep grazing on biomass and forage quality parameters.

| Biomass and quality parameters | Zone | Year | | | Grazing | | | Grazing × Year | | |
|--------------------------------|-------------------|------|-------|-------------|---------|-------|-------------|----------------|------|---------|
| | | df | F | p-value | df | F | p-value | df | F | p-value |
| Biomass (gr) | Floodmark | 1 | 11.72 | 0.00 | 1 | 0.14 | 0.71 | 1 | 0.29 | 0.60 |
| | High zone | 1 | 0.50 | 0.83 | 1 | 0.01 | 0.92 | 1 | 3.13 | 0.11 |
| | Intermediate zone | 1 | 14.37 | 0.00 | 1 | 3.57 | 0.09 | 1 | 0.98 | 0.35 |
| | Low zone | 1 | 3.26 | 0.12 | 1 | 0.33 | 0.01 | 1 | 0.01 | 0.29 |
| CP (%) | Floodmark | 1 | 33.43 | 0.00 | 1 | 0.38 | 0.55 | 1 | 3.28 | 0.12 |
| | High zone | 1 | 14.21 | 0.00 | 1 | 4.80 | 0.07 | 1 | 0.71 | 0.43 |
| | Intermediate zone | 1 | 17.53 | 0.00 | 1 | 0.06 | 0.82 | 1 | 7.33 | 0.09 |
| | Low zone | 1 | 5.15 | 0.05 | 1 | 100.9 | 0.00 | 1 | 0.37 | 0.56 |
| NDF (%) | Floodmark | 1 | 2.88 | 0.14 | 1 | 1.72 | 0.23 | 1 | 0.19 | 0.67 |
| | High zone | 1 | 3.13 | 0.13 | 1 | 2.36 | 0.17 | 1 | 0.08 | 0.80 |
| | Intermediate zone | 1 | 16.01 | 0.00 | 1 | 0.15 | 0.71 | 1 | 0.11 | 0.74 |
| | Low zone | 1 | 0.40 | 0.54 | 1 | 13.13 | 0.07 | 1 | 0.68 | 0.43 |
| ADF (%) | Floodmark | 1 | 10.32 | 0.02 | 1 | 0.44 | 0.52 | 1 | 0.00 | 0.94 |
| | High zone | 1 | 62.54 | 0.00 | 1 | 1.20 | 0.31 | 1 | 0.06 | 0.80 |
| | Intermediate zone | 1 | 22.03 | 0.00 | 1 | 0.99 | 0.34 | 1 | 0.29 | 0.60 |
| | Low zone | 1 | 0.60 | 0.46 | 1 | 105.2 | 0.00 | 1 | 1.26 | 0.29 |

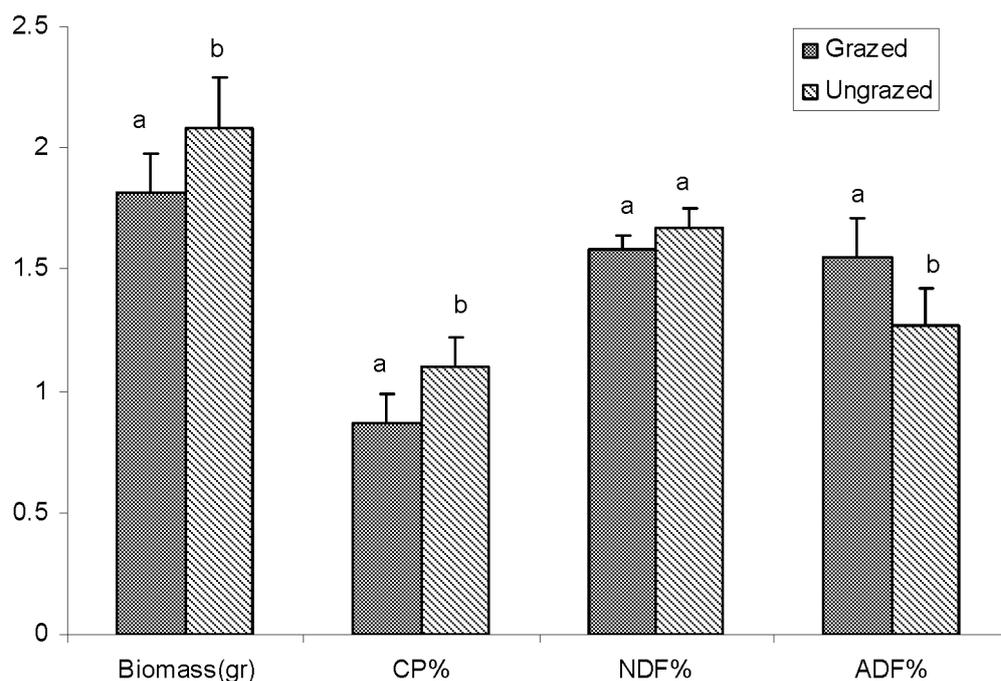


Fig. 4.2. The effect of sheep grazing on biomass and quality parameters in the low zone dominated by *Salicornia europaea*. Different successive letters indicate significant differences (at $p < 0.05$) between grazed and ungrazed; (see Table 1 for details on GLM).

4.4.3 Forage quality parameters in different individual species

CP% was significantly different between distinct species ($F = 44.14$, $df = 5$ and $p < 0.01$) being lowest in *Elymus athericus* ($8.01 \pm 3.16\%$) and highest in *Limonium vulgare* ($13.37 \pm 4.04\%$). There was no significant difference among *Puccinellia maritima* ($10.89 \pm 3.91\%$), *Salicornia europaea* ($9.46 \pm 3.54\%$), and *Suaeda maritima* ($9.76 \pm 3.24\%$) in CP%. There was a significant difference among species in NDF% being highest in *Elymus athericus* ($62.73 \pm 7.50\%$) and lowest in *Limonium vulgare* ($40.36 \pm 10.07\%$) ($F = 119.85$, $df = 5$ and $p < 0.01$). There was a significant difference among species in ADF%, being highest in *Elymus athericus* ($33.41 \pm 5.74\%$) and lowest in *Puccinellia maritima* ($22.90 \pm 7.37\%$) and *Salicornia europaea* ($22.61 \pm 9.02\%$) ($F = 46.32$, $df = 5$ and $p < 0.01$).

4.5 Discussion

The results show that sheep grazing has a positive effect on species richness in the *Elymus athericus*-dominated zone: whereas the species richness decreased in ungrazed plots, it remained high in the grazed plots. As sheep grazing does not appear to have an effect on the cover and biomass of *Elymus athericus*, it is likely that sheep increase the plant richness by trampling and creating small gaps or by dispersing seeds to the *Elymus athericus* zone rather than by grazing. Indeed sheep packing closely together in the high zone when the tide came in was often observed. Sheep are more selective than cattle in grazing (Hafer 1975; Hodgson et al. 1995) and prefer plant species which are generally short and not stemmy and have leaves of low dry matter (i.e. succulents), low tensile strength, and high crude protein content (Vallentine 2001). Our results show that *Elymus athericus* has the lowest quality among the (more dominant) species present. In addition, sheep prefer to graze forbs rather than grasses (Arthur et al. 2000). The decreasing species richness in the floodmark zone might be a result of selective grazing on some species. Selective grazing by sheep could eradicate some species from the floodmark zone. In the floodmark zone the seeds of some palatable species such as *Atriplex* spp. and *Chenopodium* spp. reach the driftline and germinate. The seedlings may be grazed by sheep intensively, consequently decreasing species richness.

Species composition in our plots changed between 2005 and 2007, but sheep grazing had no apparent effect on that natural succession. In contrast, it has been proven that grazing prevents the successional changes in plant composition that would otherwise occur as a result of continuous sedimentation in natural salt-marshes (Bockelmann & Neuhaus 1999). An eight-year permanent plot study showed that successional outcomes on the permanent plots depended on grazing intensity (Kleyer et al. 2003). In some studies, herbivory by insects accelerated plant species replacement (Brown 1990) whereas in others it retarded succession (Brown 1990; Davidson 1993). In addition, the cessation of grazing allows an accelerated

succession leading to rapid vegetation change (Kiehl et al. 1996). Our results might be attributed to the short time period of the study; differences may not be visible yet after only three years of grazing. In previous studies, the areas were grazed for longer periods, e.g. 5 years in the Kiehl et al. (1996) study, 6 years in the Jensen (1985) study and even longer in other studies (e.g. Bouchard et al. 2003).

Sheep grazing also had no significant effect on common species cover. Previous studies, however, showed that grazing could have a significant influence on cover of these species. Tessier et al. (2003) and Jensen (1985) found that in grazed conditions, vegetation was dominated by a short *Puccinellia maritima* stand in the lower and middle marshes. Concerning the response of annual species to grazing, results differ between investigations. According to Jensen (1985) and Kiehl et al. (1996), grazing largely promoted *Salicornia europaea* due to the creation of open space for seedling establishment, but it also damaged plants as a result of trampling. In contrast, Tessier et al. (2003) showed that the cover of *Salicornia europaea* was higher after cessation of grazing.

In contrast to our results, in which total cover was not influenced by grazing, Jensen (1985) showed that six years without grazing caused a marked increase in total cover and a dramatic reduction of the amount of bare ground while total cover did not change in the grazed area. The short duration and low pressure of grazing (*ca.* 1 sheep/ha) in the IJzermonding area could explain the different outcomes.

In general, grazing causes rapid turnover of plant material as plants produce fresh new leaves or tillers of a higher quality compared to the old leaves and reduces the standing dead and litter biomass (Fox et al. 1998; Mayhew & Houston 1999). Defoliation by intensive grazing is a method of improving or prolonging forage quality and palatability by delaying maturity, removal of old growth and stimulating re-growth (Valentine 2001). It seems that in this study late grazing periods (from August onwards) could not stimulate the re-growth of

species and refresh leaves and stems leading to higher quality. In this study, we observed either no effect on forage quality (intermediate, high and floodmark zone) or the reverse effect in the *Salicornia*-dominated zone, where the quality is lowered by grazing. To increase the forage quality, grazing would need to begin earlier in the growing season when the period of spring and early summer growth is not yet finished. For instance, *Salicornia* is not showing any re-growth anymore near the end of the growing season in August, when sheep are introduced in the area. A higher stocking rate might further increase general forage quality. Indeed, in the model developed by Hutchings & Gordon (2001), and the field data gathered by Arnold (1964), sheep have lower performance at low stocking rates as the probability of encountering previously grazed stands is lower under these circumstances. It was found that animals (birds) at higher densities keep the plants in a high quality by repeated defoliation and thus facilitate each other (Bos et al. 2002). A higher forage quality could be of management importance for two reasons: herbivorous, macrophyte eating bird species (like several duck and goose species) might profit from a higher forage quality, while general sheep performance would be higher as well. In that case, it can be recommended to the manager that the intensity of grazing should be increased and start earlier in the season. The results on biomass show that sheep graze more in the lower zones. In the low zone, sheep were grazing *ca.* 13% of primary production. Using 50:50 (take half and leave half) rule of Heady and Child (1994) suggests that intensity of grazing should increase three folds. Milotic et al. (2008) calculated that the grazing capacity of the study site, according to total available digestible energy, varies between 15 ewes in winter and *ca.* 60 ewes in summer.

As shown here and elsewhere unhampered natural succession in new salt-marsh leads to a dominance of clonal species such as *Elymus athericus*, eventually leading to a monospecific vegetation with a low animal diversity (e.g. Leendertse 1995). On the other hand, previous studies showed that cattle grazing could prevent the massive expansion of *Elymus athericus*

(van Wijnen et al. 1997). In addition, Schröder et al. (2002) showed that the cessation of sheep grazing enhanced the cover of the latter grass species. Therefore, the introduction of grazing to the salt-marsh seems to be a useful management tool to control the expansion of *Elymus athericus* and to increase plant and animal diversity. To eliminate the expansion of *Elymus athericus*, it is recommended to increase the intensity of grazing. Grazing intensity should be increased rather by cattle or mixed grazing (cattle and sheep). The increasing grazing intensity by sheep alone is expected to concentrate on other species that have a higher forage quality.

4.6 Conclusion

A period of three years grazing with low intensity had different effects on different zones. Although the highest intensity of grazing occurs on the more succulent and protein rich plants of the lower zone, species richness was also decreased by grazing in the floodmark zone indicating the attractiveness of this zone for sheep. Indeed, the risk of over-grazing in the floodmark and other zones should be taken into account before making the decision to increase sheep number.