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Secondary succession on a high salt marsh at different grazing intensities

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Abstract. Succession occurs on a large part of German salt marshes following abandonment or reduction of grazing. Its speed and effect on the biodiversity of salt marshes has been discussed in the literature. Permanent plot studies show site-dependent differences in successional outcome. If grazing is to be continued, there is uncertainty about the stocking rates that are optimal for the conservation of plant diversity. We present an eight year permanent plot study with different grazing treatments on a high salt marsh at the marsh island of Hallig Langeness, Germany, which is enclosed by a summer dike. The study site is owned by WWF. Successional outcomes on the permanent plots depend on grazing intensity and depth of the groundwater table which is correlated with soil salinity. Intermediate stocking rates support a mixture of halophytes and glycophytes, the relative proportion of which depends on the depth of the groundwater table. Cattle grazing at stocking rates of 0.6 livestock units per ha were found to be optimal for plant diversity conservation. At sites with deeper groundwater tables and no grazing, dominant *Elymus* spp. stands develop and diversity is strongly reduced. If the groundwater table is high, succession following grazing abandonment is retarded and small halophytes prevail.

Keywords: Competition; Conservation; Grazing effect; Groundwater table; Langeness; Permanent plot; Salinity.

Nomenclature: Wisskirchen & Haeupler (1998).

Introduction

Biological diversity is an ever increasing source of concern, with respect to species conservation and ecosystem functioning (Tilman 2000). This also applies to coastal salt marshes that represent a unique habitat for a wide range of organisms (Adam 1990; Meyer & Reinke 1995; van der Maarel & van der Maarel-Versluys 1996). Additionally, salt marshes are important staging areas for migratory waterfowl (Madsen et al. 1999).

Competitive ability, stress tolerance and regeneration following disturbance were found to be plant persistence traits that determine diversity on local scales (Grime 1979; Grace 2001) in contrast to dispersal traits on landscape scales. Predictions on species richness along environmental gradients such as fertility, stress and disturbance are provided by the 'humped-back' model of Grime (1973) and the 'intermediate disturbance hypothesis' (Connell 1978) or the 'dynamic equilibrium' model proposed by Huston (1979). In these models, dominant species competitively exclude other species if dominance is not broken by either stress at low fertility levels or by disturbance, while many species are unable to survive at high levels of either stress or disturbance. Species prevailing under these conditions display storage effects (Warner & Chesson 1985) or high regeneration abilities. At intermediate disturbance or stress levels, plant species diversity is supposed to be maximized (Grime 1973; Connell 1978; Huston 1979).

With respect to salt marshes, tolerance of stress such as submergence in salt water during inundations, saline soil water, and soil oxygen deficiency is supposed to be a prerequisite to grow seaward. In contrast, ability to attain dominance is thought to be the trait that controls plant species patterns by competitive exclusion at the upper landward elevations of the marsh where salinity and immersion frequency is lower. (Chapman 1975; Snow & Vince 1984; Pennings & Callaway 1992; Levine et al. 1998; Olff et al. 1997).

Until recently, most salt marshes at the Wadden Sea were grazed by domestic livestock (Dijkema 1984).

Following the above-mentioned predictions on the effect of disturbance on diversity, extensive grazing should periodically break the dominance of competitively superior plant species and thus support diversity. Intensive grazing should exclude those species unable to rapidly regenerate their photosynthetic tissue and thus decrease diversity. According to the hierarchical foraging model (Senft et al. 1987), grazers should select the landscape unit with the most abundant resources, then the most productive community within the landscape unit, and finally the most palatable species within a feeding station (an area the animal can graze without moving its feet). At lower stockings rates feeding selection results in patch or even random grazing, producing patterns with patches of different grazing intensity ('micro-pattern', Bakker et al. 1984). If stocking rates are increased, patch grazing may change towards homogeneous grazing which is predicted to result in lower spatial diversity of the vegetation (Adler et al. 2001). In lower salt marshes, tidal inundation frequency, salinity, aeration and drainage systems interact to form landscape units that vary in their suitability for foraging, thus obscuring the effect of grazing on plant diversity. These interactions should decrease landwards, diversity patterns should therefore be more consistent with theory at the high marsh.

Growing empirical evidence largely supports these predictions. Experiments with different stocking rates or exclosures showed that plant species diversity is fairly low at high stocking rates and increases when stocking rates are reduced. Lower stocking rates also led to higher spatial diversity of the vegetation (Bakker 1989; Berg et al. 1997; Gettner et al. 2000). Permanent plot results indicate different successional outcomes when grazing is abandoned. On a sandy back-barrier marsh (Schiermonnikoog), an artificial clayey marsh (Leybucht) and on a brackish artificial marsh (Dollart), abandonment led to almost monospecific stands: *Elymus athericus* on the high marsh, *Atriplex portulacoides* on the lower marsh, and *Phragmites australis* on the brackish marsh (Dijkema 1983; Andresen et al. 1990; Bakker et al. 1997a; Bakker et al. 1997b; Olff et al. 1997; Esselink et al. 2002). On the other hand, Schröder et al. (2002) found little evidence for the extension of dominant *Elymus athericus* stands on a clayey mainland salt marsh (Hamburger Hallig). This may be due to the period of observation that is different across the available studies. Long-term studies showed that species-poor communities developed with a time-lag of > 10 years after abandonment (Bos et al. 2002). Hence, records covering more than 10 years should be paid special attention.

Most of the German Wadden Sea salt marshes are now under protection in the framework of German nature conservation legislation. The legal criteria imply no or a small human impact for the major part of a national park area. For the salt marshes of the Wadden Sea area of Denmark, Germany and The Netherlands common management targets were elaborated in the Trilateral Wadden Sea Plan (Anon. 1998). Concerning grazing, the trilateral policy states: "It is the aim to reduce and / or diversify grazing in order to increase the diversity of vegetation and associated animal species in salt marshes" (Anon. 1998; Annex 1: 40). Within the limits of the Wadden Sea national parks in Germany, nowadays 40 to 60% of the salt marsh area are not grazed, 25% are moderately grazed and 15 to 30% are intensively grazed (different figures for Schleswig-Holstein, Hamburg, and Lower Saxony, CWSS 2001: 42). Salt marsh islands ('Halligen') are not included in the national park area. They are managed in the framework of the 'Halligprogramm', an integrated management programme. It implies stocking rates of 0.7 to 1.7 livestock units per ha (one livestock unit equals a grazer with 500 kg body weight per vegetation period), and restrictions concerning fertilization and mowing (Anon. 1986, 1987; Fleet 1999). Farmers receive subsidies to compensate for economic losses resulting from reduced stocking rates. Apart from its objective to contribute to the preservation of salt marsh biodiversity, cattle or sheep farming under the 'Halligprogramm' seeks to facilitate a sustainable future for 'Hallig' – farmers having to cope with adverse conditions on the small islands in the Wadden Sea.

According to the above-mentioned predictions and field studies, reduction in grazing intensity may have profound consequences for the biodiversity of the salt marsh system, not only with respect to plant species but also to herbivorous waterfowl and other small herbivores (van de Koppel et al. 1996; Aerts et al. 1996). It is debated whether grazing should be maintained to conserve biodiversity on salt marshes and which stocking rates are most suitable to achieve this target (Bakker et al. 1997a; Stock 1997).

In this study, the development of the vegetation under various stocking rates was monitored from 1989 to 2000 on a salt marsh owned by the World Wildlife Fund (WWF) on the marsh island of Hallig Langeness (Schleswig-Holstein, Germany). The study area is a summer polder on this marsh, thus representing different environmental conditions with less frequent inundation as compared to the field studies mentioned above. Results of year-by-year sampling in permanent plots are compared to changes in the mapped vegetation cover between 1993 and 1998. Although designed primarily to assess the effects of the 'Halligprogramm', the study may also contribute to the general discussion on the long-term effects of grazing reduction or abandonment on the succession of high salt marsh vegetation.

Methods

Study area

Most of the salt marshes on Hallig Langeness (54°38' N, 8°38' E) in the German Wadden Sea are surrounded by a summer dike, with a height between 2.20 m and 2.35 m above NN (German ordnance level). The study area (20 ha) is situated between 1.50 m and 1.80 m above NN and was flooded on average 19 times per year in the last 12 years, predominantly in autumn and winter. In contrast to artificial mainland marshes, the drainage system of the island consists of winding marsh creeks, wet depressions and, in some parts, artificial drainage furrows. Drainage after flooding is regulated by one-way valves located in the summer dike. The marshes are predominantly characterized by plants of the higher salt marsh, together with some glycophytes of fresh water soils. Mean annual precipitation is 696 mm and mean annual temperature is 8.4 °C.

The experiment was initiated in 1989 by WWF. Before the start, most of the study area was uniformly grazed from May to September with approximately 17 heifers (equalling 1.3 livestock units per ha, calculated according to Anon. 1994a). In 1989, the study area was divided into three paddocks that are since then being grazed with cattle at three different stocking rates. Means of these stocking rates between 1989 and 2000 are 0.4, 0.6, and 1.3 livestock units per ha on 2.03 ha, 3.03 ha, and 9.50 ha, respectively. Two adjacent sites with no grazing at all were also monitored, one being abandoned since 1982 (0.4 ha), the other since 1987 (4.4 ha). Marsh creeks serve as borderlines between the paddocks and therefore determine size and form of the paddocks. There is no indication that soil conditions of the abandoned sites differ substantially from the paddocks. The main reason for abandonment was that creeks hampered access to the sites. The grazing season lasted from the end of May to the end of September. Grazing intensities follow Prokosch & Kempf (1987), with 1.3 livestock units per ha representing 'high' stocking rates on salt marshes. Note that stocking rates of inland pastures are considered 'high' if they are above 3 livestock units per ha.

Sampling

In 1989, WWF installed 21 permanent plots of 2 m × 2 m in the different paddocks. Four years later, 19 permanent plots were added. Every year at the beginning of August, species coverage was estimated on a percent basis in each plot. This was done by different people, mainly by the staff of WWF and 'Schutzstation Wattenmeer' at their station at Hallig Langeness. The staff of the station at Langeness designed the study and performed the yearly monitoring according to the available personnel and funds. This restricted additional monitoring of abiotic explanatory factors such as e.g. groundwater table or salinity. In autumn 1998, all plots were surveyed for elevation and groundwater level. At 12 plots (selection stratified according to treatments), 10 soil samples per plot were taken with an auger from four layers (0-10, 10-30, 30-60, 60-90 cm) and mixed. In each layer, the soil substrate was recorded following Anon. (1994b) and soil salinity was measured. As soil salinity varies with rainfall, this measurement represents only a momentum in time but allows to show the variation among plots. Salinity was measured in water extracts with a chloride-sensitive electrode, after centrifuging of the soil suspension (50 mg air-dried soil, 100 mL distilled water). At the time of the measurement, the upper horizons of the soils were water-saturated from recent rainfalls. Soil moisture content was measured by weight loss after drying the soil at 105 °C until constant weight was reached.

The first vegetation map of the total area was compiled in 1993 by Hagge (1993). Using the same methods, we mapped the area again in 1998. Vegetation analyses were carried out in plots of 1-5 m^2; species cover was estimated according to the decimal scale (Londo 1976). Vegetation units were classified by tabular sorting and then mapped in the field (see Dierschke 1994). Vegetation change was analysed by overlaying the two maps with help of the GIS ARCView.

Statistical analysis

In our time series analysis, we only used the records from the period 1993-2000. Species cover was estimated by different people in these years. Percent cover estimations are hard to standardize across many people. We decided to absorb potential differences in the accuracy of the estimations by transforming the original percent cover values to a broader five-graded scale: 1 = 0.1-20%; 2 = 21-40%; 3 = 41-60%; 4 = 61-80%; 5 = 81-100%.

Grazing intensity in the paddocks ranged from abandonment to 1.3 livestock units per ha. We combined the five different states of land use intensity – i.e. the two dates of abandonment and the three stocking rates of the continuously grazed areas – into a variable 'disturbance intensity'. Plots on areas which are abandoned for the longest time received the lowest rank, plots on areas where high stocking rates were maintained during the experiment received the highest rank. As a second explanatory factor, we used successional time, i.e. the number of years since the start of the experiment or the year of abandonment. The third explanatory factor is depth of groundwater table in year 1998.

The analysis of the species composition and its relation to (1) successional time, (2) disturbance intensity and (3) groundwater was done with Redundancy Analysis using the CANOCO for Windows package (ter Braak & Šmilauer 1998). Redundancy Analysis is based on the assumption that there is a linear response of species to environmental factors. This was assessed by first performing a Detrended Correspondence Analysis on the data set. The lengths of the first and second ordination axis were less than 2.8 and 2.4, respectively, which indicates a linear response (ter Braak & Šmilauer 1998: 123). In all analyses, we used centring by species and no standardization by samples. All three explanatory variables were analysed separately in all combinations. The individual analyses are numbered consecutively and their results are displayed in Table 1. Variance partitioning enabled to ascribe the variability of the species composition to the individual environmental factors. The repeated sampling of the permanent plots result in time series where individual species cover values may be autocorrelated in time. In CANOCO, it is possible to account for autocorrelation by permuting the time series and specifying plot identity as a covariable.

Species richness and key species

We chose species richness per plot and four key species to exemplify the successional trends in relation to grazing intensity and depth of groundwater table. *Festuca rubra* is considered a character species of the high salt marsh and the main sward component of the grazed high salt marsh. *Aster tripolium* has been shown to react strongly to the reduction of grazing intensity (Schröder et al. 2002). *Puccinellia maritima*, a matrix species from the lower marsh, prevails in depressions on the high marsh. *Elymus* spec. has been shown to build up dense stands with low plant species diversity following abandonment (e.g. Bakker et al. 1997a).

The inherent autocorrelation of data points in time series prohibits to use logistic or linear regression procedures to show successional trends for species richness and the key species. As our intention was to visualize trends rather than test them statistically we used a spline to model trend surfaces of the time series from the permanent plots. In a non-parametric local regression method ('LOESS'; Anon. 1989), weighted least squares are used to fit linear or quadratic functions of the predictors at the centres of neighbourhoods, i.e., a specified percentage of the data points. Data points in a given local neighbourhood are weighted by a smooth decreasing function of their distance from the centre of the neighbourhood.

The relation between chloride concentration and depth of groundwater table was expressed with regression analysis by using a 2nd order polynomial.

Table 1. Redundancy Analysis runs with different combinations of explanatory variables and covariables. Dis_Int: disturbance intensity; GwaterT: depth of the groundwater table; Year: successional year.

No.	Year	Explanatory variable	Covariable	r	Var % axis 1	Var % all axes	F-value	p-value	Sum of unconstrained eigenvalues	Sum of canonical eigenvalues	Variability explained %
1	1993-2000	Dis_Int		0.73	18.4	63.1	64.54	0.005	1	0.184	18.4
2	1993-2000	GwaterT		0.62	08.5	61.2	26.45	0.005	1	0.085	8.5
3	1993-2000	Year	Plot	0.49	5.4	56.9	16.81	0.005	0.832	0.045	5.4
4	1993-2000	Dis_Int, GwaterT		0.75	19.6	55.8	51.14	0.005	1	0.264	26.4
5	1993-2000	Year, GwaterT	Plot	0.68	11.4	48.7	22.54	0.005	0.832	0.114	13.7
6	1993-2000	Year, Dis_Int	Plot	0.49	5.7	48.2	11.14	0.005	0.832	0.061	7.3
7	1993-2000	Year, Dis_Int, GwaterT	Plot	0.68	11.5	38.9	17.22	0.005	0.832	0.128	15.4
8	1993-2000	Year, GwaterT	Plot, Dis_Int	0.68	10.4	48.0	20.05	0.005	0.803	0.1	12.5
9	1993	Dis_Int		0.75	11.9	59.5	4.58	0.005	1	0.119	11.9
10	1993	GwaterT		0.77	13.0	60.3	5.06	0.005	1	0.13	13.0
11	1993	GwaterT, Dis_Int		0.77	13.8	53.6	5.40	0.005	1	0.247	24.7
12	1993	GwaterT	Dis_Int	0.77	14.5	57.6	5.61	0.005	0.881	0.128	14.5
13	1996	Dis_Int		0.80	25.9	69.2	11.89	0.005	1	0.259	25.9
14	1996	GwaterT		0.69	10.0	70.2	3.77	0.010	1	0.1	10.0
15	1996	GwaterT, Dis_Int		0.82	27.7	66.3	12.62	0.005	1	0.353	35.3
16	1996	GwaterT	Dis_Int	0.78	12.6	63.8	4.77	0.005	0.741	0.094	12.7
17	2000	Dis_Int		0.73	30.6	79.4	14.99	0.005	1	0.306	30.6
18	2000	GwaterT		0.42	5.7	78.6	2.07	0.070	1	0.057	5.7
19	2000	GwaterT, Dis_Int		0.76	32.6	73.4	9.08	0.005	1	0.355	35.5
20	2000	GwaterT	Dis_Int	0.54	7.1	72.6	2.51	0.005	0.694	0.049	7.1
21	2000	GwaterT, Dis_Int, GwaterT*Dis_Int	0.77	33.3	65.7	6.39	0.005	1	0.375	37.5	

Results

Soil conditions

The permanent plots are situated between 1-2 m above NN (German ordnance level), the groundwater table varied between 0.1 and 0.8 m below soil surface. Elevation is correlated with groundwater level: Spearman's rank correlation $r = 0.76, p < 0.0001, n = 38$. Soil salinity, i.e. concentration of chloride, increased in the lower soil horizons. Across all horizons, soil salinity increased with higher groundwater table, with a lower, not significant trend at the uppermost soil horizon (Fig. 1). The soils are mostly two-layered with an upper horizon with sandy loam and a clayey lower horizon.

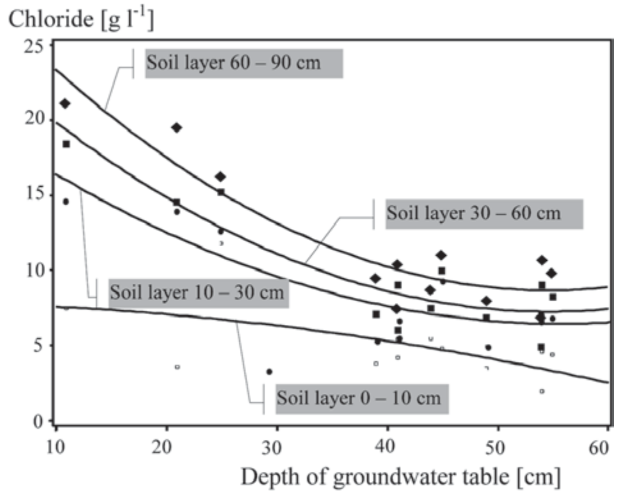

Fig. 1. Relation between chloride concentration (Cl) and depth of groundwater table (GW) for different soil layers (Regression parameters: Soil layer 0-10 cm (□), Cl = 7.8- 0.01∗GW - 0.001∗GW^2; $R^2 = 0.3$, $F = 2.14$, $p = 0.17$; Soil layer 10-30 cm (●), Cl = 21.3 - 0.53∗GW + 0.005∗GW^2; $R^2 = 0.8$, $F = 15.17$, $p = 0.0013$; Soil layer 30-60 cm (■), Cl = 26.2 - 0.69∗GW + 0.006∗GW^2; $R^2 = 0.8$, $F = 23.86$, $p = 0.0003$; Soil layer 60-90 cm (◆), Cl = 30.7 - 0.81∗GW + 0.007∗GW^2; $R^2 = 0.9$, $F = 31.17$, $p = 0.0001$).

Redundancy Analysis of permanent plots

Forward selection of the environmental variables revealed that all variables significantly contribute to the model, with the exception of groundwater table in the year 2000 (analysis 19, Table 1). When comparing the single effects of successional time, groundwater table and disturbance intensity (Table 1, analyses 1, 2, 3), disturbance intensity shows the highest correlation to the first ordination axis and explained most of the variability (18.4%). A combination of disturbance intensity and groundwater table yielded a slightly higher species-environment correlation of the first ordination axis and explained a higher percentage of the variability of the data (26.4%). When including successional time together with disturbance intensity and groundwater table into the analysis and using the plot identity as a covariable (analysis 7), the species-environment correlation of the first ordination axis, the percentage of the species variability explained by the ordination axes and the variability of the data explained by the combination of these three environmental factors is less pronounced. This indicates that there is no clear successional trend over all plots. Obviously, for certain combinations of groundwater depth and disturbance intensity, succession leads to changes in the species composition and for others not.

Fig. 2 displays the results of analysis 7. The factors time and disturbance intensity point in opposite directions, indicating that succession is halted with increasing grazing pressure. The cover of *Elymus* spp. clearly increases with successional time. *Potentilla anserina* responds in a similar way, but less pronounced. On the other hand, *Festuca rubra* increases with disturbance intensity and does not respond to successional time or depth of groundwater table. A group of halophytes (*Spergularia salina, Suaeda maritima, Plantago maritima*, and *Triglochin maritima*) only respond to increasing groundwater table, showing no changes with respect to disturbance intensity or successional time. *Puccinellia maritima, Glaux maritima, Juncus gerardii, Salicornia europaea, Spergularia maritima,* and *Aster tripolium* slightly respond to disturbance intensity in plots with a high groundwater table and subsequently higher salinity. *Armeria maritima, Leontodon autumnalis* and *Agrostis stolonifera* perform similarly on well-drained levees.

Separate analyses (9 to 21; Table 1) were done for plots of the same age (1993, 1996, 2000) to ask whether the influence of the disturbance intensity and the groundwater depth on the species composition increases over time since the start of the experiment. The percentage of the species variability explained by the ordination axes and the variability explained by the environmental factors clearly increase from 1993 to 2000 and this increase can be ascribed mainly to disturbance intensity alone. Effects of the groundwater table decrease over time, suggesting that this factor became less important during the experiment.

Trends of species richness and key species

The trend surfaces over successional time and depth of the groundwater table display apparent differences across disturbance intensities (Fig. 3). While high stocking rates maintain the number of species and the cover values of the key species at almost the same level over time, very low stocking rates (0.4 livestock units per ha)

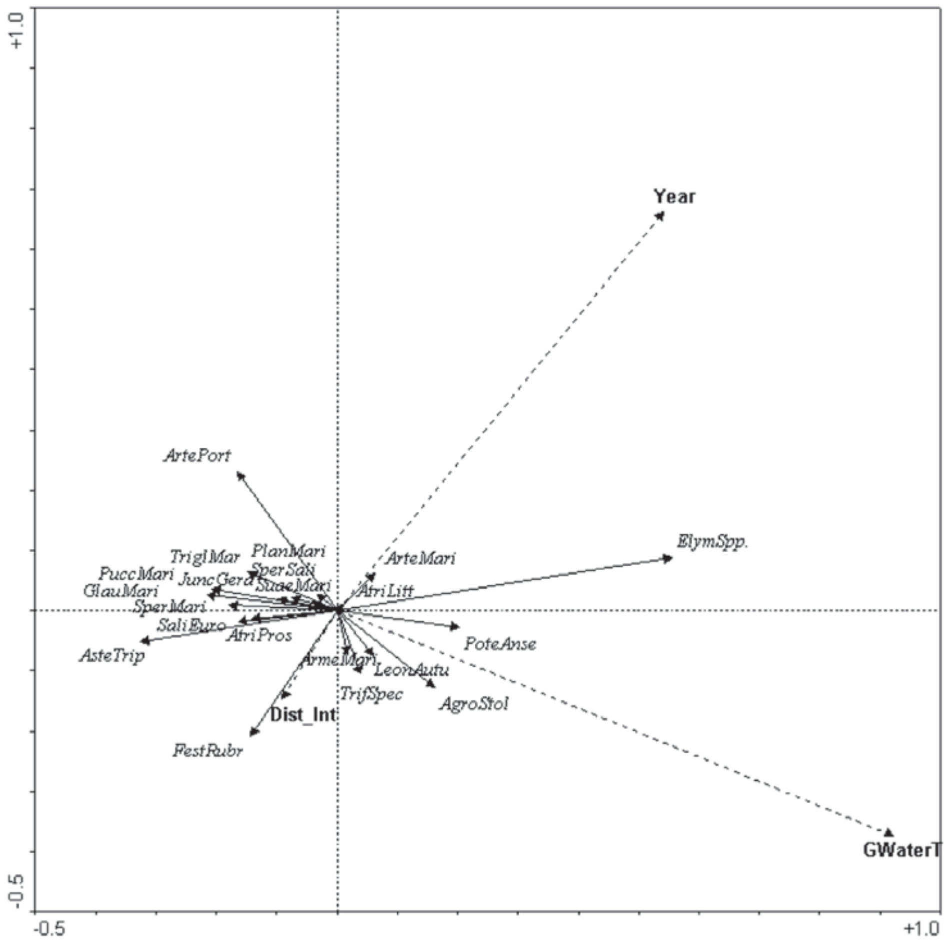

Fig. 2. Biplot of RDA No. 7. Species names are abbreviated with the first four characters of the genus and the first four characters of the species. For abbreviations of explanatory variables see Table 1.

and no grazing result in successional changes. Small successional changes already happen with 0.6 livestock units per ha. Changes are more pronounced on permanent plots with a deep groundwater table, whereas high groundwater tables lower the effects of the treatments. At high stocking rates (1.3 livestock units per ha), species richness remains almost constant over time. With 0.6 livestock units per ha, species richness increases at higher elevations, due to increasing occurrence of glycophytes such as *Leontodon autumnalis*. Species richness is declining following abandonment of grazing. The cover values of *Festuca rubra* and *Aster tripolium* are declining dramatically after 10 to 15 years following abandonment. In the same period, *Elymus* spp. is increasing towards dominance. *Puccinellia maritima* only occurs in plots with high groundwater table which are mainly found in the abandoned paddocks. Its cover slowly decreases over time.

Vegetation changes based on total area surveys

Between 1993 and 1998, the vegetation showed only minor changes in paddocks with intermediate (0.6) to high stocking rates (1.3 livestock units per ha; Table 2). Most of the area was dominated by *Juncus gerardii* – and *Festuca rubra* – swards. The most remarkable change occurred on sites covered with *Puccinellia maritima* that were converted to *Juncus gerardii* or *Festuca rubra* swards, less completely at high stocking rates.

In contrast, more than half of the *Festuca rubra* - swards changed towards stands dominated by *Elymus* or mixed *Festuca rubra*- / *Elymus* spp. stands in paddocks that are abandoned or grazed with low intensity. In 1993, a larger part of the abandoned paddock was already covered with stands dominated by *Elymus*.

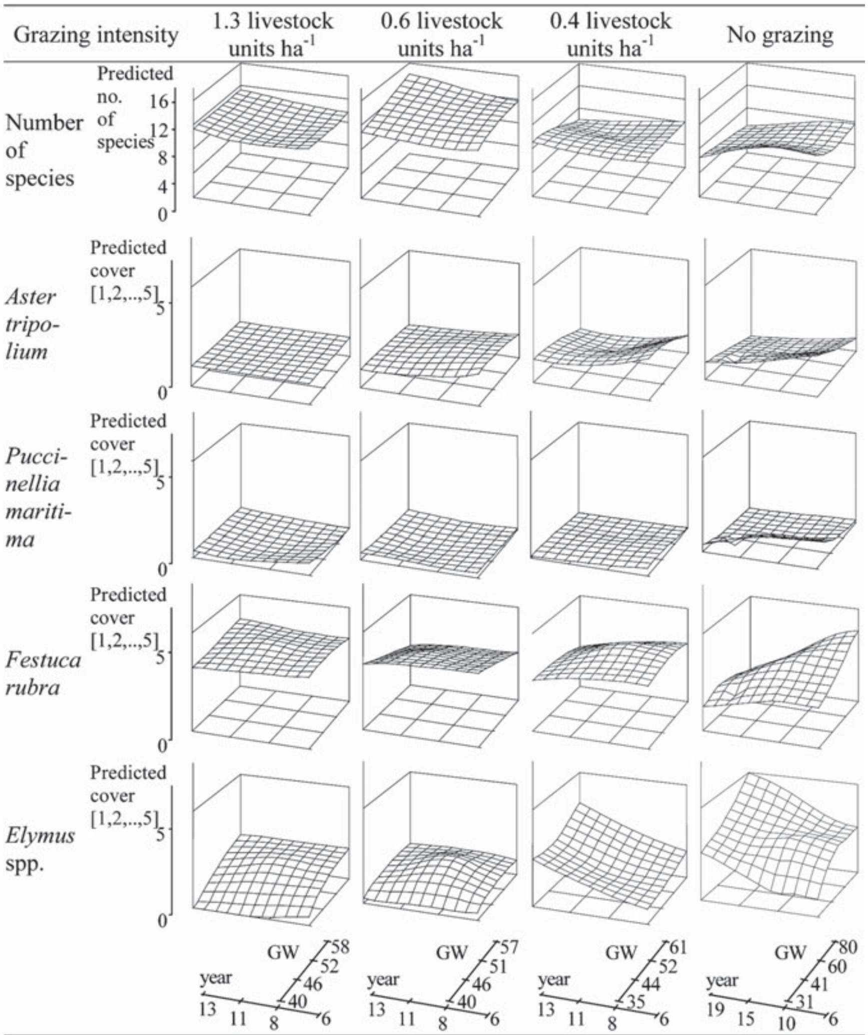

Fig. 3. Trends of species richness, *Festuca rubra, Aster tripolium, Puccinellia maritima*, and *Elymus* spp. with time ('year') and depth of groundwater table ('GW', [cm]) as explanatory variables. The beginning of the 'year' axis is 1993 which is year no. 6 after the abandonment of the first sites.

Discussion

One common result of the available permanent plot studies on salt marshes in the Wadden Sea is that successional outcomes differ with respect to the environment, e.g., elevation, inundation frequency, degree of naturalness of the marsh system. As a difference to other studies (e.g. Kiehl 1997; Bakker 1989; Esselink et al. 2002), we focus on a high marsh system which is protected from frequent inundation by a summer dike. In contrast to mainland artificial salt marshes, most of the drainage creeks are of a winding form. Although not all sites could be monitored from the beginning (especially the abandoned sites), the date of land use change is well known and soil conditions as well as previous land use were similar across the study area before the start of the experiment.

Homogenization at high grazing pressure

Our results support the prediction that homogeneous grazing through relatively high numbers of cattle decreases spatial variability (Adler et al. 2001). The intensively grazed paddock (1.3 livestock units per ha) displayed a uniform *Festuca rubra* turf which was remarkably stable over time. Although we did not measure spatial variability with e.g. variograms or autocorrelation indices, increasing γ-diversity (Whittaker 1977) following decreasing grazing intensity allows to confirm the prediction. According to Adler et al. (2001), homogeneous grazing should occur at scales that are small relative to the herbivore (i.e., relatively high numbers of cattle on small feeding areas), among generalists rather than selective grazers (i.e., cattle as compared to horses or sheep; Sambraus 1991), and in communities where differences in plant quality are small. Decreasing spatial

Table 2. Transition matrices of vegetation units between 1993 and 1998 (in percentage of the total area). Only those units are shown that covered more than 1 % of the total area in each paddock in 1993.

Mapping units 1993 (Dominant species)		Mapping units 1998 Pm	Jg	Fr	FL	FA	El	EF	*Total 93*
0.0 livestock units per ha									
Puccinellia maritima	Pm	1	0	1	0	0	6	0	*8*
Juncus gerardii	Jg	0	0	0	0	0	1	1	*2*
Festuca rubra	Fr	2	0	14	0	2	7	6	*31*
Festuca rubra, Leontodon autumnalis	FL	0	0	0	0	0	0	0	*1*
Festuca rubra, Atriplex prostata	FA	0	0	0	0	0	2	1	*4*
Elymus spp.	El	1	0	1	0	0	35	1	*39*
Elymus spp. *with Festuca rubra*	EF	0	0	2	0	1	8	5	*16*
Total 1998		*4*	*0*	*19*	*0*	*3*	*59*	*15*	*100*
0.4 livestock units per ha									
Puccinellia maritima	Pm	2	1	0	0	0	1	1	*5*
Juncus gerardii	Jg	0	13	0	0	0	0	4	*18*
Festuca rubra	Fr	1	18	0	0	0	3	23	*47*
Festuca rubra, Leontodon autumnalis	FL	0	0	0	0	0	0	1	*1*
Festuca rubra, Atriplex prostata	FA	0	0	0	0	0	0	0	*0*
Elymus spp.	El	0	0	0	0	0	4	2	*7*
Elymus spp. *with Festuca rubra*	EF	0	1	0	0	0	10	11	*23*
Total 1998		*4*	*34*	*0*	*1*	*1*	*18*	*42*	*100*
0.6 livestock units per ha									
Puccinellia maritima	Pm	0	3	1	0	0	0	0	*4*
Juncus gerardii	Jg	0	11	11	0	0	0	0	*23*
Festuca rubra	Fr	1	7	38	12	0	0	0	*59*
Festuca rubra, Leontodon autumnalis	FL	0	0	3	8	0	0	0	*11*
Festuca rubra, Atriplex prostata	FA	0	0	0	0	0	0	0	*0*
Elymus spp.	El	0	0	0	0	0	1	0	*2*
Elymus spp. *with Festuca rubra*	EF	0	0	1	0	0	0	0	*1*
Total 1998		*1*	*21*	*55*	*21*	*0*	*1*	*0*	*100*
1.3 livestock units per ha									
Puccinellia maritima	Pm	4	2	3	0	1	0	0	*11*
Juncus gerardii	Jg	2	19	2	0	0	0	0	*24*
Festuca rubra	Fr	2	3	32	7	3	1	0	*49*
Festuca rubra, Leontodon autumnalis	FL	0	0	2	3	1	0	0	*6*
Festuca rubra, Atriplex prostata	FA	1	0	6	0	1	0	0	*8*
Elymus spp.	El	1	0	0	0	0	1	0	*3*
Elymus spp. *with Festuca rubra*	EF	0	0	0	0	0	0	0	*1*
Total 1998		*9*	*25*	*45*	*10*	*6*	*2*	*1*	*100*

vegetation variability with increasing stocking rates was found also on lower marshes (Andresen et al. 1990; Kiehl et al. 1996). On the contrary, increasing spatial variability changing over time ('micropatterns') has been found following decreasing grazing intensity on salt marshes. If grazing was abandoned, micropatterns did not develop (Berg et al. 1997). Similar but more stable micropatterns were found on inland environments following moderate grazing intensities (Bakker et al. 1984).

The spatiotemporal stability of grazed turf has been explained as a positive feedback between grazing and forage quality by reduction of senescent material and increased tillering producing young leaves with high protein content (Jefferies et al. 1994). This promotes the continued use of previously grazed patches. If grazing intensity decreases, both patchy grazing and increasing biotic processes may result in a more patterned and more species-rich vegetation.

Species richness and management

At higher elevations, species richness is highest in plots that are extensively grazed (0.6 livestock units per ha) and slightly lower in plots that are intensively grazed (1.3 livestock units per ha, Fig. 3a). Similar conditions at a similar plot size were found on a high marsh of Friedrichskoog (Kiehl 1997). This contrasts with low marshes where rather species-poor communities develop under sheep grazing with stocking rates that are comparable to one livestock unit per ha (e.g. Kiehl 1997, but see Scherfose 1989 for cattle-grazed lower marshes). A reason is contribution from a different species pool: While low marsh communities consist only of halophytes, glycophytes are able to enter the high marsh communities (e.g. *Leontodon autumnalis, Trifolium* spp.; Dijkema 1983, see also phytosociological surveys, e.g. Raabe 1950; Dierssen et al. 1988). This entering occurs mainly at extensive grazing intensities and well drained sites (Fig. 2), the species displaying traits that enable grazing avoidance (i.e. small rosette) or tolerance (high regeneration by frequent tillering). Second, cattle graze less effectively than sheep (Klapp 1971; Sambraus 1991), resulting in lower damage to the individual plants, hence enabling also plants with lower regenerative abilities to survive. Third, extensive grazing is constantly breaking dominance and litter accumulation of e.g. *Festuca rubra*, allowing low growing plants as *Armeria maritima* and *Glaux maritima* to survive (Kiehl 1997).

At lower grazing intensities or abandonment, *Elymus* spp. attained dominance, concurrently with a strong decline in species richness (see also Dijkema 1983; Andresen et al. 1990; Bos et al. 2002). Similar trends of dominance were reported from *Phragmites australis* in brackish marshes (Esselink et al. 2002). In a positive feedback loop, increasing heterogeneity of canopy texture following cessation of grazing may stimulate higher sedimentation rates and subsequently higher supply of nitrogen which was found to favour *Elymus athericus* (Andresen et al. 1990; Olff et al. 1997; van Wijnen & Bakker 1999). Dominance of *Elymus* spp. in abandoned paddocks developed more strongly after 10 years of successional time (Fig. 3). Also, the degree of variation explained by the ordination axes increased over time (Table 1). This indicates that the species composition is determined more definitely, with less noise, by the experimental treatment over time. Similar delays in dominance by *Elymus athericus* were reported from the high marshes of Schiermonnikoog and Leybucht (Andresen et al. 1990; Bos et al. 2002; Bakker et al. 2003). It advocates for long-lasting permanent plot studies of successional systems before deducing management recommendations.

Succession on wet depressions

At the abandoned sites, depressions with high groundwater level display weaker successional trends towards dense stands of dominant species. High groundwater levels imply low soil aeration. A potential caveat is that the one-off groundwater measurements may not represent year-round variation among plots and do not show temporal variation of the soil aeration. The groundwater level is correlated to elevation and soil salinity (Fig. 1; see Kiehl 1997, Esselink et al. 2002), resulting in high salinities (> 20 g Cl^- per L) in lower soil horizons. As precipitation in October 1998 was almost twice as much as in the preceding years, chloride concentrations of upper horizons may have been diluted by rain water at our autumn measurement campaign. Hypersaline conditions (i.e., higher than in the low marsh) can be often encountered in upper soil horizons at depressions in the high marsh due to concentration and accumulation following longer periods of continuous evaporation (Giani et al. 1993; Srivastava & Jefferies 1995). This effect may also reach down to deeper soil horizons of high marshes protected by a summerdike as in Langeness because dilution by inundations is less frequent. Low soil aeration together with high salinities may restrict fundamental niches to strong halophytes with aerenchyma (Kiehl 1997), excluding competitively superior species of other species pools. Recent studies on root growth responses to waterlogging and nutrient availability showed that growth of *Elymus pycnanthus* was significantly reduced at waterlogged conditions but could not be correlated to root architecture responsiveness, indicating that the mechanisms are still not well understood (Bouma et al. 2001).

Plant diversity in salt marshes: management

This study was performed on the marsh island of Hallig Langeness, on sites enclosed by a summer dike. On these areas, continuous cattle grazing is supported and subsidized by a state programme (Anon. 1986, 1987). According to this study on the WWF site, cattle grazing with 0.6 livestock units per ha performs best to meet the target of conserving plant diversity. However, the *Elymus athericus* community did also spread at 0.5 cattle per ha 15 years after the start of a grazing experiment at the Leybucht (Bakker et al. 2003). This indicates that higher stocking rates may be even better suited to conserve plant diversity on such areas. In contrast, Kiehl et al. (2000) report that higher stocking rates of sheep significantly decreased plant diversity by excluding species unable to regenerate following damage. In order to assess the best grazing practice for conserving diversity it is necessary to acknowledge that sheep and cattle differ in their grazing behaviour. Sheep as well as horses byte off the plants close to the soil surface while cattle tear off the plants with the tongue thus leaving a larger part of the shoot without damage or, in contrast, uprooting the plant, especially from soft sediment. Sheep and cattle differ in plant preference, in the way they browse the area and in the way they redistribute nutrients by defecating (see Jensen 1985 for a small review). Hence, equal stocking rates of different grazer species standardized to livestock units may still represent different impacts on the vegetation.

Our study may also contribute to predict consequences of grazing cessation. The Trilateral Wadden Sea Plan management targets for salt marshes imply the increase of the diversity of the vegetation. We showed that cessation of grazing may not meet this target on high salt marshes with reduced inundation regimes (e.g. summer polders), at least on a patch scale. Clearly, the plots at Hallig Langeness are not within the geographical scope of the Wadden Sea national park but within that of the 'Halligprogramm' where grazing cessation is not a management target. However, the successional trends on the abandoned plots of this study are in line with results of several long-term permanent plot studies across the Wadden Sea showing that diversity of plant communities signifibzŒtly decreases on ungrazed compared to moderately grazed salt marshes (Bakker et al. 2003). Stock & Kiehl (2000) argue that the neglect of the artificial drainage system, sea level rise and development of natural drainage systems will increase the number and size of wet depressions, creek banks, and other kinds of habitat on the landscape scale, thus compensating for declining α-diversity on the patch scale. According to their assumption, the ungrazed salt marshes would essentially contain the same species pool as the moderately grazed salt marsh, the species however being less evenly distributed in a more patterned mosaic of habitats. In the present study, retarded succession to dominant stands of *Elymus* spp. in wet depressions point in the direction of the argument of Stock & Kiehl (2000), but see Bos et al. (2002). Several questions arise from their assumption: 1. Can a general increase in habitat variability be predicted, either by modelling the development of surface morphology or investigating the soil (e.g. winding creeks, depressions, eroded banks etc.)? 2. Do habitat models confirm the suitability of the newly developing habitats for the species pool of the moderately grazed higher salt marsh (Kleyer et al. 2000)? 3. May higher spatiotemporal variability and smaller size of the newly developing habitats impose higher extinction risks on the species (Johst et al. 2002)? This landscape perspective should be investigated with greater emphasis! However, to arrive at sound predictions on a landscape scale, long-term studies are needed that add a functional perspective on landscape – species interactions to the plot-based studies that dominate empirical succession research till to date.

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