Agriculture, Ecosystems and Environment 182 (2014) 69–79

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Scale matters: Impact of management regime on plant species richness and vegetation type diversity in Wadden Sea salt marshes

Antonia Wanner[a,*], Sigrid Suchrow[a], Kathrin Kiehl[b], Wiebke Meyer[b], Nina Pohlmann[a], Martin Stock[c], Kai Jensen[a]

[a] Applied Plant Ecology, Biocentre Klein Flottbek, University of Hamburg, Ohnhorststraße 18, 22609 Hamburg, Germany
[b] Vegetation Ecology and Botany, Faculty of Agricultural Sciences and Landscape Architecture, University of Applied Sciences Osnabrück, Oldenburger Landstr. 24, 49090 Osnabrück, Germany
[c] Administration of the Wadden Sea National Park of Schleswig-Holstein, Schlossgarten 1, 25832 Tönning, Germany

ARTICLE INFO

Article history:
Received 7 January 2013
Received in revised form 9 August 2013
Accepted 9 August 2013
Available online 7 November 2013

Keywords:
Artificial drainage system
Grazing
Monitoring
Species-area-relationship
Succession
Wadden Sea National Park of Schleswig-Holstein

ABSTRACT

After foundation of the Wadden Sea National Park, grazing and artificial drainage was ceased or reduced on large areas of the salt marshes at the Schleswig-Holstein mainland coast (Northern Germany). The effect of grazing cessation versus intensive and moderate grazing on vegetation diversity was studied on small (plant species richness on plots between 0.01 and 100 m^2) and large scale (vegetation type richness per hectare) over 18 to 20 years by analysing data from long-term monitoring programs. Plant species richness and vegetation type richness increased strongly over time in all management regimes, because grazing-sensitive species increased first in ungrazed marshes and later dispersed to and established in intensively grazed marshes. Dominance of the tall, late-successional grass *Elymus athericus* on 7% to 52% of all moderately and ungrazed (primarily high marsh) plots led to a decrease in species richness. After 18 to 20 years, species richness was highest in moderately and intensively grazed high marshes. Differences were significant only on small plots of up to 4 m^2. On the large scale, vegetation type richness in the low marsh was higher without grazing, while no differences were found in the high marsh. Our results indicate that grazing effects differ between spatial scales and that different spatial scales have to be considered for monitoring and evaluation of vegetation diversity in salt marshes. To conserve vegetation diversity on all scales, a large-scale mosaic of different management regimes should be maintained.

1. Introduction

Salt marshes represent one of the few naturally treeless ecosystems in Central Europe. They develop at shallow tidal coasts under conditions of low water currents by continuous sedimentation (Adam, 1990). The sediment is first colonised by pioneer species, which are replaced by plant species of the low and later of the high marsh after a period of continued sedimentation (Beeftink, 1977). Salt marsh vegetation is composed of specialised salt-tolerant plant species, and is thus naturally species-poor. In the course of succession from pioneer via low to the mid marsh, species richness increases (Beeftink, 1977; Kiehl, 1997). Under less extreme conditions of the high marsh, however, interspecific competition becomes more important and the dominance of competitive species can reduce species richness (e.g. Pennings and Callaway, 1992; Bockelmann and Neuhaus, 1999; Aegerter, 2011).

The Wadden Sea along the North Sea shores of The Netherlands, Germany and Denmark is the largest coherent tidal flat area of the temperate zone (Reise et al., 2010). A barrier system of sandy islands, sand bars and shoals mitigates wave exposure and allows the formation of salt marshes (Dijkema, 1987; Esselink et al., 2009). In the Wadden Sea region, salt marshes have been reclaimed and diked for hundreds of years (Bakker et al., 2002). In front of the dikes, the formation of new salt marshes was enhanced by land reclamation techniques, such as construction of brushwood groynes and sedimentation fields with a dense regular network of artificial drainage ditches ("foreland salt marsh", Dijkema, 1987; Stock et al., 1998). Wadden Sea salt marshes have traditionally been used for livestock grazing and mowing (Stock et al., 1998; Bakker et al., 2002). In recent decades, grazing has been reduced or ceased in large parts of the Wadden Sea salt marshes because agricultural economic interest has decreased and nature conservation goals gained in importance (Bakker et al., 2003).

Plant species richness often follows a hump-backed curve along environmental stress gradients (Grime, 1979; Pausas and Austin, 2001, see also Kelemen et al., 2012). At the more extreme end

* Corresponding author. Tel.: +49 40 42816 392; fax: +49 40 42816 396.
E-mail addresses: antonia.wanner@uni-hamburg.de (A. Wanner), ssuchrow@web.de (S. Suchrow), k.kiehl@hs-osnabrueck.de (K. Kiehl), wmeyer.mechtersen@web.de (W. Meyer), pohlmann.nina@googlemail.com (N. Pohlmann), martin.stock@lkn.landsh.de (M. Stock), kai.jensen@uni-hamburg.de (K. Jensen).

0167-8809/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.agee.2013.08.014

of the gradient, abiotic stress such as low water or nutrient availability or high salinity limit species richness, whereas competition decreases species richness at the less extreme end of the gradient (Grime, 1973, 1979; Huston, 1979). Likewise, a hump-backed curve of species richness has been described for disturbance gradients as the "intermediate disturbance hypothesis" (Connell, 1978). At the same time, diversity is a scale-dependent phenomenon (Dengler, 2012), and the impact of disturbances can differ between spatial scales (Chaneton and Facelli, 1991; Turtureanu et al., 2014).

Grazing as a form of disturbance can enhance the diversity of vegetation, but the effects depend on the intensity of biomass reduction and plant damage due to trampling and foraging. However, the scale-dependent grazing effects on diversity can also depend on abiotic factors such as nutrient availability (Proulx and Mazumder, 1998), climate (Milchunas et al., 1988; De Bello et al., 2007) or salinity (Bakker, 1989; Olff and Ritchie, 1998). In addition, intensive grazing on a large scale can reduce the species pool by strongly selecting grazing-tolerant species, thereby reducing species diversity on a larger scale (of e.g. hectares, Chaneton and Facelli, 1991; Olff and Ritchie, 1998).

In grazed salt marshes, low marsh species and vegetation types occur at higher elevations than in ungrazed salt marshes (Bakker, 1989; Kiehl, 1997), triggered by direct and indirect grazing effects on plants and soil conditions, e.g. salinity, nitrogen mineralisation, compaction and waterlogging (Bakker et al., 1985; Van Wijnen et al., 1999; Schrama et al., 2012). Consequently, during (secondary) succession after grazing has ceased, high marsh species and vegetation types increase and spread towards lower elevations (Bakker, 1989; Kiehl et al., 1996, 2001). The effect of grazing and grazing cessation on vegetation structure, composition and species richness of salt marshes has been studied in different regions of the Wadden Sea (e.g. Bakker, 1989; Berg et al., 1997; Schröder et al., 2002). Nevertheless, it is still discussed controversially, whether cessation of grazing decreases diversity in the long run or not (Bos et al., 2002; Bakker et al., 2003; Kleyer et al., 2003). Up to now, the scale-dependence of grazing effects on species richness has been investigated only in few studies in foreland salt marshes (Kiehl, 1997; Bakker et al., 2003) or Baltic salt grasslands (Dupré and Diekmann, 2001; Wanner, 2009) with contrasting results.

After decades of sheep grazing with high stocking rates on more than 90% of the area (Kempf et al., 1987), the establishment of the Wadden Sea National Park of Schleswig-Holstein in 1985 led to large-scale land use changes in mainland salt marshes in the early 1990s (Kiehl et al., 1996; Stock et al., 1998). According to the conservation goal of allowing natural processes within the National Park, mainland salt marshes are today ungrazed on 53% and moderately grazed on 6% of the area. Additionally, the maintenance of the artificial drainage system was abandoned in ungrazed marshes (Stock et al., 1998, 2005). As a consequence, vegetation structure and species composition of the salt marshes have changed (Kiehl, 1997; Schröder et al., 2002; Kiehl et al., 2007). Grazing-sensitive species and the diversity of salt marsh vegetation increased in many areas. In other areas, however, highly competitive species (such as *Elymus athericus*) started to dominate with negative effects on small-scale species richness (Stock et al., 2005; Esselink et al., 2009).

Since 1997, the three Wadden Sea countries of Denmark, The Netherlands and Germany have developed a common trilateral monitoring and assessment program (TMAP), which also includes salt marshes (Wolff et al., 2010). Based on a common methodology for the monitoring of vegetation changes in salt marshes, a regular large-scale mapping of vegetation types is carried out every five years. In addition, species composition on small-scale permanent plots is monitored annually in several regions. By analysing data originating from this long-term monitoring program of the Schleswig-Holstein National Park (Stock et al., 2005, 2012a) and from earlier mapping (Van Bernem et al., 1992), we addressed the following questions: (1) how does management regime (intensive grazing, moderate grazing, no grazing) affect species richness and vegetation type richness in foreland salt marshes over time, after the management changes?; and (2) do these effects differ between spatial scales from 0.01 m^2 up to 1 ha?

2. Methods

2.1. Study area

The Wadden Sea, located at latitude of 53° to 55°N, is influenced by the Gulf Stream. The temperate climate is characterised by mild winters (mean temperature in January approx. 0.5 °C) and cool summers (mean temperature in July approx. 16 °C), and an annual precipitation of approx. 700 mm (Rieke, 1998).

The study area comprises the mainland coast of the Schleswig-Holstein Wadden Sea (Northern Germany, Fig. 1). In this area, approx. 8000 ha of foreland salt marshes with clay-rich soils have developed (Wanner et al., 2014), representing about 40% of all foreland salt marshes of the Wadden Sea region (Esselink et al., 2009). The tidal range varies between 180 cm on the island of Sylt and 280 cm at the mouth of the river Elbe, reaching up to 340 cm in some bays (BSH, 2010). Salinity of the inundating seawater decreases from 25–32 ppt in the northern parts to 10–22 ppt in the southern parts of the study area (Becker, 1998). Vegetation types of the low salt marsh are mostly dominated by *Puccinellia maritima* or *Atriplex portulacoides* and – with increasing elevation – these are continuously replaced by *Artemisia maritima*, *Festuca rubra* and *Juncus gerardii*, and higher up by *E. athericus* (Suchrow and Jensen, 2010; Wanner et al., 2014).

All studied marshes were intensively grazed with a stocking density of approx. 10 sheep/ha until the early 1990s (cf. Kempf et al., 1987; Stock et al., 1998). After the establishment of the Wadden Sea National Park of Schleswig-Holstein, grazing was reduced in many areas, and from 1992 onwards, three different management regimes were applied: intensive grazing (10 sheep/ha); moderate grazing (0.75 to 1.5 sheep/ha) continuously between March and November; and no grazing (for spatial distribution of grazing regimes see Stock et al., 2005). In the ungrazed and moderately grazed salt marshes, the maintenance of drainage ditches was abandoned. Since the consequences of grazing reduction on the one hand and the abandonment of the artificial drainage system on the other interact and thus cannot be separated, we refer to the three variants as "management regimes".

2.2. Plant species richness

To analyse the temporal development of small-scale species richness, vegetation data of permanent plots were used from: (a) 31 transects spread along the entire mainland coast of Schleswig-Holstein (hereafter referred to as "mainland transects"); and (b) salt marshes of the "Hamburger Hallig" which is the largest contiguous salt marsh complex along the mainland coast of Schleswig-Holstein comprising approx. 1100 ha.

Vegetation changes along the entire mainland coast were analysed by using relevés of 369 permanent plots of 1 m^2 along 31 mainland transects. In a large survey between 1987 and 1989 (hereafter referred to as "1987"), vegetation was recorded on 2781 plots along 121 transects positioned perpendicular to the coastline with a distance to each other of 1000 to 3000 m, spreading along the entire coast of Schleswig-Holstein (Suchrow and Jensen, 2010). Plots along transects were selected to represent all visually distinguishable vegetation units and micro-topographic structures. In 2007, 31 of these transects were re-sampled (after relocation by