Community Ecology

Processes, Models, and Applications

EDITED BY

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Preface

In 2001 H.A.V. started a course for second-year undergraduate biology students at the Vrije Universiteit Amsterdam entitled Community Biology. This course has now been running successfully for 8 years. The course was obligatory for all biology students, and it differed from other courses in that it was multidisciplinary and provided the students with opportunities to perform their own research. The multidisciplinarity was emphasized by the different disciplines of the teachers on the course: soil ecology, plant ecology, systems ecology, microbial physiology and theoretical biology. The important task of finding a textbook that could link all disciplines and encourage participating lecturers to deliver a unified course was solved by using *Community Ecology* by P.J.M. That book linked the different subjects of community ecology, and integrated the more theoretical parts on modelling with the empirical studies, including topics such as biodiversity and applied studies. Subsequently, H.A.V. and P.J.M. met at an international meeting on food webs, and discussed the possibility of participating in a similarly themed graduate-level course. And, thus, our current collaboration began. In The Netherlands PhD students from different universities are organized into interdisciplinary thematic groups, called research schools, that provide an intellectual support base for instruction and research. For example, students working in the field of socioeconomic and natural sciences of the environment belong to the Research School SENSE. In 2005, H.A.V., André de Roos, Claudius van de Vijver and Johan Feenstra organized a PhD course on Community Ecology for the SENSE PhD programme. During this 1 week course held in Zeist, leading researchers in the field of Community Ecology from Europe and the USA were asked to deliver lectures on recent and often unpublished developments in their areas of expertise. The lecturers were accompanied by some of their PhD students, creating an international group of community ecologists. The course was not intended to be encyclopaedic, but rather it focused on the areas of expertise of the invited speakers, many of which share the theme of patterns and processes emerging from ecological networks. Participants addressed the state of the art in theory and applications of community ecology, with special attention to topology, dynamics, the importance of spatial and temporal scale and the applications of community ecology to emerging problems in human-dominated ecosystems, including the restoration and reconstruction of viable communities. The course finished with speculations about future research directions. During the course, it became clear that this international group of students appreciated the information presented by the various lecturers, despite the fact that research topics exhibited great diversity. It was during this very stimulating course that the idea for this book took form. H.A.V. and P.J.M., the editors, convinced most lecturers to transform their lectures into book chapters, and asked other colleagues to fill in some gaps. The result captures much of the excitement about community ecology expressed during the course, and expands the coverage of topics beyond what we were able to discuss in an intensive week-long course. We recognize at the outset that certain subdisciplines of community ecology are not covered here, and we do not claim otherwise. We know that the topics addressed here will be of interest to advanced students and practitioners of community ecology. Ultimately, 19 colleagues participated in writing this book. We thank them all for their important contributions. Writing book chapters, strangely enough, is less valued than writing articles for scientific journals in some academic circles. Still, like the multidisciplinary course mentioned above, we find that the interactive writing that happens when people from different subdisciplines work together is a fascinating, synergistic and productive process.

We would like to thank friends and colleagues who were indispensable during the process of writing: H.A.V. thanks Nico van Straalen, who by writing his book *Ecological Genomics* for Oxford University Press acted as an instigator for this book. H.A.V. also thanks his colleagues who made the Community Biology course a success for so many years: Wilfred Röling, Bob Kooi, Matty Berg, Wilfried Ernst, Tanja Scheublin, Diane Heemsbergen, Stefan Kools, Marcel van der Heijden, Susanne de Bruin, Lothar Kuijper, Rully Nugroho and Henk van Verseveld. H.A.V. acknowledges colleagues who were directly involved in the organization of the PhD course: André de Roos, Claudius van de Vijver, Johan Feenstra and Ad van Dommelen. H.A.V. is very grateful to his critical friend, John Ashcroft (Durham), for supportive focusing.

P.J.M. thanks the many students who participated in the Zeist Community Ecology Course, as well as the students who have taken the community ecology course that he has taught at Rutgers University since 1983. Their collective comments and feedback have helped to refine his perspectives about the nature of community ecology over the years. Thanks also go to participants in a recent seminar on Ecological Networks for critical feedback on some of the writing that appears here, including Mike Sukhdeo, Maria Stanko, Wayne Rossiter, Tavis Anderson, Faye Benjamin, Denise Hewitt, Kris Schantz and Chris Zambel.

H.A.V. and P.J.M. both thank Ian Sherman of Oxford University Press, who was immediately enthusiastic about this book project, and Helen Eaton, who as assistant commissioning editor played a crucial role in the development of the book.

H.A.V. thanks Emilie Verhoef, without whom this book probably would never have been produced. P.J.M. thanks Marsha Morin for her understanding and support during another extended writing project.

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CHAPTER 10

Community ecology and management of salt marshes

Jan P. Bakker, Dries P.J. Kuijper and Julia Stahl

10.1 Introduction

Salt marshes are ecosystems at the edge of land and sea. They are influenced by tidal movement. It is the interaction of the vegetation and sediment trapped from inundating water that creates a salt marsh. Currently, there are about 176 000 ha of salt marsh around the Baltic and Atlantic coasts of Europe. For the Wadden Sea the area of the salt marshes can be subdivided into ~13 000 ha of salt marshes on the barrier islands and ~26 000 ha of salt marshes along the mainland coast (Bakker *et al*. 2005a). Back-barrier marshes develop at the lee side of the sand dune system of barrier islands in front of the mainland coast, where foreland marshes develop.

Salt marshes are considered to represent one of the few pristine ecosystems in North-West Europe. That may be true for some marshes, others are distinctly influenced by humans (Davy *et al*. 2009). The role of salt marshes along the coast has been transformed from primarily coastal protection tasks to a combination of the former with nature conservation interest. Large areas are nowadays assigned to nature reserves or national parks. These designations initiated critical debates on naturalness and suitable management of marshes and concern especially the need and intensity of livestock grazing (Bakker *et al*. 2003a).

Naturally developed salt marshes feature a self-stimulated development and geomorphological condition and growth that are not affected by humans. They show a natural drainage system with meandering creeks and levees with higher elevation than the adjacent depressions. Erosion protection measures, coastal defence or agricultural purposes play no critical role. They occur in sandy back-barrier conditions on islands such as Mellum, Spiekeroog (Germany), eastern parts of Ameland and Schiermonnikoog (The Netherlands). On the other hand, semi-naturally developed salt marshes either have an extensive wide-stretched natural creek system but are affected by measures to enhance livestock grazing (e.g. back-barrier conditions at the peninsula of Skallingen (Denmark) or feature a salt marsh within sedimentation fields with a man-made drainage system by ditches and are grazed by livestock or left fallow after previous grazing (e.g. artificial marshes along the mainland coast of The Netherlands, Germany and Denmark; Bakker *et al*. 2005a).

Abiotic conditions on salt marshes are related to the inundation period and frequency depending on an elevation gradient running from the upper marsh at the foot of a dune at the back-barrier marshes, or the foot of the seawall along the mainland coast to the intertidal flats. This elevational gradient also influences the rate of sedimentation, which is the main driver of plant succession. The rate of sediment input on salt marshes varies from < 5 mm/year on sandy back-barrier marshes to up to 20 mm/year on marshes in sedimentation fields (Bakker *et al*. 2002). This results in a distinct zonation of plant communities (Bakker *et al*. 2002), invertebrate communities (Andresen *et al*. 1990), avian herbivores (Stahl *et al*. 2002) and mammals (D.P.J. Kuijper unpublished data).

In this chapter we will discuss the naturalness of salt marshes and their plant cover and the interaction of the vegetation with abiotic conditions, such as sediment and nutrient input, and with biotic conditions, such as wild herbivores and livestock. We will particularly address the long-term dynamics of salt-marsh communities. We will demonstrate to what extent the findings of small-scale experiments on individual salt marshes can be generalized to add to our understanding of community ecology of salt marshes, and how this knowledge can be applied for management purposes.

10.2 Natural salt marsh: the back-barrier model including a productivity gradient

Barrier islands in the Wadden Sea feature sandy beaches along the North Sea and silty salt marshes along the Wadden Sea. Sedimentation of fine suspended material (silt or clay) can take place in the shelter of dunes. The geomorphological conditions of the sandy subsoil show a gradual slope from the foot of the dunes towards the intertidal flats. As the period of inundation is longer and the frequency higher at low elevation, the input of sediment is higher at the low marsh than at the higher marsh. Apart from the zonation from low to high marsh, the thickness of the sediment layer changes over time from a young marsh to an older marsh. The back-barrier salt marsh of the Dutch island of Schiermonnikoog shows such a successional pattern. The eastern part of the island gradually extends further eastward. Hence, a chronosequence representing vegetation succession (De Leeuw *et al*. 1993; Olff *et al*. 1997) has established with very young marsh (from 0 years onwards) at the far east and older marshes (up to 150 years) more to the west (Fig. 10.1). Increasing age of the marsh coincides with a thicker layer of sediment resulting from tidal inundation. Thus, the eastern part of Schiermonnikoog features a matrix of two phenomena: zonation and succession. While walking from east to west at high or low elevation levels, succession of the higher and lower marsh can be studied, respectively. With the sediment, organic matter including nitrogen is imported. The nitrogen pool of the top 50 cm of the soil, i.e. the rooting depth of most plant species, is positively related to the thickness of the sediment plus underlying sandy soil. By comparing various back-barrier systems

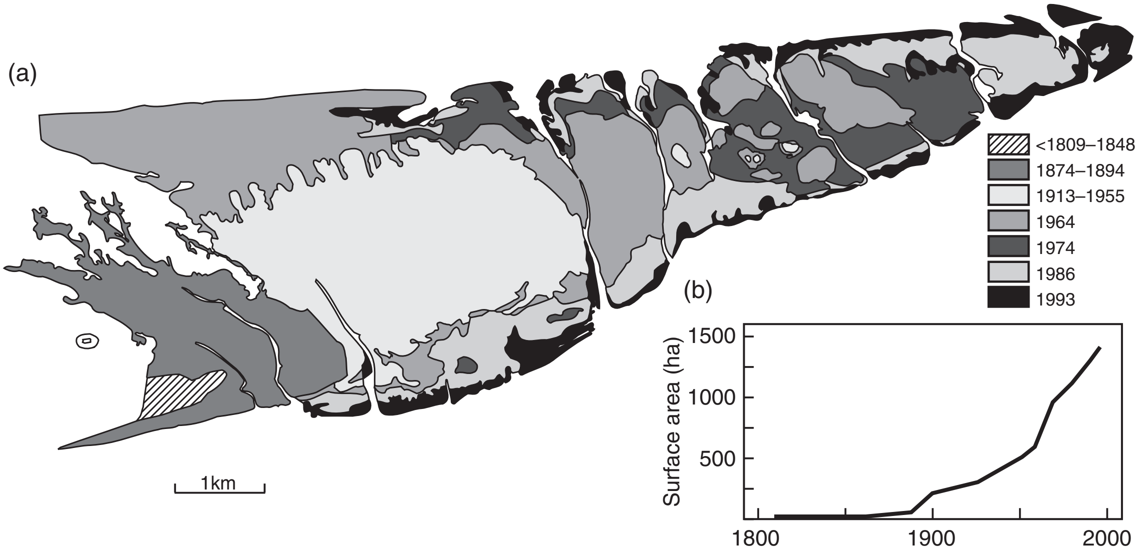

Figure 10.1 (a) The development history of the eastern part of the Dutch Wadden Sea island of Schiermonnikoog. The different shadings represent different age classes on the basis of maps and aerial photographs. (b) Development of the size of the vegetated marsh and dune area on the eastern part of Schiermonnikoog from 1989 onwards. After Van der Wal *et al*. (2000b).

in the Wadden Sea (Schiermonnikoog, The Netherlands; Terschelling, The Netherlands; Skallingen, Denmark), this appeared to be a general phenomenon (Olff *et al.* 1997; Van Wijnen and Bakker 1997).

Soil nitrogen is a limiting factor for plant production in salt-marsh systems (see overview in Davy *et al*. 2009). As the nitrogen availability is positively related to the nitrogen pool (Bakker *et al*. 2005b), the plant productivity increases with a growing thickness of clay layer (Van de Koppel *et al*. 1996). In other words the chronosequence of increasing thickness of sediment represents a productivity gradient.

10.3 Effects of plants on herbivores (bottom-up control)

Along the productivity gradient the density of the wild herbivores such as different species of Arctic geese (e.g. brent goose *Branta bernicla bernicla,* barnacle goose *Branta leucopsis*), brown hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) initially increases to an optimum at intermediate productivity, but declines at sites with high productivity (Van de Koppel *et al*. 1996). According to theory, at sites with low productivity, plant biomass is too low to support a herbivore population, and plant growth will be regulated by bottom-up effects such as nutrient availability (Oksanen and Oksanen 2000). With increasing productivity a shift from bottom-up to top-down effects is expected to occur. Top-down regulation of plant biomass occurs at sites of intermediate levels of productivity, and herbivore population will be top-down regulated by carnivores at high productivity (Oksanen and Oksanen 2000). However, in the absence of carnivores (e.g. one of our study systems, Schiermonnikoog) bottom-up effects remain to play an important role even at highly productive sites. Herbivore density can decrease even in the absence of carnivores. Intake rate of geese levels off or declines with biomass above a certain threshold (Van der Graaf *et al*. 2006). Forage quality declines at sites of high biomass and tall canopy (Van der Wal *et al*. 2000a; Kuijper and Bakker 2005) featuring a decreasing leaf–stem ratio. This bottom-up control of herbivore density at high productivity sites is referred to as the ‘quality threshold hypothesis’ (Van de Koppel *et al*. 1996; Olff *et al*. 1997; Huisman *et al*. 1999).

The productivity gradient (chronosequence) on Schiermonnikoog is accompanied by plant species replacement. The unproductive lower salt marsh is dominated by *Salicornia* spp., *Puccinellia maritima*, *Plantago maritima* and *Limonium vulgare*, whereas the oldest stages are dominated by *Atriplex portulacoides*. The unproductive higher marsh features *Puccinellia maritima* and *Festuca rubra* followed by *Artemisia maritima* and, eventually, *Elymus athericus* (*Elytrigia atherica*) at the productive marsh (Olff *et al*. 1997; Van der Wal *et al*. 2000a). Both at the low and high salt marsh, succession eventually features a tall canopy of *Atriplex portulacoides* or *Elymus athericus*, respectively. Recently, it was noticed that *Elymus athericus* spread into lower elevation at older marshes (Olff *et al*. 1997). These tall plant species outcompete other species by light interception (Huisman *et al*. 1999; Van der Wal *et al*. 2000a), with subsequent decline in plant species richness (Bakker *et al*. 2003b).

Herbivores are evicted by plant succession. Goose numbers were estimated at young, intermediate and older parts of the salt marsh on Schiermonnikoog between 1971 and 1997 (Fig. 10.2). In the late 1970s brent goose numbers were high in the old marsh. However, goose numbers declined significantly in the following 20 years (Van der Wal *et al*. 2000b). This decrease is not related to a decrease in size of the area. On the contrary, the surface area increased over the years as a result of sedimentation (Fig. 10.1). Goose numbers increased in the intermediate aged salt marsh followed by a slight but significant decrease towards 1997. Development of new young marsh in the east led to a further eastward movement and an increase of goose abundance (Van der Wal *et al*. 2000b). The decrease in number of brent geese at the older marsh coincided with a change in vegetation composition. In 1977, when goose abundance was still high, the clonal shrub *Atriplex portulacoides* was lacking. Since then, the *Atriplex* community has spread into the lower elevation salt marsh, and this coincided with the observed decline in goose numbers. Part of the *Limonium* community was transformed into the *Atriplex portulacoides* community. The open *Limonium vulgare* community harbours the preferred goose food plants such as *Puccinellia maritima*, *Festuca rubra* and *Triglochin*

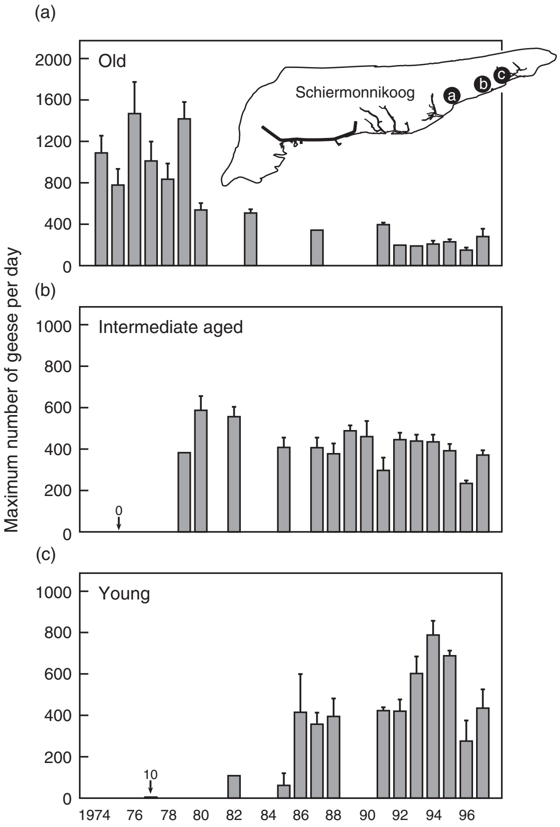

Figure 10.2 The number of brent geese in (a) old, (b) intermediate and (c) young parts of the salt marsh of Schiermonnikoog between 1974 and 1997. Maximum numbers of geese counted per day ± SE is given for all years separately. The location of the three parts of the marsh is indicated in the inset in (a). The absence of bars indicates no data, unless stated otherwise. The sizes of the study areas were 58.2 ha, 39.8 ha and 78.9 ha in 1977, and 97.4 ha, 37.5 ha and 79.2 ha in 1996 for the old, intermediate and young marsh, respectively. After Van der Wal *et al*. (2000b).

maritima, which were replaced by non-preferred species such as *Artemisia maritima*, *Atriplex portulacoides* and *Limonium vulgare* itself (Van der Wal *et al*. 2000b). However, the losses of the *Limonium vulgare* community were compensated for by an increase in this community in newly developed parts of the salt marsh at the east. We observed that ongoing plant succession pushed the geese eastward and geese had to follow the changing vegetation or, in other words, 'vegetation succession evicted spring-staging geese' (Van der Wal *et al*. 2000b).

Comparably, on the high elevation salt marsh, foraging patch choice and spatial distribution of brown hares is influenced by the ongoing vegetation succession. The tall-growing plants *Elymus athericus* and *Artemisia maritima* are invading at these sites with short vegetation consisting of the preferred food plant for hares, *Festuca rubra* (Kuijper *et al*. 2008). The increasing abundance of these tall-growing plants, which are not preferred as food plants, reduces the grazing intensity of hares. As a result, hare numbers decrease with increasing salt-marsh age; hence, they are also evicted by vegetation succession (Kuijper and Bakker 2008).

10.4 Effects of intermediate-sized herbivores on plants (top-down control)

Are small herbivores only a victim of plant succession? Studies on American salt marshes show that small- to medium-sized herbivores can regulate plant biomass. For instance, grazing by insects (Bertness and Shumway 1992), crabs (Bortolous and Iribarne 1999), snails (Silliman *et al*. 2005) and greater snow goose (*Chen caerulescens atlantica*) (Smith and Odum 1983) can regulate plant biomass in *Spartina*-dominated marshes. The effects of lesser snow goose (*Chen caerulescens caerulescens*) on sub-arctic marshes along the Hudson Bay, Canada, are another example (Jefferies *et al*. 2006). But what is known about the effects of intermediate-sized herbivores in European salt-marsh systems?

10.4.1 Experimental evidence

Theory predicts the effects of herbivory to change along a productivity gradient. The strongest top-down effects are predicted at sites of intermediate productivity (Oksanen *et al*. 1981). At the back-barrier salt marsh on Schiermonnikoog the wild brown hares occur year round, whereas brent and barnacle geese are spring-staging visitors on their way to arctic breeding grounds (Stahl 2001). Although rabbits are also found at the salt marsh, their grazing pressure is more than a factor of 10 lower than that of hares and geese, and they mainly forage along the foot of the dunes high on the marsh (Kuijper and Bakker 2005). Hence, their role on salt marshes is expected to be low. Exclosures were established at four sites along the chronosequence on the island of Schiermonnikoog. The sites were established 1, 8, 20 and 30 years previously, when experiments started. At each site, four exclosures were established in autumn 1994: two in the high marsh and two in the low marsh. Every exclosure plot included three treatments. 'controls' were freely accessible to geese and hares. 'goose exclosures' kept geese out and allowed hares to enter freely. 'full exclosures' excluded both geese and hares (Kuijper and Bakker 2005). Dropping counts demonstrated that different herbivores were successfully excluded in the treatments. The vegetation was monitored from 1995 to 2001.

10.4.2 Effects of herbivores at high marsh

Multivariate analyses revealed that full exclosures in the 1-, 20- and 30-year-old marshes showed overall a different shift in plant species composition compared with goose exclosures and control plots (Kuijper and Bakker 2005), whereas the goose exclosures did not differ from the control plots. However, these changes in cover of individual plant species did not show consistent responses to treatments. To study the effects on vegetation species composition, detrended correspondence analysis (DCA) was used. This analysis orders a data set and plots data points that are most similar close together in a diagram. DCA can be used to show graphically how the plant community structure, taking the changing abundances of all plant species into account, is changing in response the different treatments. First, when all vegetation relevés were ordered in the DCA, typically early successional species such as *Elymus farctus*, *Parapholis strigosa* and *Ammophila arenaria* were located at the left-hand side of the diagram. The typically late successional species *Elymus athericus* was at the right-hand side, and *Festuca rubra* and intermediate successional species were in the middle of the diagram (Fig. 10.3a). The ordination showed an ordering of plant communities typical of young marshes (left in Fig. 10.3) to older marshes (right in Fig. 10.3). Second, the positions of all exclosures (and controls) at the start and at the end of the experiment were included in these diagrams to show the changes in plant community. The centroids of each treatment, indicative of the averages of treatments, at each site revealed different starting positions in the diagram. This resulted from the different species composition at the establishment of the exclosures. The centroids of all treatments (control, goose exclosure and full exclosure) at the youngest sites moved in the direction of increasing cover of *Festuca rubra*, whereas all other centroids moved towards increased cover of *Elymus athericus*.

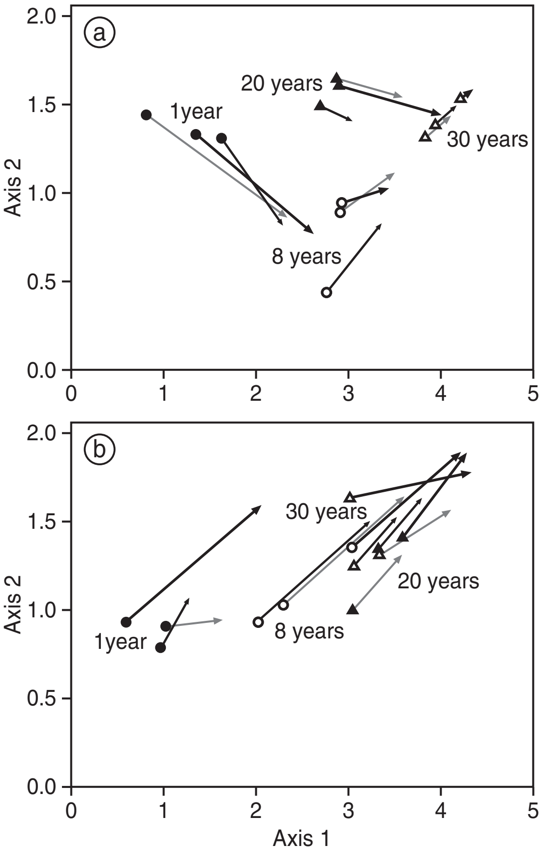

Figure 10.3 The change of position of the centroids of the quadrats in the ordination diagram between 1995 and 2001 is shown by arrows on (a) the high marsh and (b) the low marsh on Schiermonnikoog. Note the differences in scale between (a) and (b). Treatments are indicated by thick lines (full exclosure), thin lines (control) and dashed lines (goose exclosure). Sites of different ages are indicated by different symbols: closed circle, 1 year old; open circle, 8 year old; closed triangle, 20 year old; and open triangle, 30 year old marsh. After Kuijper and Bakker (2005).

The magnitude of this change did not show consistent differences between treatments, as indicated by the lengths of the arrows. Only the full exclosures in the 20 year-old marsh showed larger changes than the other treatments. This shows that, at all but the youngest sites, *Elymus athericus* increased at the expense of *Festuca rubra*, and, despite of the significant treatment effects, no clear pattern in the direction of plant communities could be detected.

10.4.3 Low marsh

The effects of the treatments on the species composition in the low marsh were more pronounced than those in the high marsh. On the low marsh, the full exclosures showed a different shift in species composition in the 1-, 8- and 30-yr-old marshes, but not in the 20-year-old marsh where highest herbivore density occurred (Kuijper and Bakker 2005). Overall, the full exclosures explained most of the variation in the shift in species composition. Typical plant species that increased in cover inside full exclosures at the 1-year-old marsh were *Atriplex portulacoides* and *Festuca rubra*, whereas *Salicornia* spp. increased the least compared with the other treatments. Also, the typically late successional species *Elymus athericus* had become established, whereas it could not be found in the area surrounding the exclosures at the young marsh site. At the 8-year-old marsh, *Festuca rubra* increased most in the full exclosures at the expense of *Puccinellia maritima*. At this site the goose exclosures showed a shift in species composition that was intermediate between the full and control treatments. At the oldest site (30 years) two typically late successional species increased in cover and dominated the vegetation: in one full exclosure *Elymus athericus*, in the other exclosure *Atriplex portulacoides*.

In the DCA diagram, typically early successional plant species such as *Salicornia* spp., *Spartina anglica*, *Spergularia maritima* and *Suaeda maritima* were in the bottom left-hand corner whereas late successional species such as *Elymus athericus* and *Atriplex portulacoides* were in the upper right-hand corner (Fig. 10.3b). All treatments showed a similar direction in the shift of species composition, i.e. they moved in the direction of increasing cover of late successional species and decreasing cover of early successional species. Moreover, all sides converge to the same point, indicating that all sites started to resemble each other in species composition. The largest changes in plant species occurred in the full exclosure at the 1 yr-old marsh; this is indicated by the largest vector (Fig. 10.3), which describes the change in community composition. Here, the largest increase in vegetational cover of late successional species occurred in the absence of herbivores (Kuijper and Bakker 2005).

These experiments revealed that grazing by intermediate-sized herbivores retards vegetation succession and that these top-down effects are most pronounced at low, young salt marshes. The open vegetation in the young unproductive marshes offers the opportunity for late successional species to become established as long as selective grazing by herbivores is absent. Once late successional species have established, they will spread more rapidly in the absence of herbivores, indicating that establishment is actually the limiting factor in this invasion and herbivory can retard further spread. In the absence of herbivores, late successional species can directly invade, during the ‘window of opportunity’ in young marshes, and will dominate the vegetation at an earlier stage. Hence, the top-down effects of the herbivores combined with the bottom-up effects of the vegetation can retard vegetation succession in these salt-marsh systems for several decades (Kuijper *et al*. 2004).

A second conclusion is that small migratory herbivores such as geese alone do not show a long-lasting impact on the vegetation, but the combination with hares is essential to retard succession. It was argued that the hare is the most important of these two herbivores in determining the effects. First, migratory geese use the salt marsh in spring before peak productivity periods of most plant species. This allows plants to recover from goose grazing once the geese have left the salt marsh. Second, in spring, hares and geese have a strongly overlapping diet, namely early successional plant species such as *Festuca rubra*, *Puccinellia maritima*, *Triglochin maritima* and *Plantago maritima*. However, in winter, hares eat late successional woody species which are sensitive to grazing, such as *Atriplex portulacoides*, *Artemisia maritima* and *Elymus athericus* (Van der Wal *et al*. 2000c).

During undisturbed succession at the high marsh in temperate European marshes, the low-statured species *Festuca rubra* eventually will be replaced by the tall-growing grass *Elymus athericus* (Leendertse *et al*. 1997). Both species were affected when herbivores were excluded, indicating local effects of grazing by intermediate-sized herbivores, because the herbivores are not able to prevent the increase of *Elymus athericus* at the high marsh (Kuijper and Bakker 2005). The main reason for this may be that *Elymus athericus* is not preferred by any herbivore (Prop and Deerenberg 1991; Van der Wal *et al*. 2000a; Kuijper *et al*. 2008), and grazing pressure drops dramatically once this species dominates the vegetation (Kuijper *et al*. 2008).

10.5 Large-scale effects of an intermediate herbivore on salt-marsh vegetation

The small-scale exclosure experiments and studies on individual plants on the salt marsh on Schiermonnikoog revealed that plant species replacement is retarded by herbivory. The effects of hare grazing especially were dominant and were most pronounced in young salt marshes (Kuijper and Bakker 2005). Grazing by hares retarded succession by more than 25 years (Van der Wal *et al*. 2000c). This implies succession should proceed fast when hares are not present at the initiation of salt-marsh development. Hence, late successional species should dominate at an earlier stage of development compared with salt marshes that developed in the presence of hares. This idea was tested by comparing the hare-grazed salt marsh on Schiermonnikoog with those of two Wadden Sea islands without hares, namely Rottumerplaat (The Netherlands) and Mellum (Germany).

On all three islands, sites were selected where salt-marsh development had started in the early 1970s. Transects of 1000 m running from the foot of a dune towards the intertidal flats were matched for surface elevation with respect to the level of mean high tide and sediment thickness (Kuijper and Bakker 2003). Early to mid-successional plant species *Puccinellia maritima* and *Plantago maritima,* which are the preferred food plant of geese, occurred at a similar elevation with higher cover on Schiermonnikoog than on Rottumerplaat and Mellum (Fig. 10.4). *Plantago maritima* was rarely found on Rottumerplaat and Mellum. *Festuca rubra*, a preferred food plant for both geese and hares, occurred over a large part of the elevation gradient on Schiermonnikoog, but was found at only a small part of the gradient on Rottumerplaat and Mellum (Kuijper and Bakker 2003). In contrast, the typically late successional species *Atriplex portulacoides* dominated the lower elevations on both Rottumerplaat and Mellum, whereas it had low cover on Schiermonnikoog (Fig. 10.4). *Elymus athericus*, a characteristic late successional species of the high marsh, occurred with higher cover at both low and high elevation on Rottumerplaat and Mellum compared with that on Schiermonnikoog. At the upper part of the elevation gradient on Rottumerplaat and Mellum a monoculture of *Elymus athericus*, covering 100%, was found. In contrast, on Schiermonnikoog, *Elymus* cover did not reach values higher than 70% (Kuijper and Bakker 2003).

It can be concluded that the small-scale exclosure experiments on Schiermonnikoog are not applicable only to understanding the local effects of grazing, but can also be extrapolated to a larger scale. Intermediate-sized herbivores affect the community structure of large-scale salt-marsh systems on the back-barrier Wadden Sea islands.

10.6 Interaction of herbivory and competition

Apart from experiments focusing on the level of the entire vegetation, detailed experiments with individual plant species may reveal which mechanisms play a role in plant species replacement along the productivity gradient. In addition to plant–plant competition, plants have to deal with changing levels of herbivory. The small highly herbivore-preferred *Triglochin maritima* is hardly present at the very young and old marshes, but is very abundant at intermediate-aged marshes. Competition and grazing are closely linked: when grazing pressure is relaxed, competition with neighbouring plants is intensified. Grazing is shown to influence these competitive interactions between plants, acting

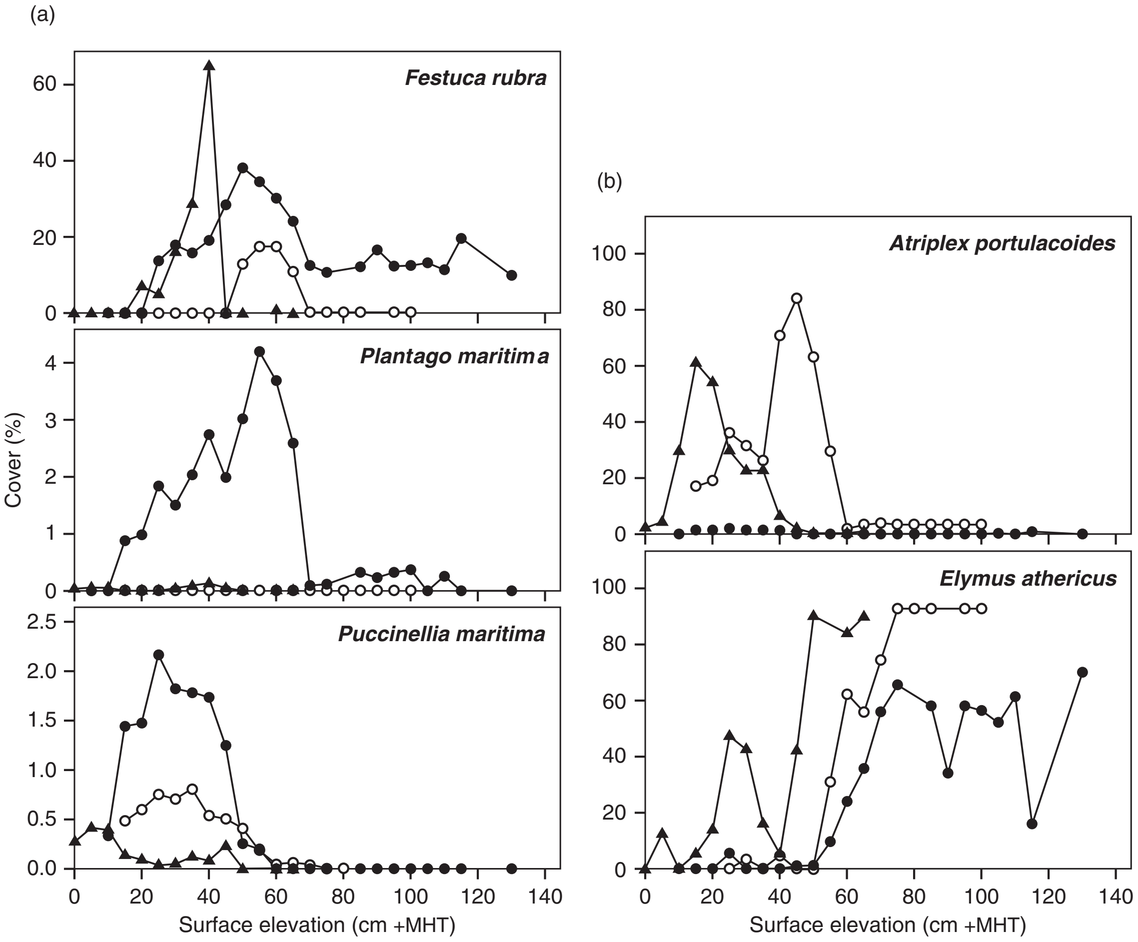

Figure 10.4 Average cover of (a) important food plant species for hares and geese, *Festuca rubra, Plantago maritima* and *Puccinellia maritima*, and of (b) typically late successional, unpalatable species, *Atriplex portulacoides* and *Elymus athericus*, at different marsh surface elevation (cm + mean high tide (MHT)) for Schiermonnikoog (island with hares), Rottumerplaat and Mellum (islands without hares). Closed circles, Schiermonnikoog; closed triangles, Rottumerplaat; open circles, Mellum. After Kuijper and Bakker (2003).

both directly on the target plant and indirectly through its neighbours. The significance of competition and herbivory largely depends on plant stature relative to the neighbouring vegetation. Although establishment of *Triglochin maritima* starts from seed, the high grazing pressure at younger marshes determines its abundance in the sward. However, at productive old marshes this small-statured plant is outcompeted by tall-growing late successional species. The distribution of *T. maritima* is 'sandwiched' between intense grazing in the younger marsh and increasing competition for light in the older marsh (Van der Wal *et al*. 2000a).

Adult plants of *Elymus athericus* are tall and not preferred by any of the herbivores. However, experiments in which grazing and competition were manipulated along the productivity gradient show that herbivory negatively affects the survival of seedlings (being a good food source) in the unproductive sites. At the productive sites, plant competition becomes an overruling factor. When seedlings grow in natural vegetation, the increased competition prevents any increase in biomass, whereas in the absence of competition the plant can grow fast because of high nutrient availability along the productivity gradient. Even though *Elymus athericus* is an unpalatable superior competitor as an adult plant at highly productive sites, in its seedling phase its growth is strongly reduced by herbivory at unproductive stages and competition with neighbouring plants at the productive stages (Kuijper *et al*. 2004).

10.7 Competition and facilitation between herbivores

10.7.1 Short-term competition and facilitation between hares and geese

For a large part of the year hares and geese forage on the same food plants, hence competitive interactions may also occur. Exclusion of brent geese at scales ranging from 30 m^2 to 1 ha at the salt marsh on Schiermonnikoog enhanced the level of utilization by hares in both *Festuca rubra*- and *Puccinellia maritima*-dominated marshes. The more geese were excluded from a site, the stronger the increase of hare grazing pressure. When geese were excluded, the 'original' decrease in *Festuca* consumption by geese was completely matched by increased hare grazing, while for *Puccinellia* only part of the surplus was grazed. Apparently, competition for food between hares and brent geese also occurs and plays a role in the habitat use of hares (Van der Wal *et al*. 1998).

Competitive and facilitative interactions between geese (barnacle and brent geese) (Stahl 2001) and geese and hares were studied on Schiermonnikoog (Stahl *et al*. 2006). Biomass (through temporary exclosures) and quality (by fertilizer application) of grass swards were manipulated and the foraging preferences of the herbivores were recorded. Captive barnacle geese were used to set the stage for a choice experiment with captive brent geese, as the latter species normally exploits the vegetation 'on the heels' of the former. Brent geese preferred to forage on vegetation previously grazed by barnacle geese, probably reacting to enhanced quality of the regrowth, in spite of the higher biomass of the ungrazed swards (Stahl 2001). In another experiment with captive barnacle geese, it was demonstrated that grazing affected the sward characteristics significantly: the proportion of dead biomass in the vegetation was reduced, and the production of additional axillary tillers increased

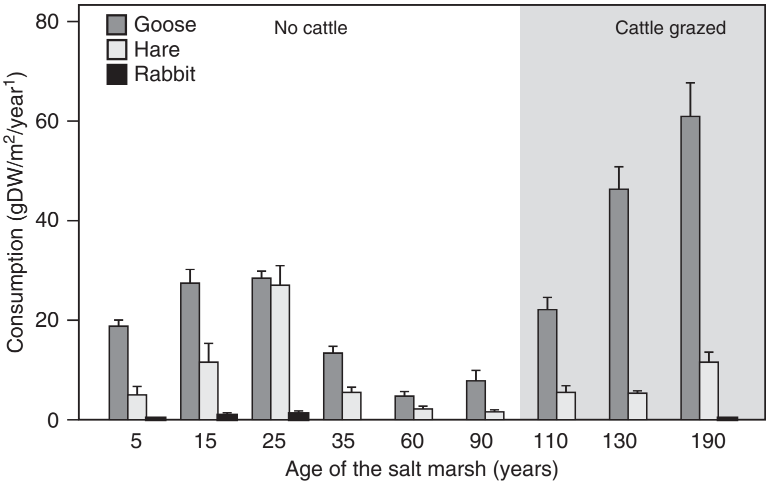

Figure 10.5 Total plant consumption of geese, hares and rabbits in salt marshes of different ages at Schiermonnikoog. Cattle grazing occurs only at the older marshes. Consumption was calculated on the basis of total droppings weight by multiplying the cumulative amount of droppings during 1 year (1999–2000) by the droppings weight per species. Subsequently, consumption was calculated from: total faecal mass/(1 – DE). Digestive efficiency (DE) for hares and geese was obtained from literature (Van der Wal *et al*. 1998). After Kuijper (2004).

(Van der Graaf *et al*. 2005). Both barnacle and brent geese selected plots with plants that have a high nitrogen content. Barnacle geese avoided plots with high biomass. Geese mainly selected plots that have been previously grazed by either geese or hares within the same season. Grazing by both geese and hares leads to an increased quality of the sward. Under these circumstances, herbivores profit from the increased tissue quality as a result of an elevated rate of nutrient intake. However, when the forage resource is used jointly by more than one herbivore species, a shift towards less preferred plots by one species may take place. Hares prefer the combination of high biomass with high plant quality in the absence of geese (Stahl *et al*. 2006). Van der Wal *et al*. (1998) suggested that large flocks of socially foraging geese rapidly deplete preferred salt-marsh sites in spring and evict hares to alternative less favourable foraging sites.

10.7.2 Long-term facilitation between herbivores

The previous section showed that the cover of species that are selected as food plant by both geese and hares, such as *Puccinellia maritima*, *Plantago maritima* and *Festuca rubra*, is higher at hare-grazed islands, whereas the cover of unpreferred plants, such as *Atriplex portulacoides* and *Elymus athericus*, is lower. Hare grazing may thus facilitate food supply for geese (Kuijper and Bakker 2003). This idea was tested experimentally at the salt marsh on Schiermonnikoog. The woody shrub *Atriplex portulacoides* is unpalatable for geese. It can overgrow the preferred food plant *Pucinellia maritima*. When *Atriplex portulacoides* was removed, goose grazing, expressed as the number of droppings found, was higher than in the control plots. In contrast, goose grazing declined when *Atriplex portulacoides* individuals were planted in a *Pucinellia maritima* sward (Van der Wal *et al*. 2000c). Knowing that hares forage on *Atriplex portulacoides* during winter, this experiment clearly demonstrated the effect of grazing facilitation by hares for geese.

Although hares can retard vegetation succession for several decades (Van der Wal *et al*. 2000c; Kuijper and Bakker 2005), they eventually lose control in the higher ranges of the productivity gradient. Large herbivores, such as livestock, are needed to set back the successional clock. Indeed, at the older cattle-grazed salt marsh in the chronosequence on Schiermonnikoog, grazing pressure of hares and geese increases again compared with the ungrazed older marsh (Kuijper 2004; Fig. 10.5). An experiment with exclosures on the cattle-grazed marsh revealed that after 30 years of cessation of cattle grazing no hares grazed inside the exclosures when the cover of tall plants, such as *Elymus athericus,* was $> 30\%$. Thus, clear facilitative effects of cattle on the feeding opportunities of hares were found (Kuijper *et al*. 2008). This finding is in contrast to studies from other areas that reported only competitive interaction between hares and livestock (Hulbert and Andersen 2001; Smith *et al*. 2004). The contrasting conclusions of these studies may be the result of the timescale of the experiments. Facilitative effects between cattle and hares on Schiermonnikoog were observed only when looking at the long-term effects, including the effect of cattle on the competitive replacement of plant species. Only when species replacement did occur in the absence of cattle was an effect on the abundance of hares observed. In contrast, in a short-term experiment on Schiermonnikoog in which cattle were excluded for 5 years, plant biomass increased inside the exclosure, but the period was too short for plant species replacement to occur. In this short-term study no effect on the abundance of hares was detected (Kuijper *et al*. 2008). This suggests that at a short timescale no effect of cattle grazing on hare abundance is apparent, whereas at a longer timescale facilitation occurs (Kuijper *et al.* 2008).

It can be concluded that competition between different species of herbivores occurs only in the short term, i.e. within one spring season. In the long-term, facilitation plays an important role. At the salt marsh on Schiermonnikoog, barnacle geese facilitate for brent geese within one season, hares facilitate for geese for several decades, and ultimately cattle facilitate for hares and geese, when hares have lost control of the vegetation.

10.8 Exclusion of large herbivores: effects on plants

10.8.1 Natural marshes

The effects of large herbivores on salt marshes is restricted to that of livestock. In fact, livestock grazing is the most common land use of North-West European salt marshes (Bakker *et al*. 2005a; Davy *et al*. 2009). Hence, the obvious way to study the effects of livestock grazing is to establish exclosures. In 1973 at the oldest part of the chronosequence on Schiermonnikoog (> 150 years) that was always cattle grazed, two exclosures were established, one at the higher and one at the lower marsh. At the higher marsh *Elymus athericus* was already present in the grazed area. The *Elymus athericus* community established at the expense of the *Juncus maritimus* community within five years after the cessation of grazing. The deposition of driftline material initiated temporary spots with the annual *Atriplex prostrata*, but within two years these were taken over again by the *Elymus athericus* community. This community also spreads at the transition to the low dune, but only gradually, and after 27 years remnants of the *Festuca rubra* community with *Armeria maritima* were still present. It seems that *Elymus athericus* is also spreading in the grazed area, but this is mainly due to the fact that the tall *Juncus maritimus* is not preferred by cattle and protects *Elymus athericus* from grazing, thus acting as a 'natural' exclosure (Bakker *et al*. 2003a).

At the lower marsh *Elymus athericus* was lacking in the grazed area at the start of the experiment. The *Artemisia maritima* community dominated within five years in the relatively higher parts inside the exclosure. It took 12 years before the first clone of *Elymus athericus* found its window of opportunity and became established. After 22 years the *Elymus athericus* community expanded. The initially bare soil at the lowest places became covered by the *Plantago maritima/Limonium vulgare* community after about ten years, after which the *Atriplex portulacoides* community took over after 22 years. The last has locally been replaced by the *Elymus athericus* community, 27 years after the cessation of grazing (Bakker *et al*. 2003a).

Taking into account the aforementioned natural succession without livestock grazing, it is likely that the oldest part of the salt marsh with a thick layer of clay in most sites will eventually be covered by the *Elymus athericus* community at both the high and the low salt marsh. That is exactly what happens after the long-term exclusion of livestock. The cessation of livestock grazing produces two main conclusions. Initially, the vegetation transforms into a 'flower garden' as many existing species have the opportunity to flower during the first few years before tall species become dominant and replace the present plant community with another one. Eventually, most plant communities are replaced by the *Elymus athericus* community at the salt marsh on Schiermonnikoog. Another part of the salt marsh on Schiermonnikoog was abandoned in 1958 for cattle grazing and grazed anew from 1972 onwards. Permanent plots in exclosures revealed that different plant communities converged into the *Elymus athericus* community after various periods of cessation of grazing: the *Juncus maritimus* community, the *Plantago maritima/Limonium vulgare* community and the *Artemisia maritima* community after 30 years and the *Juncus gerardi* community after 35 years. The only exception was the *Festuca rubra/Armeria maritima* community, which was not replaced 35 years after cessation of livestock grazing (Van Wijnen *et al*. 1997). Perhaps the combination of a thin layer of sediment (low nutrient pool) at this high elevation site and evapotranspiration during dry summer periods with subsequent high soil salinity have until now prevented replacement.

The natural marsh of Süderhafen (Germany) developed in the shelter of the former salt-marsh island of Nordstrand after 1925. The site was hardly grazed before 1968, and not at all since 1971. Repeated vegetation mapping in 1968 and 1995 revealed an expansion of the *Elymus athericus* community at the expense of the *Festuca rubra* community, and of the *Atriplex portulacoides* community at the expense of the *Puccinellia maritima* community (Bakker *et al*. 2003a).

Combining permanent plot data from experimentally ungrazed sites on the back-barrier marshes on Schiermonnikoog (The Netherlands), Terschelling

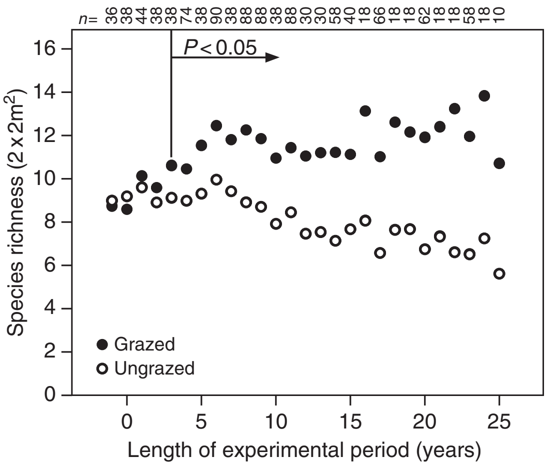

Figure 10.6 The development of plant species richness over time in paired livestock-grazed and ungrazed permanent plots in the Wadden Sea. Sample sizes (*n*) per year since the start of the treatment are indicated in the top of the diagram. After a period of three years the differences between grazing treatments were significant, indicated by the arrow with text $P < 0.05$. Observations for two sites started one year before the treatment was established. After Bos *et al*. (2002).

(The Netherlands) and Skallingen (Denmark) revealed that the convergence to the *Elymus athericus* community after the exclusion of livestock grazing is a general phenomenon (Bos *et al*. 2002).

Not only the diversity of plant communities declined after the cessation of livestock grazing. The species richness within plant communities in paired permanent plots in experimentally ungrazed and control plots also decreased significantly after five years (Fig. 10.6). (Data have been combined from the back-barrier marshes on Schiermonnikoog, Terschelling and Skallingen (Bos *et al*. 2002; Bakker *et al*. 2003a).) These permanent plots also revealed that out of 30 frequently occurring plant species only four had a significantly higher occurrence at ungrazed than at grazed marshes, namely *Artemisia maritima*, *Atriplex portulacoides*, *Atriplex prostrata* and *Elymus athericus*. Three species were indifferent, namely *Festuca rubra*, *Juncus maritimus* and *Lotus corniculatus*. All remaining 23 species had a significantly higher occurrence at grazed than at salt-marsh sites excluded for more than 20 years (Bos *et al*. 2002).

10.8.2 Artificial salt marshes

There are experimentally ungrazed plots in artificial marshes in Dollard Bay, The Netherlands. In these brackish, highly productive marshes the exclusion of cattle resulted in the increase of *Elymus repens* within six years, mainly at the expense of *Puccinellia maritima*. Species richness was higher in grazed than in excluded plots (Esselink *et al*. 2002). When salt marshes are broad enough, a gradient in grazing intensity emerges. Cattle and sheep tend to concentrate near the seawall, where fresh drinking water is available. Hence a reduction in grazing is found at the seaward site of salt marshes resulting in a taller canopy. Indeed, gradients of increasing canopy height towards the marsh edge were reported in the Dollard (Esselink *et al*. 2000), the Ley Bucht (Andresen *et al*. 1990) and Sönke-Nissen-Koog (Germany) (Kiehl *et al*. 1996).

No controlled large-scale grazing experiments have been established along the Dutch mainland coast with artificial marshes. However, three good examples can be found along the German coast. The first site is located at Friedrichskoog in Lower Saxony. It developed after 1854 and was long-term sheep grazed. The experiment was established in 1988 to study the effects of different stocking rates on soil and vegetation (Kiehl *et al*. 1996; Kiehl 1997). The stocking rate was expressed in sheep-units, i.e. adult sheep including their lambs (1 sheep-unit equals 2.8 sheep). The area was heavily grazed 'as a golf course' by 3.4 sheep-units/ha at the end of the grazing season. The control area with 3.4 sheep-units/ha was compared with 1.5 and 1.0 sheep-units/ha and cessation of grazing. At the start of the experiment this salt marsh harboured mainly *Festuca rubra* community, at the lower marsh *Puccinellia maritima* community, and at the intertidal flats *Spartina anglica* and *Salicornia* spp. communities were found (Kiehl 1997). The vegetation revealed a relatively small coverage of the *Elymus athericus* community after the cessation of grazing 11 years after the start of the experiment (Bakker *et al*. 2003a).

Apart from the above large-scale patterns, the Friedrichskoog experiment also revealed different micropatterns in the vegetation with the various stocking rates seven years after the start of the experiment. The micropatterns were formed by a mosaic of short and tall *Festuca rubra* stands on a scale of square decimetres in transects of 2 m × 10 m. In the most intensively grazed and the abandoned paddocks, no micropattern was found. The vegetation in the transects was homogeneously short or tall, respectively. However, micropatterns occurred in the three intermediately grazed paddocks with the highest spatial diversity in the 1.5 sheep-units/ha (Berg *et al*. 1997).

The second site is located at Sönke-Nissen-Koog in Schleswig Holstein. It developed after 1924 and was long-term sheep-grazed. The experimental treatments were established at the same time and had the same layout as at the Friedrichskoog site. At the start of the experiment this salt marsh mainly harboured the *Puccinellia maritima* community with locally some *Festuca rubra* and *Elymus athericus* communities, and with *Spartina anglica* and *Salicornia* spp. near the intertidal flats (Kiehl 1997). The marsh showed a large coverage of the *Elymus athericus* community after the cessation of grazing. The community covered smaller areas at the lower stocking rates, 11 years after the start of the experiment (Bakker *et al*. 2003a).

The third site is in the Ley Bucht (Germany). The site was cattle-grazed since its formation after 1950. The site was established as an experiment in 1980. The area with 2 cattle/ha was compared with areas with stocking rates of 1 and 0.5 cattle/ha and cessation of grazing. The zonation included *Elymus repens/Elymus athericus* and *Festuca rubra* communities close to the seawall, the *Agrostis stolonifera* community at the transition, the *Puccinellia maritima* community at the lower marsh, and *Spartina anglica* and *Salicornia* spp. communities near the intertidal flats. Eight years after the cessation of grazing, the *Elymus athericus* community covered large areas at the higher salt marsh and one spot at the lower marsh. It hardly occurred at the other grazing regimes (Bakker *et al*. 2003a). The *Elymus athericus* community quickly spread over both the higher and the lower marsh, and covered nearly the entire gradient 20 years after the cessation of grazing, at the expense of the *Festuca rubra* and the *Agrostis stolonifera* communities, and the *Puccinellia maritima* community, respectively. Also the 0.5 cattle/ha regime revealed a spread of the *Elymus athericus* community 15 years after the start of the experiment at both the higher and the lower marsh, but to a lesser degree than at the abandoned area.

Both artificial and the natural back-barrier salt marshes tend to transform into a dominance of the *Elymus athericus* community after the cessation of livestock grazing within 10–30 years, as could be predicted from succession without livestock grazing. However, a correlation between the number of years of exclusion of livestock grazing and the spreading of *Elymus athericus* is not always found. The salt-marsh sites that do not follow this rule seem to have a low sediment (nitrogen) input (Schröder *et al*. 2002). In these sites exclusion of livestock grazing did not result in a dominance of *Elymus athericus* within 30 years. A complication may be that because of the low sediment input these sites are building a sedimentation deficit due to continuous sea-level rise, and hence are becoming wetter. This may be an extra factor preventing the establishment of *Elymus*. Another conclusion is that grazing with low stocking rates cannot prevent the spread of *Elymus athericus*, but only retards the spread. In contrast to intensive grazing and no grazing at all, intermediate grazing can create small-scale patterns in the vegetation.

10.9 Exclusion of large herbivores: effects on invertebrates

On the natural mainland salt marsh in Mont Saint-Michel Bay (France), the invasive species *Elymus athericus* outcompetes *Atriplex portulacoides*. Apart from changes in plant communities, this results in changes in invertebrate communities, particularly spiders. The invasion of *Elymus athericus* led to an increase in the overall species richness. Causes may be the formation of a dense, tall sward which allows colonization of web-spinning species such as *Argiope bruennichi*, *Neoscona adianta* and *Larinioides cornutus*. The building of a deep litter layer favours nocturnal wanderers (Gnaphosids, Clubionids), ambush hunters (Thomisids) and litter-sensitive sheet-weavers. Non-coastal species such as the ground-living nocturnal *Pachygnatha degeeri* and the halophilic sheet-web spinning *Arctosa fulvolineata* increased. However, the dominant halophilic species *Pardosa purbeckensis* was strongly negatively affected by the invasion of *Elymus athericus* (Pétillon *et al*. 2005). Some halophilic ground beetle species were more abundant in grazed than in abandoned sites and vice versa. In general, no effect of management on species richness was found for ground beetles. Generally, spiders seem to be more dependent on vegetation and litter structure than ground beetles (Pétillon *et al*. 2008).

The aforementioned experiment in the artificial marsh of the Ley Bucht aimed to study the effect of various stocking rates on the invertebrate fauna (Andresen *et al*. 1990). For invertebrates, it may not only be the plant species composition that is important. Non-flowering *Asters* were found only at the higher salt marsh within the highest stocking rate. The canopy height of the understorey was higher in the abandoned site than in the grazed sites (Andresen *et al*. 1990). In the third year of cessation of grazing, positive effects for several invertebrate groups were recorded for Collembola, Aranea, Amphipoda, Coleoptera and Diptera. This was attributed to the accumulation of litter, increase of flowering plants and hence availability of pollen and nectar and therefore higher aboveground biomass for leaf- and stem-dwelling species (Irmler and Heydemann 1986). *Erigone longipalpis*, a halophilic species, is the most important spider species in the *Puccinellia maritima* community. Other species occur mainly in the *Festuca rubra* community and cannot be considered halophilic, namely *Oedothorax retusus*, *Pardosa agrestis* and *Pachygnata clerki*. Whereas *Erigone longipalpis* still occurred in high abundance in the *Festuca rubra* community at the start of the experiment in 1980, it has since 1982 moved to the lower *Puccinellia maritima* and *Salicornia* spp. communities in the abandoned site. The other species spread into the lower salt marsh at different rates (Andresen *et al*. 1990). A distinct zonation of the invertebrate communities was observed in the first three years of the experiment. The community diversity was highest in the abandoned site, since communities of the higher marsh spread into the lower marsh. In 1988, however, the community of the higher marsh had spread over the entire elevation gradient, and completely replaced the communities of the lower marsh in the abandoned site. Hence, eventually the community diversity was lowest at the abandoned site. However, the number of species became highest at the abandoned site, partly as a result of immigration from adjacent grassland. But the main reason was that many species are damaged by grazing (Irmler and Heydemann 1986). The authors especially stress the damaging effects of grazing on many arthropod communities.

Two and three years after the start of the aforementioned grazing experiment in Friedrichskoog and Sönke-Nissen-Koog, invertebrates were monitored. Mainly herbivorous and flower visitors were positively affected by cessation of sheep grazing and the resulting flowering of *Aster tripolium* and *Plantago maritima*. A minor part of the herbivorous fauna profits from enhanced plant growth in moderately grazed sites. Typical soil dwellers benefit from grazing owing to greater amounts of bare soil (Meyer *et al*. 1995).

In general, the community structure changes from a dominance of detritivores to a dominance of herbivores after the cessation of sheep grazing, and after the cessation of cattle grazing. The number of species and individuals increases shortly after the cessation of grazing, but after a longer period of cessation of grazing typical halophilic species may decrease. For the time being it is not possible to discuss top-down or bottom-up concepts with respect to the interaction between vegetation and invertebrates. Food web studies could help in this discussion and are currently being carried out.

10.10 Exclusion of large herbivores: effects on birds

10.10.1 Migrating birds

In order to evaluate the importance of livestock grazing for habitat use by geese in the Wadden Sea, a large-scale inventory was made. Sixty-three transects were established, subdivided over 38 sites. Only those sites with a stable and clearly defined management regime for at least six preceding years were included. Management was subdivided into 'long-term ungrazed'($>$ 10 years), 'short-term ungrazed' (6–10 years), 'lightly grazed' (low stocking rates, i.e. $\leq$ 4.5 sheep/ha or $\leq$ 1 cow/ha), and 'intensively grazed' (i.e. with high stocking rate). Only marshes with sufficiently large surface area (> 5 ha), large enough for a flock of geese to land on, were included. The sites were distributed over the entire Danish ($n = 11$), German ($n = 17$) and Dutch ($n = 10$) Wadden Sea. Twenty-two sites harboured transects with at least two different grazing regimes under similar abiotic conditions. Seventeen sites with paired transects were visited twice, once in April and once in May 1999. The transects on back-barrier marshes were, with one exception, visited only by brent geese, whereas most transects on artificial marshes along the mainland coast were utilized by both brent and barnacle geese. For each management regime at each site, one transect was established perpendicular to the seawall and the coastline, along the entire extent of the marsh. Hence, transects were variable in length, ranging from 100 m to 1000 m, and included high-marsh, mid-marsh and lower marsh sections. Twenty plots of 4 m^2 were sampled per transect, and the accumulated number of goose droppings were counted and the plant community was assessed (Bos *et al*. 2005).

The communities of *Elymus athericus*, *Artemisia maritima* and *Atriplex portulacoides* had a significantly taller canopy, but a lower goose dropping density than the communities of *Agrostis stolonifera*, *Festuca rubra* and *Puccinellia maritima*. Dropping density at the transect level declined with decreasing livestock grazing regime. However, only the long-term ungrazed regime combined for barrier marshes and artificial marshes had significantly lower dropping densities than the other regimes (Fig. 10.7). These results are valid for May, the end of the staging period for both goose species. In April, goose-dropping densities at the transect level did not differ between grazing regimes. There were no significant differences in dropping densities by geese between transects grazed by sheep or cattle (Bos *et al*. 2005). We conclude that the long-term exclusion of livestock on salt marshes will result in a decline in utilization of these areas by spring-staging geese.

10.10.2 Breeding birds

The effects of excluding livestock grazing on breeding birds cannot be studied in small-scale exclosure experiments as for plants and invertebrates. Also a comparative study in the entire Wadden Sea, as for migrating birds, has not been carried out so far. We derive our knowledge from a small number of studies describing differences in ungrazed and differently grazed marshes. At the natural marsh on Schiermonnikoog, including some low dunes, the breeding population was monitored in 1973 and 1978. The 83 ha of marsh ungrazed since 1958 harboured maximally 31 species with in total 850–1000 breeding pairs, the 77 ha continuously cattle-grazed marsh hosted maximally 25 species with in total 550–600 breeding pairs. In 1978, the grazed marsh harboured 133 breeding territories for oystercatcher, 10 for lapwing and 71 for redshank, whereas the grazed marsh harboured 85, five and 48 territories, respectively (Van Dijk and Bakker 1980).

Studies on the relationship between management and vegetation, and the occurrence of breeding birds have been summarized by Koffijberg (in press). Most studies have been carried out on artificial marshes in Germany (Hälterlein 1998; Eskildsen *et al*. 2000; Hälterlein *et al*. 2003; Oltmanns 2003; Schrader 2003; Thyen and Exo 2003, 2005; Thyen 2005). They reveal a trend that relaxation of formerly heavily grazing regimes results in an increase in species richness, particularly due to a species group shift from waders, gulls and terns towards ducks and songbirds. Another trend is the decrease of avocet (*Recurvirostra avosetta*), great ringed plover (*Charadrius hiaticula*), Kentish plover (*Charadrius alexandrinus*), common tern (*Sterna hirundo*) and Arctic tern (*Sterna paradisaea*) after the cessation of grazing and subsequent vegetation succession. A problem in these studies is that the results represent snapshots, describing ‘pioneer situations’ a few years after transition of management, and do not include the long-term effects of cessation of grazing.

For some species more detailed information is available. Increased grazing negatively affects the number of redshanks. This was attributed to the destructive effects of trampling of nests and hatchlings, whereas changes in the vegetation composition were considered less important (Schultz 1987). However, in salt marshes in Great Britain the occurrence of redshank densities were positively related to the extent of the *Elymus athericus* community. This relation could be explained by the variation in vegetation structure. Cattle-grazed plots, with

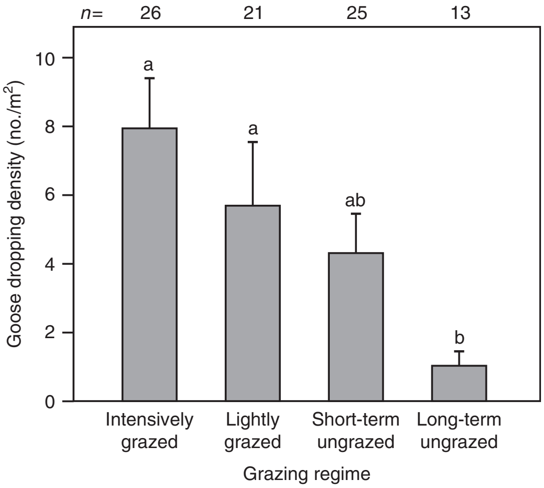

Figure 10.7 Average goose grazing pressure at the transect level in relation to livestock grazing regime for all transects that were paired within the same site. Bars that do not share the same letter differ significantly ($P < 0.05$). After Bos *et al*. (2005).

Elymus athericus covering up to 30%, supported the most structurally diverse vegetation and the highest breeding densities. In contrast, ungrazed plots of similar habitat contained tall, uniform vegetation and supported significantly lower breeding densities (Norris *et al*. 1997). The period of abandonment was not indicated. However, a survey on 77 salt-marsh sites in Great Britain revealed that breeding redshank densities were lowest on heavily grazed marshes and tended to be highest on lightly or ungrazed marshes (Norris *et al*. 1998). Redshanks breeding on salt marshes partly feed on nearby intertidal flats and build their nests hidden among vegetation of intermediate height, avoiding areas with low cover or with very tall vegetation (Cramp and Simmons 1983). In the Dollard (The Netherlands) cattle-grazed salt marsh, densities of redshanks were approximately two breeding pairs per hectare at a grazing regime of ~200 cattle-days/ha in 1984, and decreased to less than one breeding pair per hectare in 1998. Within the same period cattle grazing was reduced to ~50 animal-days/ha. The redshanks preferentially breed in the *Elytrigia repens* community, and in the less preferred short-grass stands with *Festuca rubra*, *Agrostis stolonifera* and *Puccinellia maritima*. Especially the latter stands were partly replaced by bare soil and secondary pioneer community of *Salicornia* spp. and *Suaeda maritima*, which was, however, attributed to increasing numbers of spring-staging barnacle geese and not to decreased cattle grazing (Esselink 2000).

We have to conclude that the effects of cessation of livestock grazing on breeding birds need further study. From the results so far, we suppose an initially positive, but in the long term negative, effect.

10.11 Ageing of salt marshes and implications for management

As long as the area of salt marshes increases, marshes will feature the successional series of pioneer, young and older mature marshes. When these extension processes stabilize eventually, only mature marshes will be found. This happens at back-barrier marshes that do not expand. It also happens along the mainland coast where the present area is maintained, and no further expansion into the intertidal flats takes place. In the past, it was economically feasible to embank marshes, and start new sedimentation fields (Esselink 2000). Nowadays, it is no longer economically feasible for many farmers to graze livestock at the marshes. The combination of decrease in the pioneer zone, and hence maturation of the marshes, and abandonment of livestock grazing results in the encroachment of *Elymus athericus* on artificial marshes (Dijkema 2007).

What are the implications for management (often livestock grazing) in view of these ageing processes of salt marshes? According to the 'wilderness concept' (a contradiction in itself for an artificial marsh), the solution with respect to the question 'to graze or not to graze' (Bakker *et al*. 2003a) is easy: the management option will be 'no grazing'. This will undoubtedly result in a loss of biodiversity at the local scale. However, at the scale of the entire Wadden Sea, it should be a preferred option for the marshes that have never been grazed by livestock such as the eastern parts of Terschelling (The Netherlands), Schiermonnikoog (The Netherlands), Ameland (The Netherlands) and Spiekeroog (Germany). In the long run, these areas will demonstrate whether there is a world beyond *Elymus athericus*.

According to the 'biodiversity concept' the answer to the question 'to graze or not to graze' will be: define the biodiversity target at a distinct scale, and decide to what extent livestock grazing as a management tool may help to reach the biodiversity target.

It is known that no grazing results in a low diversity for plants and less favourable feeding conditions for hares and spring-staging geese. High-intensity livestock grazing is a good option for spring-staging geese. Low-intensity grazing renders a pattern of intensively grazed short swards and lightly or no-grazed taller patches of vegetation. The difference with respect to the options *no grazing* or *intensive grazing* seems the patchiness and the spatial scale. However, our knowledge of the consequences of such a mosaic for the diversity of breeding birds and invertebrates is fragmentary.

Another option with respect to grazing is rotational grazing. Livestock grazing can be abandoned after a period of intensive livestock grazing. The result will be flowering of the plants and the possibility of replenishing the soil seed bank. Flowers and taller stems will attract invertebrates, which can be the prey items for breeding birds. Before *Elymus athericus* invades, the intensive grazing regime should be re-installed. The results of such a *rotational grazing regime* have not been monitored so far. Salt-marsh communities and their management will profit from large-scale and long-term experiments in which the interactions of plants, invertebrates and birds are studied.

In summary, in order to have a full display of salt-marsh communities, including many species of plants, vertebrates and invertebrates, the best management option is to have variety in the structure of the vegetation. This can be achieved by variation in grazing management, both in space and time.

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Chapter 6

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Chapter 9

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Chapter 14

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