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The impact of tidal inundation on salt marsh vegetation after de-embankment on Langeoog Island, Germany—six years time series of permanent plots

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Abstract Salt marsh succession after de-embankment was monitored on the East Frisian barrier island Langeoog by investigating permanent plots. Seventy years after embankment salt marsh plants were once again influenced mainly by the tidal regime. From 2002 to 2004 the former high marsh and glycophytic vegetation died out and was replaced by species of lower salt marsh zones. Nitrophytic halophytes like *Suaeda maritima, Atriplex prostrata* and *Artemisia maritima* established first because of the high nutrient content in the soil, a direct result of former vegetation decay. With decreasing nitrogen afterwards other species became more competitive. Until 2007 *Atriplex portulacoides* became more dominant in the lower marsh and *Elymus athericus* reached dominance in areas where grazing has been abandoned in the high marsh. The dynamics in the study area is much lower than in natural marshes due to the still existing drainage system. Therefore vegetation units with low species diversity are widespread.

Keywords De-embankment · Permanent plots · Salt marsh · Vegetation succession · East Frisian Barrier Island

Nomenclature Wisskirchen and Haeupler (2000)

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Abbreviations

PP	Permanent plot
NN	German ordnance datum
TDN	Total dissolved nitrogen

Introduction

Climate change and sea level rise are a great concern today, especially along shallow coastlines existing in the southern part of the North Sea. Extended salt marshes are a good natural defence against the sea, because the vegetation reduces wave energy (Cooper et al. 2001; Wittig et al. 2004; Wolters et al. 2005a). However, most (over 90%) parts of these areas are embanked or are still in anthropogenic use (Reise 2005). More than that, salt marshes along the North Sea are mostly narrow areas which in many regions of the coastal mainland eroding because of the coastal squeeze (Adam 2002; Doody 2004; Hughes 2004; Wolters et al. 2005c). In the future it might be necessary to breach more of the existing seawalls to allow development of potentially natural salt marshes. An important question is: How long will natural succession last after de-embankment of several hundred hectares of former embanked salt marshes? Wolters et al. (2005a) present an overview where mostly smaller areas were de-embanked, but there are few studies dealing with the detailed change in salt marsh vegetation in large de-embanked areas. One example for an area including 350 ha on the Baltic Sea is described by Bernhardt and Koch (2003) in detail. Wolters et al. (2005b) postulate that the reestablishment of the potentially natural vegetation will take years because of the limited seedbank and the short distance transport of diaspores by the tides. Therefore there is an essential need for long-term monitoring (Wolters et al.

2005b). Especially permanent plots (PPs) are a very common method to document changes in vegetation succession (Bakker 1978; Bakker et al. 1996; Beeftink et al. 1978; Bernhardt and Koch 2003; Kiehl et al. 2007; Roozen and Westhoff 1985; Wolters et al. 2005a). The great advantage of analysing PPs is that a detailed overview of the changes in species coverage due to influence of apparently less important factors is obtained. Vegetation mapping is often more related to point out changes in vegetation units than to single species, so a combination of both methods is useful (Barkowski 2003, Vegetationskundliche und paläoökologische Untersuchungen auf dem Langeooger Sommerpolder—Westteil. Unpubl. Thesis, Universität Hannover, Institut für Geobotanik, 111 p; Barkowski and Freund 2006; Freund et al. 2003). This study gives answers to important questions concerning vegetation succession following de-embankment by monitoring PPs from 1 year before to 4 years after de-embankment. How do the salt marsh zones differ in their succession following tidal inundation? How do single species react? Wolters et al. (2005a) postulate an increase in species number as a measurement for restoration success, but after the former vegetation dies how long will it take? Important local factors such as the drainage system or grazing intensity have to be taken in account.

Methods

Study area

The salt marshes on Langeoog Island can be considered as three separate areas. One area is located on the west end of Langeoog Island (Fig. 1) and second in the east. Both of them are natural grown salt marshes. The study area includes the third region, a 378.5 ha area of salt marsh which was under intensive anthropogenic influence. It is completely ditched for drainage and in 1934/35 a summer dike was build to allow for grazing by cattle. A total of 218 ha were excluded of regular inundation in this so called summer polder. The dike was between 2 m NN and 2.25 m NN high (Ahlhorn and Kunz 2002; Harnischmacher 1949, Gutachten über die Entwicklung der domänenfiskalischen Hellerwiesen auf der Nordseeinsel Langeoog nach Ausführung der Sommerbedeichung in den Jahren 1935/36 bis zum Jahre 1948. Unpubl. expert report) and the salt marsh behind was only flooded 15 to 25 times a year during storm surges. Forty-six PPs were made in 1936 and monitored to document the effect of embankment in the vegetation. In 1948 they were controlled again (Harnischmacher 1949, Gutachten über die Entwicklung der domänenfiskalischen Hellerwiesen auf der Nordseeinsel Langeoog nach Ausführung der Sommerbedeichung in den Jahren 1935/36 bis zum Jahre 1948. Unpubl. expert report) so the data serves as a baseline study.

As a measure for nature conservation the former summer dike on Langeoog Island was partly removed in 2003/2004 (Fig. 1). Altogether 218 ha were exposed to the normal tidal regime again. The whole summer polder was grazed by cattle intensively until 1992. Grazing was abandoned in most parts of the area after 2002 before dike breaching (Barkowski 2003, Vegetationskundliche und paläoökologische Untersuchungen auf dem Langeooger Sommerpolder—Westteil. Unpubl. Thesis, Universität Hannover, Institut für Geobotanik, 111 p; Steffens 2003, Vegetationskundliche und paläoökologische Untersuchungen auf dem Langeooger Sommerpolder—Ostteil. Unpubl. thesis, Universität Hannover, Institut für Geobotanik. 122 p).

In 2000 the permanent plots where reactivated and additionally new permanent plots (PP 50 to 84) were made (Fig. 2) (Freund et al. 2003). In 2002 all plots were examined in order to obtain the reference state of vegetation 1 year prior to de-embankment.

De-embankment started in 2003 by removing the sluices within the summer dike and the whole project was completed in September 2004. To protect the dunes and to allow safe travelling to the east end of Langeoog Island a new dike with a crest height of 3.2 m NN was built (Fig. 1). The construction of this dike caused the separation of the

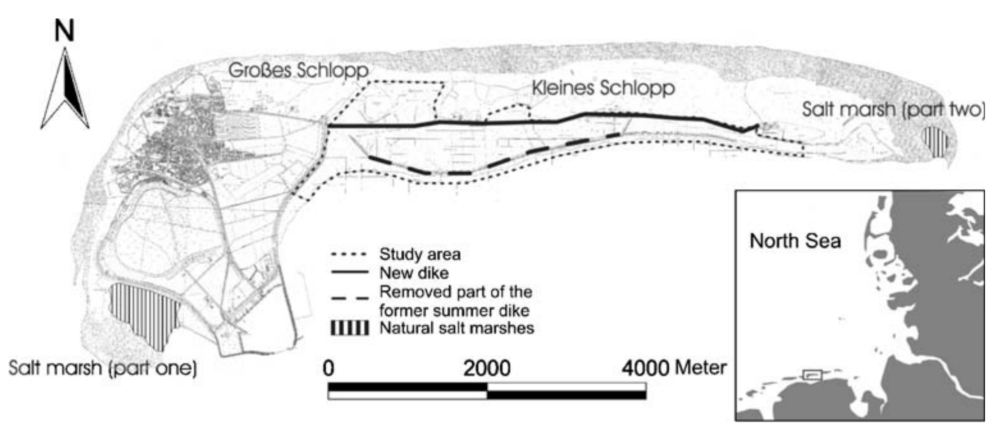

Fig. 1 Investigation area (marked by the short dashed line) and natural salt marshes on Langeoog Island. Position of the former summer dike and the new dike. Insert shows the position of Langeoog in the North Sea

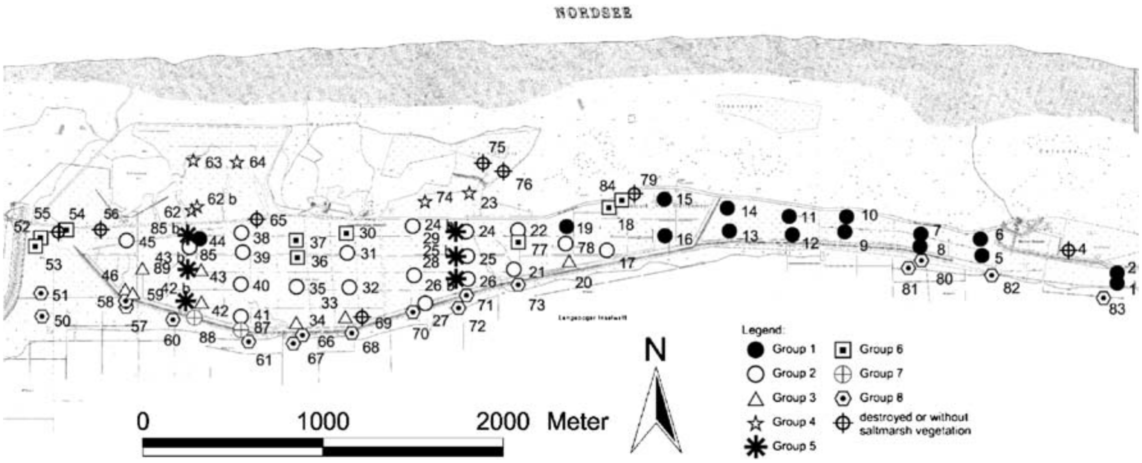

Fig. 2 Position of 83 PPs in the investigation area and their membership to the group, as well as, those PPs which were not considered in this studying

"Großes" and "Kleines Schlopp" from the rest of the salt marsh. These two areas resulted from a storm surge in 1717 which divided the island in three parts. It took until the beginning of the 20th century to close the dune ridges, followed by the development of salt marsh vegetation.

To document the daily impact of tidal inundation on the former sheltered vegetation within the summer polder from 2004 to 2007 the PPs were monitored. This research was part of a project in which geochemistry (Kolditz et al. 2009) was combined with vegetation data.

The PPs are marked on each corner with a magnet located 25 cm deep. In addition two wooden poles were set at the northern corners of each site. Each PP is approximately 4 m^2 and is predominately square. In 2005 five new PPs were made at locations of special interest (PP 85 to 89), for example where the former summer dike was located (Fig. 2). The top soil was removed at seven locations (PP 24b, 25b, 26b, 42b, 43b, 62b and 85b) to document how succession starts without former vegetation.

In this paper the years 2002 to 2007 are primarily considered in order to show the effects of de-embankment while the history of the vegetation of the summer polder before has already been well described in Barkowski (2003, Vegetationskundliche und paläoökologische Untersuchungen auf dem Langeooger Sommerpolder—Westteil. Unpubl. Thesis, Universität Hannover, Institut für Geobotanik, 111 p), Barkowski and Freund (2005), Freund et al. (2003), Harnischmacher (1949, Gutachten über die Entwicklung der domänenfiskalischen Hellerwiesen auf der Nordseeinsel Langeoog nach Ausführung der Sommerbedeichung in den Jahren 1935/36 bis zum Jahre 1948. Unpubl. expert report), Petersen (2001), Petersen (2003) and Steffens (2003,Vegetationskundliche und paläoökologische Untersuchungen auf dem Langeooger Sommerpolder—Ostteil. Unpubl. thesis, Universität Hannover, Institut für Geobotanik. 122 p).

The salt marsh was subdivided into four zones: high marsh, middle marsh, low marsh and pioneer zone. Splitting up the middle marsh from the high marsh follows partly the definition of Freund et al. (2003), Petersen (2001) and Roozen and Westhoff (1985). In this article the zones are defined as: Pioneer zone—dominated by *Salicornia stricta, Spartina anglica or Suaeda maritima* with a coverage of Puccinellion species under 15%; low marsh—dominated by *Atriplex portulacoides, Puccinellia maritima* and mixed units of Puccinellion species; middle marsh—dominated by *Limonium vulgare, Juncus gerardii* and mixed units of Puccinellion and Armerion species (for example *Artemisia maritima* and *Atriplex portulacoides*); high marsh—dominated by *Festuca rubra, Elymus athericus, E. repens, Ononido-Caricetum distantis, Artemisietum maritimae* and salt influenced grassland.

The vegetation inside the summer polder was mainly covered by vegetation units of the middle and high marsh in 2002 (Fig. 3). Additionally many glycophytic species had colonized the study area since 1936. The distribution of vascular plants did not follow salinity or inundation gradients but were strongly affected by other factors such as grazing intensity inside the summer polder, however outside the summer polder the opposite was true. Here the abiotic factors caused a normal salt marsh zonation which was predominant until 2002.

Sampling relevès

A total number of 83 PPs is located in the investigation area (Fig. 2). The number of examined PPs varies during the investigation period (72 PPs in 2002, 33 PPs in 2004, 82 PPs in 2005, and 83 PPs in 2006 and 2007). Additionally, since 2005 seven PPs with removed top soil were investigated. Coverage estimation was carried out by the same person at the beginning of August in each listed year

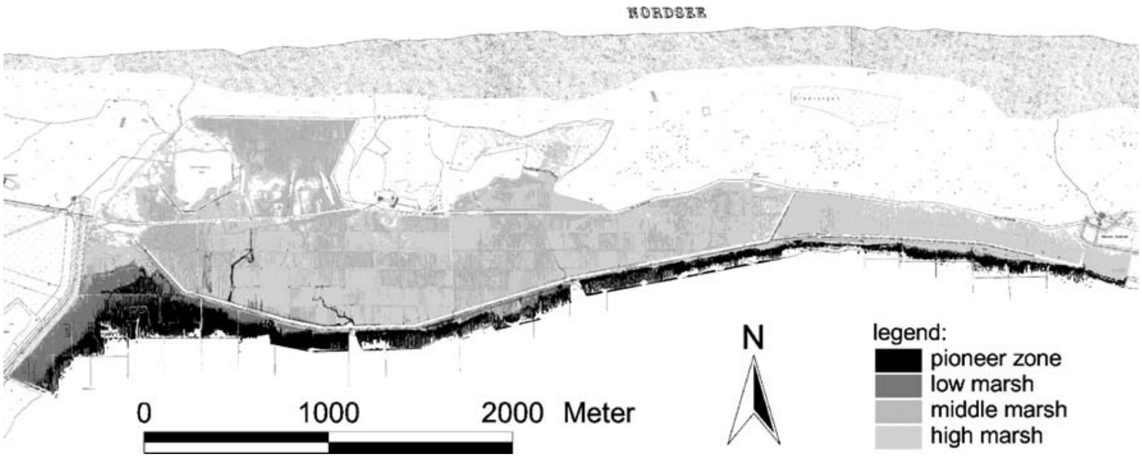

Fig. 3 Salt marsh zones in the investigation area on Langeoog Island in 2002

using a decimal scale (Londo 1976). This procedure ensures a high comparability of the single investigations.

Key species

Thirteen species were chosen as key species. The criteria were: presence in a representative number of PPs; characteristic species for a special salt marsh zone; proof of an important process, for example the increased appearance of nutrients. The key species are: *Salicornia stricta* and *Suaeda maritima* for the pioneer zone; *Aster tripolium, Atriplex portulacoides* and *Puccinellia maritima* for the lower marsh; *Limonium vulgare* and *Juncus gerardii* for the middle marsh; *Atriplex prostrata* and *Artemisia maritima* belong to the middle and high marsh depending on their accompanying vegetation; *Festuca rubra, Elymus athericus, E. repens* and *Potentilla anserina* are key species for the high marsh.

An example of why a particular species was not considered a key species is *Spartina anglica*. It was not chosen because it only dominates in a few PPs outside the former summer polder and is barely present inside the summer polder during the time of monitoring.

The appearance of species each year is always calculated based on the total number of PPs. The year 2002 is considered as the condition before de-embankment, so every species which is present in this year is treated as established. To calculate changes in vegetation, every coverage value has been set to the maximum percent value of the scale (compare Londo 1976), for example scale 3=35% coverage.

Groups of permanent plots

To characterize the changes in salt marsh vegetation in the different zones the PPs were divided into eight functional groups to describe succession processes easier (Table 1 and Fig. 2). The criteria for characterizing the groups were: a similar position in the investigation area and/or a similar succession since 2002. The presence and dominance of key species and other characteristic species were also important criteria. For each group only examples of the PPs are described in detail. The following PPs were not considered in this study (PP 4, 55, 56, 65, 69, 75, 76 and 79) because they were destroyed, located outside the investigation area or were colonized each by non salt marsh vegetation. An increasing species number is often defined as restoration success (compare Wolters et al. 2005a) so the average species number for each group was calculated for every year of monitoring (Table 3).

The vegetation data of the PPs was supplemented by information of the average monthly inundation from the "Wasser- und Schifffahrtsdirektion Nordwest" WSA Emden. In addition chemical data was used to describe succession processes for some PPs on a north to south transect through all salt marsh zones. For measuring pH a WTW pH/Cond 340i device with a pH-electrode SenTix 20 was used. Conductivity was examined with a TetraCon 325 electrode.

To obtain information about elevation above NN and distances to tidal channels of the PPs, aerial pictures from the "Nationalparkverwaltung Niedersächsisches Wattenmeer" and an elevation class model were analysed using a Geographical Information System (ArcGis).

Nutrient analysis

Pore water samples were taken with portable capillary lances at different depths for analysis of nitrogen. Sampling always took place adjacent to PPs in order to combine nutrient data directly with the vegetation. For determining Total Dissolved Nitrogen (TDN) the analysis was carried out according to Grasshoff et al. (1999). Three replicates per sample depth were made and average values were calculated. A Dr Lange Xion 500 photometer was used for analysing TDN.

Table 1 Functional groups of PPs with their salt marsh zonation before and after de-embankment, characteristics and grazing intensity

Group	Salt marsh zone in 2002	Salt marsh zone after de-embankment	Supplementary characteristics	Grazing	PPs belonging to group
1	high marsh	high marsh	*Elymus athericus*	abandoned 1992 to 1994	1, 2, 5 to 16, 19, 44
2	high marsh	middle marsh	-	abandoned 2002	17, 21, 22, 24 to 29, 31, 32, 35, 38 to 41, 45, 78, 85
3	high marsh	low marsh; pioneer zone	-	abandoned 2002	20, 33, 34, 42, 43, 46, 59, 89
4	high marsh	high marsh; glycophytic vegetation	embanked by the new dike	grazed by cattle	23, 62 to 64, 62b, 74
5	not existent	pioneer zone; low marsh; middle marsh	top soil removed	no grazing	24b, 25b, 26b, 42b, 43b, 85b
6	high marsh	high marsh	constant characteristic species	partly grazed by horses	18, 30, 36, 37, 52 to 54, 77, 84
7	not existent	pioneer zone; low marsh	former summer dike	no grazing	87, 88
8	low marsh; pioneer zone	low marsh; pioneer zone	outside the former summer dike; expansion of *Atriplex portulacoides*	no grazing	50, 51, 57, 58, 60, 61, 66 to 68, 70 to 73, 80 to 83

Results

Distribution of key species within the PPs

The key species and their increase or decrease after de-embankment is documented below. The species are listed in order of their appearance from the pioneer zone to the high marsh in the investigation area. Only species with a relevant validity for the whole area or an important part were chosen.

Species of the pioneer zone

In 2002 the pioneer species *Salicornia stricta* was only present in PPs outside the summer polder with exception in PP 59. Altogether *S. stricta* was found in 22.9% of all 83 PPs. The coverage was between 1% and 55% (Fig. 4). It was primarily an element in vegetation units of the lower marsh at this time, however, *S. stricta* dominated in PP 73 and 81 in the pioneer zone (Figs. 2 and 3). Since 2004 *Salicornia stricta* expanded into the area of the former summer polder. It was found in 4 PPs where it was absent in 2002. Because of the low number (33) of investigated PPs in 2004 where *S. stricta* was situated, it appears that the portion of colonized PPs decreased (Table 2). This can be considered a sampling artefact. In 2005 *S. stricta* was present in 25 additional PPs so that the portion of all PPs where it was growing increased considerably. On 25.5% of the PPs which were already inhabited by *S. stricta* the coverage increased as well. There were only decreases in coverage outside the former summer polder. In the two following years *Salicornia stricta* continued to spread out onto more PPs, however in 2007 the coverage decreases by 10–20% in 47.1% of the PPs. From 2002 to 2007 the

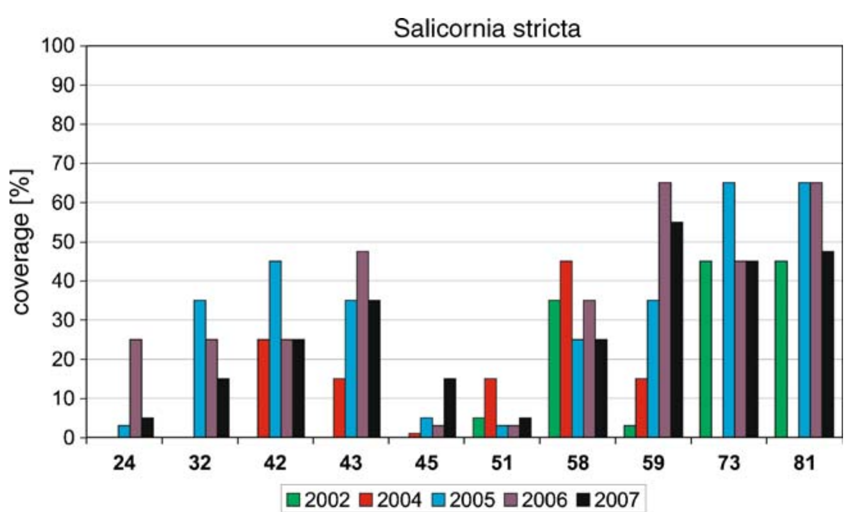

Fig. 4 Coverage of *Salicornia stricta* at selected PPs. PP 73 and 81 were not monitored in 2004

Table 2 Proportion of colonized PPs, percentage of already inhabited PPs where species coverage decreased and increased

	Colonized PPs [%]	PPs where coverage decreased [%]	PPs where coverage increased [%]		Colonized pps [%]	PPs where coverage decreased [%]	PPs where coverage increased [%]
Salicornia stricta (pioneer species)				**Suaeda maritima (pioneer species)**			
2002	22.9			2002	16.9		
2004	10.8	22.2	33.3	2004	14.5	8.3	25.0
2005	56.6	14.9	25.5	2005	56.6	4.3	27.7
2006	59.0	28.6	34.7	2006	56.6	51.1	27.7
2007	61.5	47.1	25.5	2007	65.1	20.4	40.7
Aster tripolium (low marsh species)				**Atriplex portulacoides (low marsh species)**			
2002	14.5			2002	13.3		
2004	19.3	12.5	25.0	2004	18.1	6.7	26.7
2005	25.3	38.1	14.3	2005	30.1	16.0	28.0
2006	37.4	12.9	32.3	2006	39.8	6.1	45.5
2007	55.4	10.9	34.8	2007	48.2	10.0	45.0
Puccinellia maritima (low marsh species)				**Limonium vulgare (middle marsh species)**			
2002	12.1			2002	9.6		
2004	12.1	20.0	0.0	2004	4.8	25.0	0.0
2005	21.7	33.3	5.6	2005	12.1	20.0	30.0
2006	18.1	13.3	33.3	2006	9.6	25.0	50.0
2007	36.1	6.7	16.7	2007	14.5	33.3	16.7
Juncus geradii (middle marsh species)				**Atriplex prostrata (middle and high marsh species)**			
2002	27.7			2002	34.9		
2004	21.7	44.4	27.8	2004	31.3	7.7	38.5
2005	21.7	13.0	60.9	2005	56.6	6.4	55.3
2006	30.1	32.0	24.0	2006	49.4	48.8	22.0
2007	31.3	53.9	15.4	2007	43.4	41.7	22.2
Artemisia maritima (middle and high marsh species)				**Festuca rubra (high marsh species)**			
2002	39.8			2002	61.5		
2004	20.5	11.8	52.9	2004	27.7	26.1	56.5
2005	41.0	35.3	23.5	2005	54.2	37.8	33.3
2006	44.6	18.9	46.0	2006	57.8	33.3	31.3
2007	45.8	29.0	29.0	2007	59.0	26.5	34.7
Elymus athericus (high marsh species)				**Elymus repens (high marsh species)**			
2002	19.3			2002	26.5		
2004	8.4	0.0	28.6	2004	6.0	60.0	40.0
2005	22.9	26.3	36.8	2005	21.7	38.9	27.8
2006	31.3	19.2	34.6	2006	27.7	17.4	43.5
2007	36.1	16.7	56.7	2007	24.1	70.0	5.0
Potentilla anserina (high marsh species)							
2002	57.8						
2004	25.3	81.0	0.0				
2005	34.9	58.6	13.8				
2006	32.5	37.0	40.7				
2007	24.1	30.0	45.0				

number of PPs where this species is present increased significantly (Table 2).

Like *Salicornia stricta Suaeda maritima* was located in 2002 primarily in PPs in front of the summer dike (group 8 in Fig. 2). However, in none of the PPs was *Suaeda maritima* a dominant species (Fig. 5). In 2004 *S. maritima* colonized further PPs as well as increased its coverage on already inhabited PPs (Table 2). This upward trend

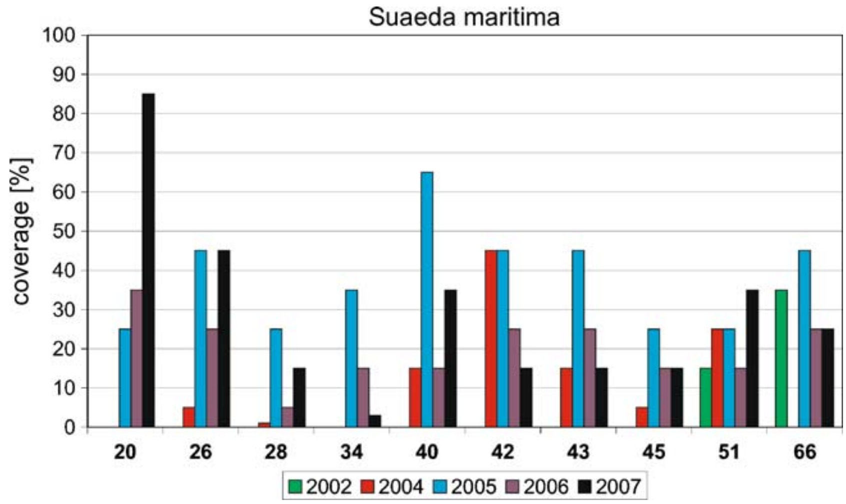

Fig. 5 Coverage of *Suaeda maritima* at selected PPs. PP 34 and 66 were not monitored in 2004

continued through to 2005. In this year *S. maritima* was present in 56.6% of the PPs. On some PPs it was clearly dominant, for example PP 40 (Fig. 5 and Table 2). In 2006 the expansion stagnated. On 51.1% of the already colonized PPs the coverage decreased up to 50%. This trend switched 2007 again and *Suaeda maritima* extended onto 65% of the PPs. Yet it did not reach the average coverage of 2005 on most sample plots, e.g. PP 40 (Fig. 5).

Species of the low marsh

The focus of the distribution area of *Aster tripolium, Atriplex portulacoides* and *Puccinellia maritima* in 2002 was outside the summer polder. Inside they were only present in PP 59. Some single specimens of *Aster tripolium* inhabited PP 40, 42 and 45. *Atriplex portulacoides* was also present in PP 26 (Fig 2). In 2004 after de-embankment *Aster tripolium* spread out on more PPs within the former summer polder and increased its coverage on the already colonized PPs (Table 2 and Fig. 6). The following year was characterized by equilibrium between new inhabited PPs and places where *Aster tripolium* disappeared (Table 2 and Fig. 6). Additionally coverage of *A. tripolium* decreased on many of the already occupied PPs. In 2006 this trend changed in favour of *A. tripolium*. The species spread out on new locations and increased its coverage (Table 2). This tendency continued until 2007 where *Aster tripolium* inhabited 55.5% of all PPs.

As mentioned before *Atriplex portulacoides* was mainly situated outside the summer polder in 2002. The coverage of this species was quite heterogeneous. In some PPs *A. portulacoides* reached absolute dominance (Fig. 7) but in PP 70 only a single small specimen was present (coverage< 5%). In 2004 *A. portulacoides* colonized additional PPs mostly inside the former summer polder with a low coverage (Table 2). In the already inhabited PPs the species increased its coverage. Until 2007 the expansion of *A. portulacoides* persisted. The portion of inhabited PPs increased continuously from 13.3% in 2002 to 48.2% in 2007, as well as, the species coverage (Table 2). On some

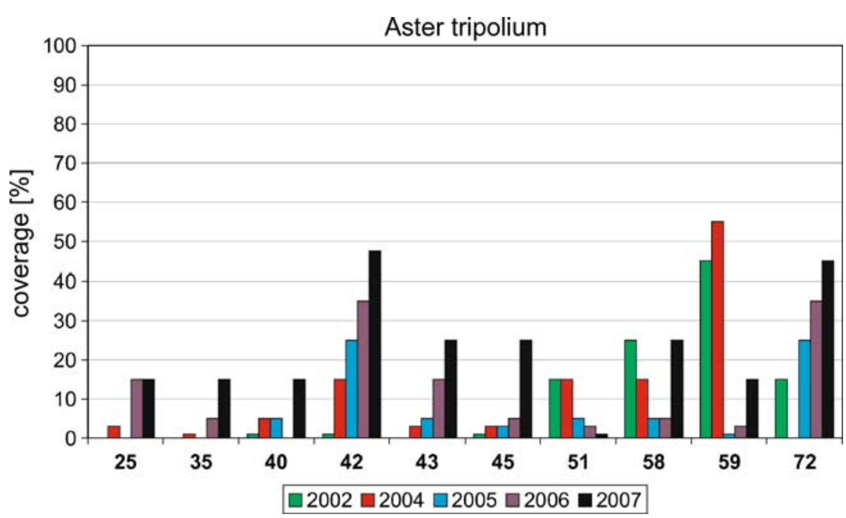

Fig. 6 Coverage of *Aster tripolium* at selected PPs. PP 72 was not monitored in 2004

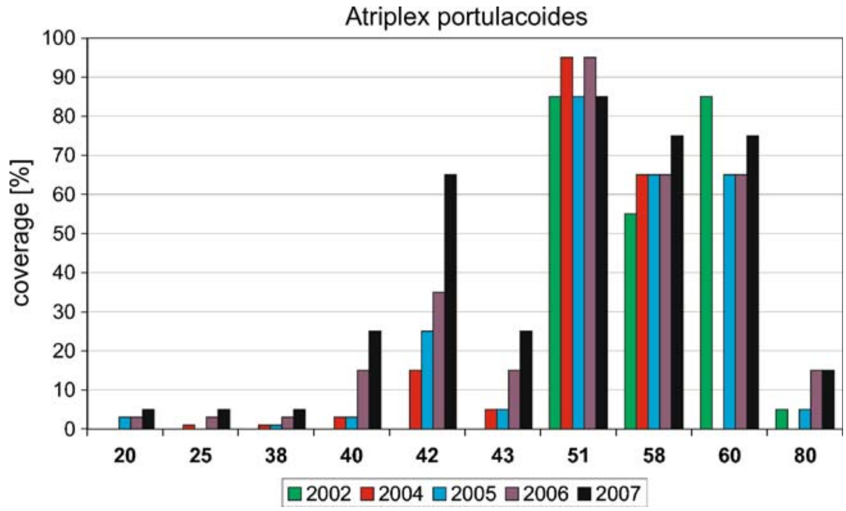

Fig. 7 Coverage of *Atriplex portulacoides* at selected PPs. PP 60 and 80 were not monitored in 2004

sites *A. portulacoides* was able to establish itself after absence in 2002 and became dominant (PP 42 in Fig. 7).

Puccinellia maritima only dominated PPs outside the summer polder in 2002 (PP 68 and 70) but usually it only accompanied other species. In 2004 *P. maritima* established itself in some PPs within the summer polder with low coverage (Table 2 and Fig. 8). On the already situated PPs coverage decreased. This tendency continued in 2005 and switched completely in 2006. *P. maritima* was found at fewer locations, but was able to increase its coverage on 33.3% of the remaining PPs. The following year was characterized by a doubling of the situated PPs and a small increase of coverage on some of the PPs. Altogether *Puccinellia maritima* was able to expand its territory from 2002 to 2007 (Table 2).

Species of the middle marsh

The two key species allocated only to the middle marsh show different succession after de-embankment. In 2002 *Limonium vulgare* was only distributed outside the summer polder except in PP 9 (Fig. 2). Until 2005 *L. vulgare* expanded its distribution a bit (Table 2), but it decreased in 2006. In 2007 *L. vulgare* colonized some new PPs (Table 2 and Fig. 9). The main focus of the distribution area of *Limonium vulgare* was located outside the former summer polder pre and post de-embankment.

In contrast to *Limonium vulgare, Juncus gerardii* was only distributed in PPs within the summer polder in 2002 with exception of PPs 52 and 54. These PPs are situated very high about NN (Fig. 2). In fact *J. gerardii* supported by grazing (Bakker et al. 1985) expanded massively during embankment. Most of the sites were still grazed by cattle in 2002 or grazing was abandoned a short time before (compare Barkowski 2003, Vegetationskundliche und paläoökologische Untersuchungen auf dem Langeooger Sommerpolder—Westteil. Unpubl. Thesis, Universität Hannover, Institut für Geobotanik, 111 p). On many PPs *J. gerardii* dominated with coverage over 50% (Fig. 10). In 2004 *J. gerardii* colonized further PPs and increased its coverage at 44.4% of

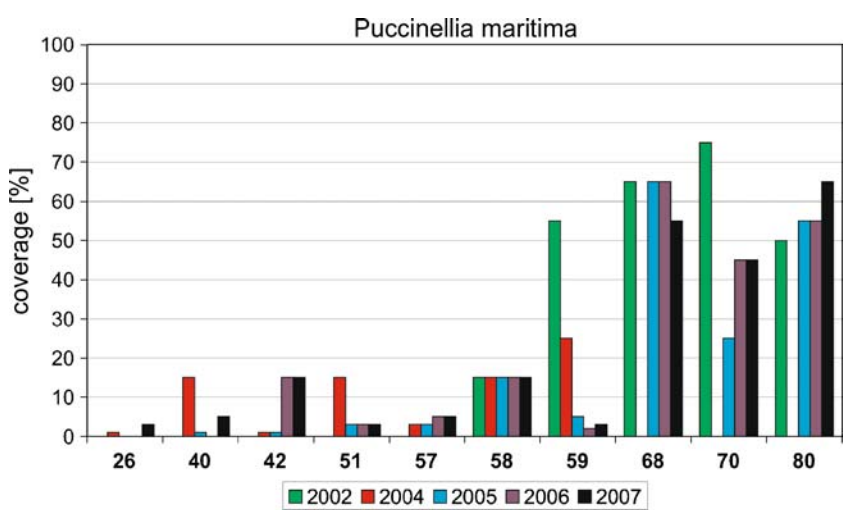

Fig. 8 Coverage of *Puccinellia maritima* at selected PPs. PP 68, 70 and 80 were not monitored in 2004

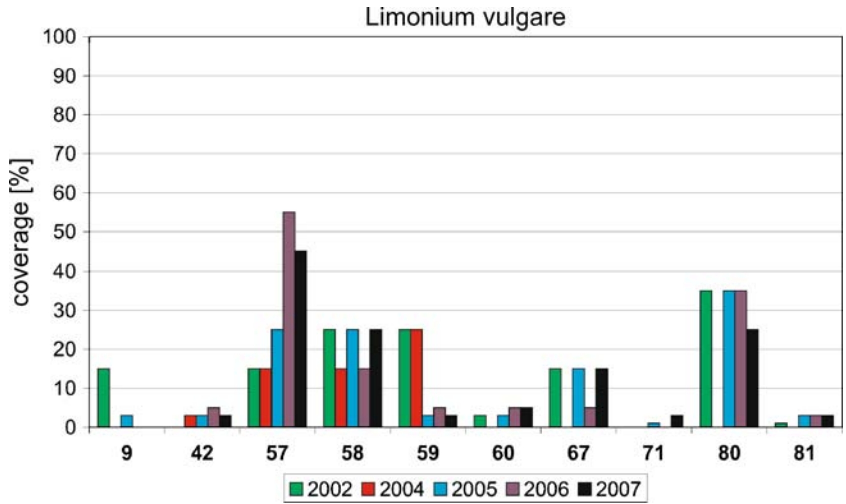

Fig. 9 Coverage of *Limonium vulgare* at selected PPs. PP 9, 60, 66, 71, 80 and 81 were not monitored in 2004

the already situated PPs (Table 2 and Fig. 10). One year later there was a sharp decrease in coverage of *J. gerardii*. The species lost ground in 60.9% of the colonized PPs. This trend only lasted for 1 year and in 2006 *J. gerardii* again spread out onto new PPs and increased in coverage on most of the PPs (Table 2, Fig. 10). In 2007 the species increased coverage in 53.9% of the colonized PPs. Until 2007 *J. gerardii* was able to establish itself on PPs again which were colonized in 2002, as well. This process of die out after de-embankment and reestablishment after 5 years appears to be an adaptation to the new conditions. The colonization of new PPs (PP 29 in Fig. 10) was more an exceptional case.

Species between middle and high marsh

Atriplex prostrata and *Artemisia maritima* are the species placed in this group. The PPs colonized by *Atriplex prostrata* in 2002 were located within the summer polder except PP 52. In most of the PPs just a few specimens were present with low coverage. Only on some places within a gull breeding colony where grazing had been abandoned it was able to expand a bit more (compare Figs. 2 and 11). In 2004 the portion of PPs where *A. prostrata* was present increased and additionally the species enlarged its coverage on the already colonized PPs (Table 2). The expansion of *A. prostrata* reached its maximum in 2005. In this year the species inhabited 57.9% of the PPs and increased in coverage in most of the colonized PPs. The following years were characterized by a decrease. Until 2007 *A. prostrata* existed in only 43.3% of the PPs and it lost much coverage, with the result that in many PPs only individual specimens were present. An exception was in the east of the investigation area (Fig. 2). Here *A. prostrata* spread out in some PPs (PP 8 and 16 in Fig. 11) dominated mostly by *Elymus* species.

In contrast to *Atriplex prostrata, Artemisia maritima* was situated in PPs outside the summer polder, as well as, inside in 2002. These places were mostly non grazed and located in areas surrounding bird breeding colonies. The range of coverage varied between one single specimen (PP 37) and absolute dominance (PP 41). In 2004 the portion of

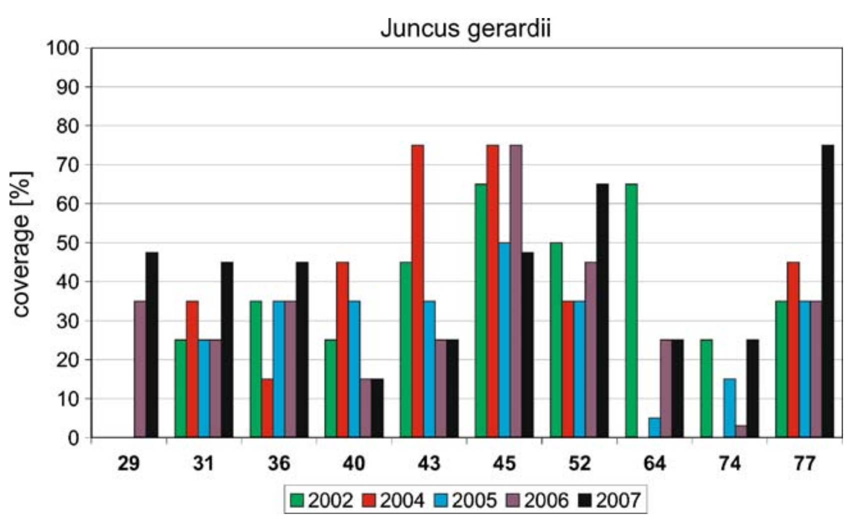

Fig. 10 Coverage of *Juncus gerardii* at selected PPs. PP 64 and 74 were not monitored in 2004

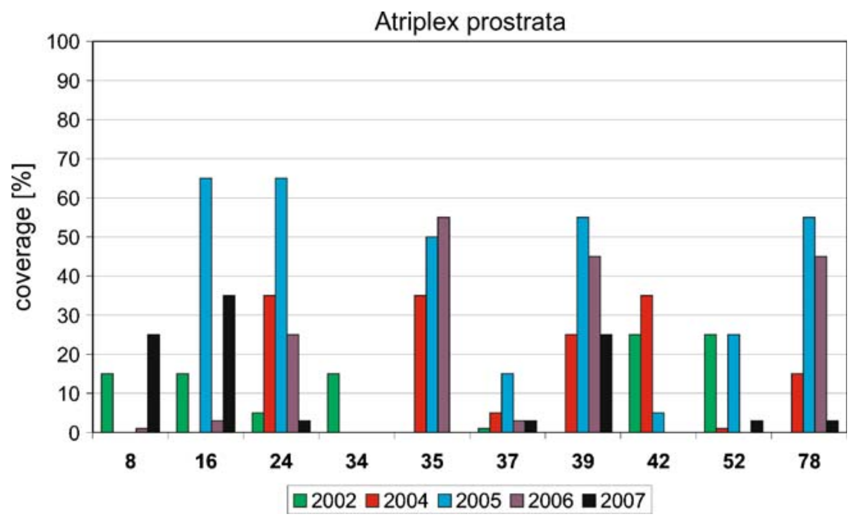

Fig. 11 Coverage of *Atriplex prostrata* at selected PPs. PP 8, 16 and 34 were not monitored in 2004

colonized PPs remained constant but *A. maritima* increased in coverage in more than half of the PPs (Table 2). One year later the expansion continued in some PPs, but mostly coverage was constant or decreased (Table 2 and Fig. 12). Expansion of *A. maritima* stagnated in 2007 and finally it inhabited 45.8 of the PPs.

Species of the high marsh

Festuca rubra, Elymus athericus, E. repens and *Potentilla anserina* belong to this group but their succession after de-embankment differed markedly.

Elymus athericus and *E. repens* were only present in PPs within the summer polder in 2002. Their focus of distribution was located in the eastern part of the investigation area (group 1 in Fig. 2). On many sites one or both became dominant with coverage between 50% and 100% (Figs. 13 and 14). After de-embankment succession of the two *Elymus* species was quite different. *E. athericus* further colonized PPs in 2004 which are located more in the western part of the investigation area and it increased in coverage on the already inhabited PPs. In 2005 an equilibrium concerning the expansion and decline of *E. athericus* was reached, but a tendency was identified when the position of the PPs was considered. In the east *E. athericus* increased and it decreased in the west. The following 2 years showed a clear expansion tendency in the whole investigation area. In 2007 *E. athericus* even became absolutely dominant on the colonized PPs in the east (PP 5, 7, 12, 15 and 19 in Figs. 2 and 13). From 2002 to 2007 *E. athericus* spread out from 19.3% of the PPs to 36.1%.

In 2004 only a few potential habits of *E. repens* were monitored, so the decrease of this species must be interpreted carefully. In 2005 however, this tendency of decline was clearly proved. Especially on the western locations *E. repens* was replaced by other species mostly by *E. athericus*. The coverage of *E. repens* decreased in 38.9% of the inhabited PPs (Table 2). In the following year *E. repens* expanded on locations in the west again and increased in coverage in the PPs in the east, as well. The

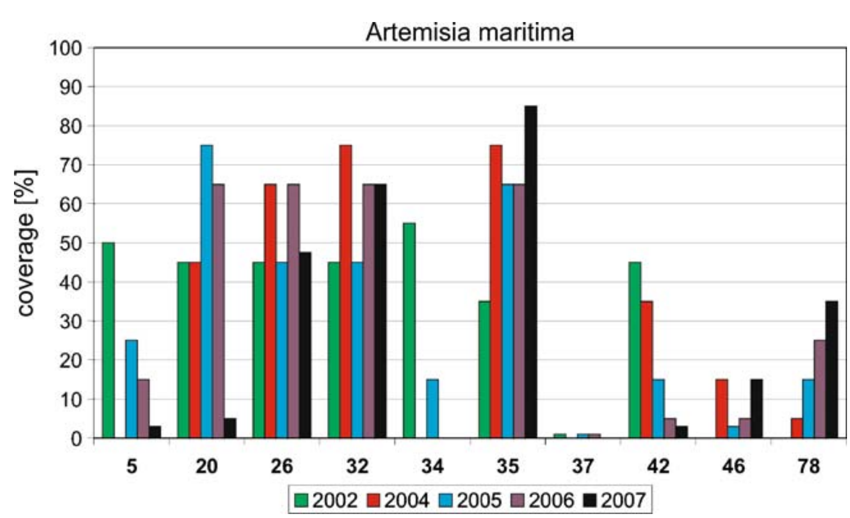

Fig. 12 Coverage of *Artemisia maritima* at selected PPs. PP 5 and 34 were not monitored in 2004

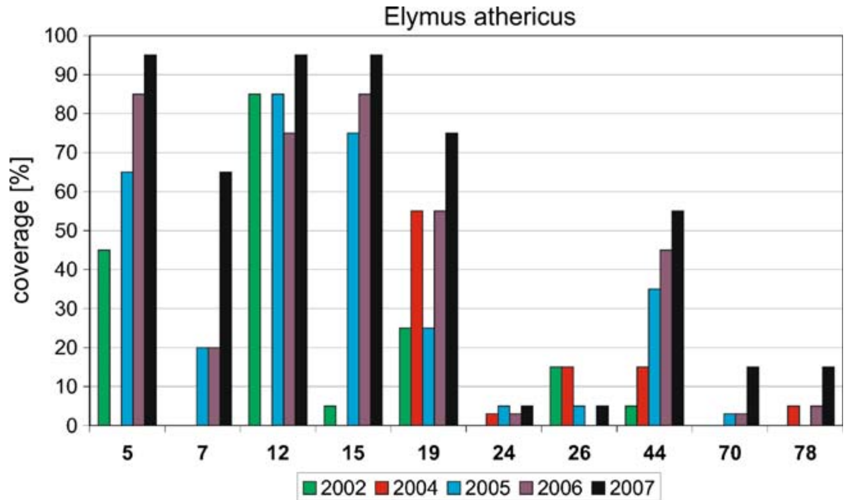

Fig. 13 Coverage of *Elymus athericus* at selected PPs. PP 5, 7, 12, 15 and 70 were not monitored in 2004

expansion process switched again in 2007, with the result that *E. repens* was absent in most of the former situated western PPs. In addition it lost coverage on the majority of all colonized PPs. Since 2002 the number of colonized PPs only decreased by 2.4%, but coverage of *E. repens* within these locations decreased more clearly (Fig. 14). The decrease of *E. repens* was linked to an increase of *E. athericus* in most of the colonized PPs.

Festuca rubra was present in almost all PPs inside the summer polder and on two locations outside in 2002. The average coverage was between 30% and 50%. In 2004 the portion of inhabited PPs decreased slightly and in addition in most of the colonized PPs the coverage decreased, as well (Table 2). One year later the number of PPs inhabited by *F. rubra* remained constant. There was no clear tendency in changing coverage by *Festuca rubra*, as it nearly decreased in as many PPs as it increased (Table 2). In 2006 and 2007 there was a small expansion on new PPs but this was accompanied with a loss of coverage. Since 2002 the number of PPs inhabited by *F. rubra* stayed relatively constant but within the majority of these PPs the species lost its dominance (Fig. 15).

Like the other three mentioned high marsh species, before de-embankment *Potentilla anserinas* distribution was focused inside the summer polder. There it was found in almost all PPs in 2002, but it inhabited only one PP outside. A total of 57.8% of the PPs were colonized by *Potentilla anserina*. On most of these locations *P. anserina* covered more than 50% and some PPs were completely dominated by this species (PP 20, 21, 28, 32, 39 and 78 in Fig. 16). In 2004 the portion of PPs inhabited decreased slightly (Table 2) but *P. anserina* decreased significantly in coverage on 81% of these PPs. The loss of coverage reached up to 70% (PP 32). In the following year *P. anserina* died off in most of the eastern PPs (compare Figs. 2 and 16) and it decreased again in coverage on 58.6% of the still colonized PP. Both 2006 and 2007 were characterized by the further loss in presence of *P. anserina* (Table 2). Additionally, coverage decreased on the remaining locations in the south and east within the investigation area. However, *P. anserina* was able to spread

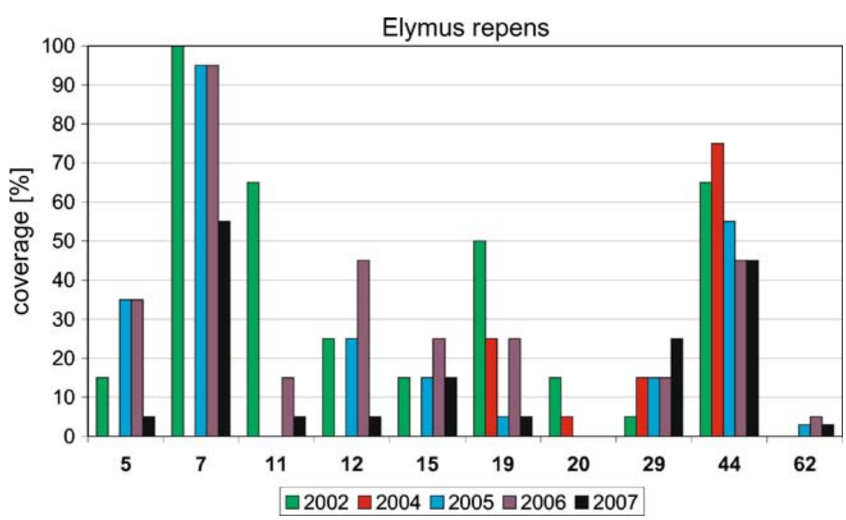

Fig. 14 Coverage of *Elymus repens* at selected PPs. PP 5, 7, 12, 15 and 62 were not monitored in 2004. PP 11 was not monitored in 2004 and 2005

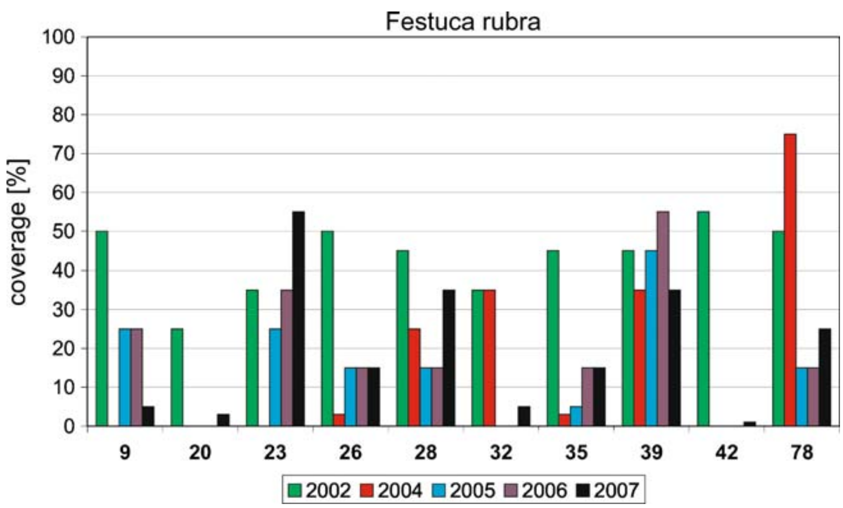

Fig. 15 Coverage of *Festuca rubra* at selected PPs. PP 9 and 23 were not monitored in 2004

out a little on northern PPs close to the new dike (Fig. 2) and especially on locations behind it. Until 2007 *Potentilla anserina* had disappeared from 58.3% of the PPs inhabited in 2002.

Vegetation succession of the permanent plots from 2002 to 2007

Wolters et al. (2005a) defined success of salt marsh restoration as the increase and presence of characteristic species. One important problem is to determine how long it takes after de-embankment until it is possible to assess this situation. In the following sections the vegetation succession of the functional groups of PPs (Table 1) is described dealing with this question.

Group 1: High marsh; *Elymus* sp. (non grazed since 1992 or 1994)

All PPs in this group are located in the eastern part of the investigation area, except PP 44, which is placed on dune remnants situated within the summer polder (Fig. 2 and Table 1). The height above NN of these PPs is between 1.9 m and 2.6 m. Grazing by cattle was stopped on these locations in 1994 or in 2002 at PP 19 (compare Barkowski 2003, Vegetationskundliche und paläoökologische Untersuchungen auf dem Langeooger Sommerpolder—Westteil. Unpubl. Thesis, Universität Hannover, Institut für Geobotanik, 111 p; Steffens 2003, Vegetationskundliche und paläoökologische Untersuchungen auf dem Langeooger Sommerpolder—Ostteil. Unpubl. thesis, Universität Hannover, Institut für Geobotanik. 122 p). The vegetation of these PPs was mainly characterized by *Elymus athericus* and *E. repens*. Some of the higher located PPs in this group showed an increasing portion of *Phragmites australis* (PP 10 and 14 in Fig. 2). Due to the composition of species all PPs are classified as high marsh from 2002 to 2007 (Fig. 17).

PP 12 is described as an example for this group (Fig. 18). Since 2002 especially *Elymus athericus* dominated the vegetation in this PP and was able to increase its

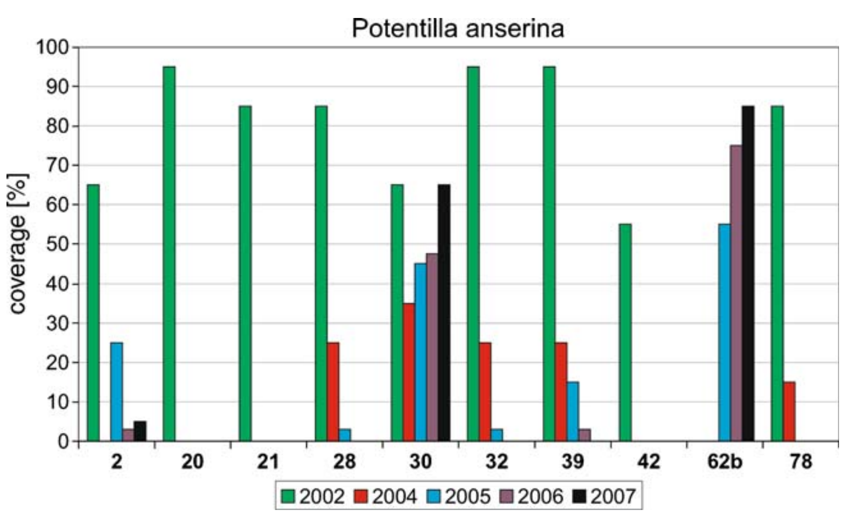

Fig. 16 Coverage of *Potentilla anserina* at selected PPs. PP 2 and 21 were not monitored in 2004. PP 62b was not monitored in 2002 and 2004

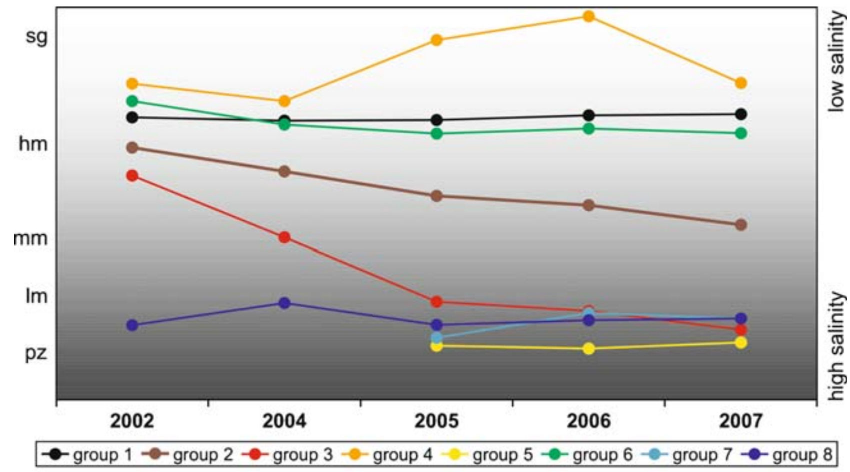

Fig. 17 Vegetation zonation of functional PP groups from 2002 to 2007: sg (*salt influenced grassland*); hm (*high marsh*); mm (*middle marsh*), lm (*low marsh*); pz (*pioneer zone*)

coverage until 2007. Species like *Artemisia maritima, Agrostis stolonifera* and *Potentilla anserina* disappeared in 2005. The coverage of *Festuca rubra* clearly decreased after de-embankment, as well. *Elymus repens* and *Atriplex prostrata* were also present in this PP and varied in coverage from year to year. In 2006 *E. repens* increased in coverage, but in 2007 a decrease in coverage followed (Table 2 and Fig. 14)

The average number of species situated in a PP in this group decreased continuously from 8.3 in 2002 to 5.9 in 2007 (Table 3).

Group 2: high marsh to middle marsh; unspecific (grazed extensive until 2002)

This group includes PPs which composition of species from 2002 to 2007 showed a clear tendency form higher marsh to middle marsh (Fig. 17). All sites are located 1.5 m to 2.2 m above NN and belong to the western part of the summer polder (Fig. 2 and Table 1). The PPs of this group are situated 0.5 m below the average altitude of PPs of group 1. Predominantly vegetation units dominated by *Festuca rubra, Juncus gerardii, Carex distans* and *Ononis spinosa* represented the state of 2002. Until 2007 the former dominant species disappeared or decreased in coverage. Since 2004 species like *Artemisia maritima, Atriplex prostrata, Atriplex portulacoides* and *Suaeda maritima* started to invade the PPs in this group and partly became dominant.

As an example for this group the succession of PP 78 will be presented in detail (Fig. 18). In 2002 the vegetation was characterized by a high coverage of *Potentilla anserina* (85%), *Festuca rubra* (50%) and *Agrostis stolonifera* (45%). In addition species of the upper Armerion (*Carex distans, Trifolium fragiferum*) and glycophytic species like *Lolium perenne, Trifolium repens, T. pratense, Cirsium arvense* and *Poa pratensis* were present. Only *Juncus gerardii* was present as an element of the lower Armerion. In the year 2004 a clear decrease of all glycophytes was evident and until 2005 they had disappeared like the upper Armerion species with the exception of *Festuca rubra*. Instead of these plants *Artemisia maritima* and *Atriplex prostrata* started to expand. Until 2006 the two pioneer species *Salicornia stricta* and *Suaeda maritima* were increasing in coverage, as well. In 2007 *Salicornia stricta* further increased its coverage whereas *Suaeda maritima* decreased. Additionally *Festuca rubra* and *Juncus gerardii* recovered and expanded a little (Fig. 18). *Elymus athericus* was able to establish itself as an element of the high marsh. The composition of the vegetation in 2007 was a mixture of species from all salt marsh zones. The number of species in this group decreased until 2005 as a result of the decline of more glycophytic related species. In the following 2 years the number of species rose again and mostly salt marsh species of the middle and low marsh replaced former vegetation.

Group 3: high marsh to low marsh or pioneer zone; unspecific (non grazed until 1994)

The PPs in this group are 1.3 m and 1.6 m above NN so they are clearly located lower the PPs in group 1 and 2. All sites of group 3 were situated directly behind the former summer dike or completely located in the west of the polder (Fig. 2 and Table 1). In 2002 these PPs were characterized by vegetation of the high marsh especially by *Festuca rubra, Juncus gerardii* and *Artemisia maritima*. Until 2007 the succession in group 3 led to vegetation units of the lower marsh and the pioneer zone (Fig. 17). Species like *Salicornia stricta, Atriplex portulacoides* and *Suaeda maritima* dominated these PPs 4 years after de-embankment. Although PP 89 was made in 2005 it was assigned to this group because its state of vegetation in 2002 could be reconstructed using vegetation mapping from that year (Barkowski 2003, Vegetationskundliche und paläoökologische Untersuchungen auf dem Langeooger

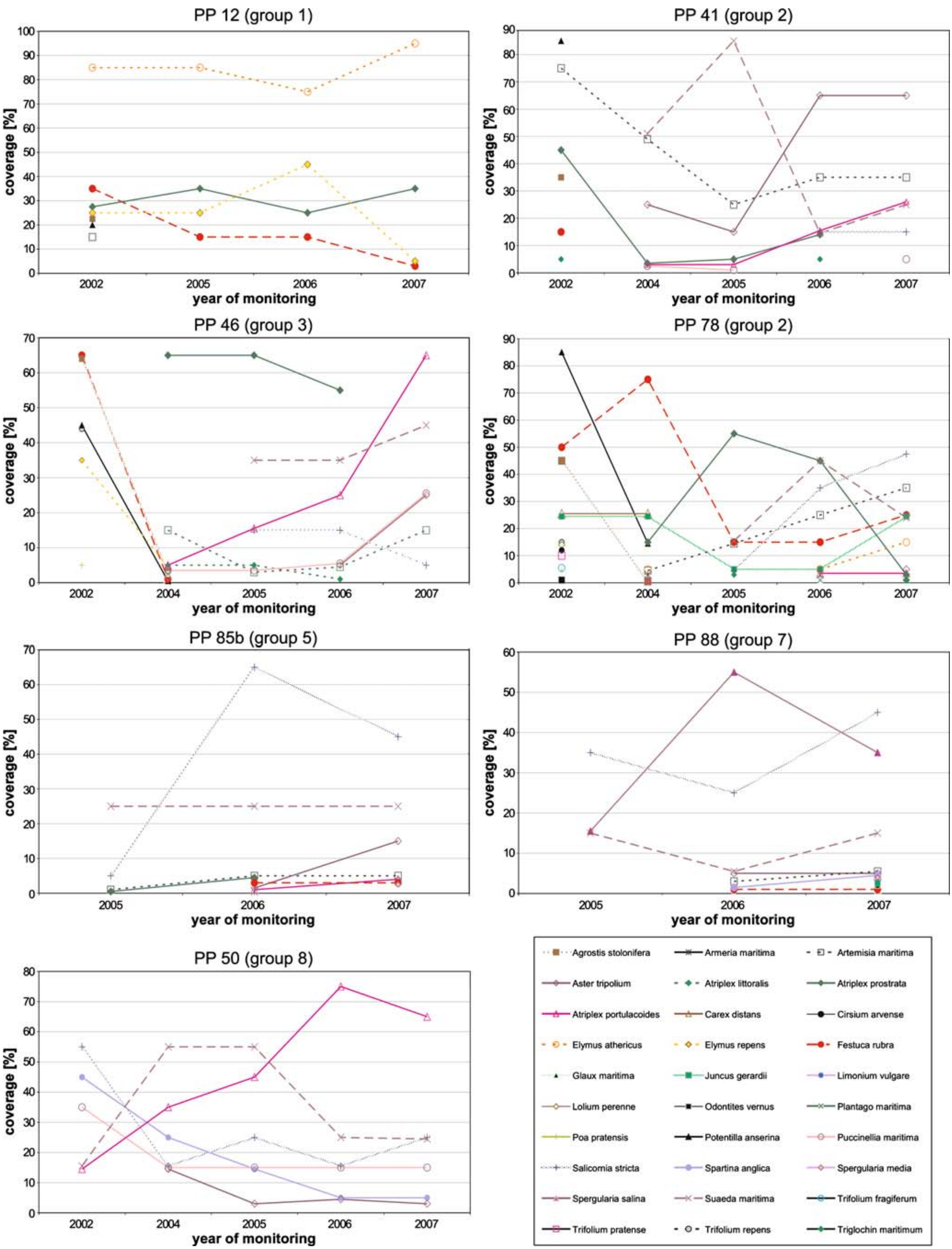

Fig. 18 Vegetation succession of PP 12, 41, 46, 50, 78, 85b and 88 from 2002 to 2007

Table 3 Average number of species for the PP groups from 2002 to 2007. The values from group 1 and 8 in 2004 (bold) have to be carefully interpreted due to monitoring only a small number of PPs belonging to these groups. In 2002 PPs of group 5 and 7 have not been monitored, as well as, the PPs of groups 4, 5 and 7 in 2004

	2002	2004	2005	2006	2007
group 1	8.3	**8.0**	6.2	6.3	5.9
group 2	10.1	9.1	8.3	9.2	9.4
group 3	8.6	7.6	6.1	6.0	5.8
group 4	12.6	-	12.6	14.5	12.6
group 5	-	-	1.3	3.8	5.0
group 6	15.2	13.0	12.7	14.4	10.9
group 7	-	-	2.5	5.5	9.0
group 8	5.2	**6.3**	5.8	5.8	6.4

Sommerpolder—Westteil. Unpubl. Thesis, Universität Hannover, Institut für Geobotanik, 111 p). In 2002 *Juncus gerardii* dominated this PP and in 2007 it was *Salicornia stricta*.

PP 46 was taken as an example for the detailed description of this group (Fig. 18). In 2002 there were only species of the upper Armerion (for example *Festuca rubra, Elymus repens*) and glycophytic species (*Trifolium repens, Potentilla anserina* and *Poa pratensis*) present in this PP. Two years later these species had disappeared or were only represented by a few specimens. *Atriplex prostrata* was dominating this PP in 2004 with coverage of 65%. Species having a lower degree of coverage were among others *Artemisia maritima, Atriplex portulacoides* and *Puccinellia maritima* in PP 46 (Fig. 18). In 2005 the pioneer species *Salicornia stricta* and *Suaeda maritima* colonized PP 46. The glycophytes and the upper Armerion species completely disappeared, whereas *Atriplex prostrata* still dominated this PP. Until 2007 *A. prostrata* disappeared but *Atriplex portulacoides* increased its coverage and became dominant. The only Armerion species in this PP was *Artemisia maritima* with coverage of 15%. *Suaeda maritima, Puccinellia maritima, Aster tripolium* and *Salicornia stricta* were growing in this PP as companions (Fig. 18). This succession from vegetation related to the high marsh over a state of middle marsh vegetation to the low marsh was representative for group 3. During the investigation period the number of species decreased continually from 8.6 in 2002 to 5.8 in 2007. Additionally the composition of species changed dramatically.

Group 4: high marsh; glycophytes (still grazed and embanked)

This group contains PPs located within the so called Großes and Kleines Schlopp (Figs. 1 and 2, Table 1). These areas were separated from the rest of the investigation area by the new dike. Because of its crest height (3.2 m above NN) the PPs of this group were inundated less often than during the time of the former summer dike (crest height 2–2.25 m above NN). A further difference to the other groups is the continuous grazing of this area. The PPs located in the Großes Schlopp (PP 62, 63 and 64 in Fig. 2) were characterized by a decrease of *Juncus gerardii* since 2002 (PP 64 in Fig. 10) and an increase of glycophytic species. A change in succession was recognizable in 2007 after controlled and natural flooding after storm surges in this area. Salt marsh species like *J. gerardii* were able to expand a little but more important was the decrease of fresh grassland species (compare Fig. 17). PP 62b is different than the other PPs within the Großes Schlopp because the top soil was removed in February 2005. This was done to obtain information about species which were able to establish themselves first on blank soil. Since 2005 this PP has been dominated by *Potentilla anserina* (PP 62b in Fig. 16). In the first year of monitoring *Trifolium repens* was also present with 55% coverage but it decreased especially in 2007 when the PP was inundated several times. *Festuca rubra* and *Agrostis stolonifera* increased their coverage from 2002 to 2007. Most of the other species present in this PP were represented by only a few specimens. There was no great difference between PP 62b and the three other sites within the Großes Schlopp (PP 62, 63, 64).

The two PPs located in the Kleines Schlopp (PP 23 and 74) were characterized in 2002 by *Carex distans, Ononis spinosa* and *Juncus gerardii*. Following completion of the new dike salt marsh species decreased and glycophytic species like *Lolium perenne* and *Trifolium repens* expanded. Both species were present in 2002 as companions. In 2007 after the area had been inundated like the Großes Schlopp the glycophytes decreased slightly and the salt marsh species *Juncus gerardii* and *Festuca rubra* were able to claim more coverage (PP 74 in Fig. 10; PP 23 in Fig. 15). The number of species stayed constant at 12.6 from 2002 to 2005. In 2006 it increased up to 14.5 because of the establishment of glycophytes. One year later the average number of species declined again to 12.6 (Table 3).

Group 5: top soil removed; unspecific

In this group PPs are summarized where the top soil (approximately 10 cm) had been removed in February 2005. The PPs were arranged in two “north to south” transects and each of them was placed next to a PP where the topsoil had not been removed (Fig. 2, Table 1). They are located between 1.5 m and 1.8 m above NN. After removing the top soil the species number was zero in this group in spring 2005. As expected it rose continuously in the first years after de-embankment (Table 3). The PPs of the eastern transect (24b, 25b, 26b) were not colonized by vascular plants except some *Suaeda maritima* specimens in

26b. In 2006 the pioneer species *Salicornia stricta* and *Suaeda maritima* were dominating these three PPs. However, in 25b and 26b there were already species of the middle and high marsh present (*Atriplex prostrata* and *Elymus athericus*). In the following year species like *Artemisia maritima, Atriplex portulacoides, Aster tripolium* and *Puccinellia maritima* colonized one or more of the PPs but *Salicornia stricta* and *Suaeda maritima* remained dominant.

There was a similar succession of the vegetation of the western transect (PP 42b, 43b and 85b). In 2005 *Salicornia stricta* and *Suaeda maritima* were the dominating species in all three PPs. In addition in PP 85b *Artemisia maritima* and *Atriplex prostrata* were also present. Until 2007 species like *Atriplex portulacoides, Aster tripolium* or *Puccinellia maritima* inhabited the PPs. In this year PP 85b was already colonized by eight species from all salt marsh zones (Fig. 18).

Group 6: high marsh; unspecific (very heterogeneous group, but constant characteristic species for each PP)

Group 6 is a more heterogeneous group which contains PPs with vegetation of the high marsh (Fig. 2, Table 1). They all stayed quite constant in their composition of species and salt marsh zonation (Fig. 17). This group is composed of PPs located outside the summer polder (52, 53 and 54) as well as PPs embanked in 2002 (18, 30, 36, 37, 77 and 84). They are situated on an altitude level (1.9 m and 2.6 m above NN) similar to group 1. In contrast to group 1 these PPs were not dominated by *Elymus* species. Most of the sites inside the summer polder were grazed until 2002 and PP 30 and 37 are still grazed by horses very restrictively. In PP 30 and 77 *Elymus athericus* was present since 2006 respectively 2007 with a few specimens and in PP 18 both *Elymus* species were present since 2002 but were still not dominant. Otherwise the PPs were characterized by changing coverage of *Juncus gerardii, Festuca rubra, Potentilla anserina* and *Agrostis stolonifera*. Additionally in PP 30 and 84 *Carex distans* and *Ononis spinosa* were an important element of the vegetation.

Outside the summer polder the PPs of group 6 were characterized by completely different types of vegetation. PP 53 was dominated by *Bolboschoenus maritimus* and *Cotula coronopifolia* from 2002 to 2007. Only the composition of the accompanying species changed from year to year. In PP 52 characterizing species (*Juncus gerardii, Glaux maritima, Plantago maritima* and *Odontites vernus*) showed a great constancy from 2002 to 2007 whereas the composition of companions changed.

The PP 54 exhibited a vegetation type similar to the *Centaurio—Saginetum nodosae* (Diemont, Sissingh et Westhoff 1940) from 2002 to 2006. In 2007 the vegetation changed to a *Festuca rubra* dominated type, after a ditch has been dug adjacent to the PP.

The number of species was quite different in this group for each PP, but there was a tendency of a decreasing number of species from 2002 to 2007. A temporary increase was only documented in 2006 (Table 3).

Group 7: unspecific (situated where the former summer dike was located)

Only two PPs (87 and 88) belong to this group. They have to be separated from the other PPs because of their unique position at the location of the former summer dike (Fig. 2, Table 1). In contrast to the PPs of group 5 which also showed no vegetation in February 2005, PP 87 and 88 were covered in August 2005 with vegetation up to 40% (Fig. 18). The dominating species were *Salicornia stricta* and *Suaeda maritima*, but in PP 88 *Spergularia salina* was present in 2005 with coverage of over 10%. In the following 2 years the number of species rose rapidly. Especially in PP 88 12 species were present in 2007. These plants represented all salt marsh zones (Fig. 18). Like group 5 the number of species increased continually from zero in 2004 to nine in 2007.

Group 8: Low marsh and pioneer zone; *Atriplex portulacoides* and unspecific (outside summer polder)

In this group all PPs were selected which were located outside the former summer polder (Fig. 2, Table 1) except the PPs of group 6 (52, 53, 54). The sites were never embanked and are between 1.3 m and 1.8 m above NN. They were characterized by vegetation of the low marsh or the pioneer zone (Fig. 17). A tendency which most of these PPs had in common was the expansion of *Atriplex portulacoides*. There were however in some PPs great differences in coverage (compare Fig. 7). The locations 51, 58, 60 and 72 were dominated by *A. portulacoides* from 2002 to 2007. In PP 50 this species was able to replace *Salicornia stricta* and *Spartina anglica* which were the dominant species in 2002 (Fig. 18). Additionally *A. portulacoides* increased in coverage in PP 57, 61, 71 and 80.

PP 82 was dominated constantly by *Spartina anglica*. In PP 57, 61, 66, 67, 71, 73, 81 and 83 *Spartina anglica, Salicornia stricta* and *Suaeda maritime* were able to compete against other species and had various coverage. Among others *Limonium vulgare* and *Puccinellia maritima* were frequent companions. *P. maritima* reached dominance in PP 68, 70 and 80. These PPs were situated on the highest places in group 8 and contained the greatest number of species. Even middle and high marsh species like *Artemisia maritima* and *Elymus athericus* were able to establish themselves here.

In this group the average number of species rose from 5.2 in 2002 to 6.4 in 2007. The year 2004 is excluded because only four of 17 PPs of this group had been monitored.

Discussion

In this chapter the results already presented separately as key species and functional groups are now combined to draw an overall picture of salt marsh succession after de-embankment on Langeoog Island.

Until 2002 vegetation expanded in the entire area within the Langeooger summer polder composed primarily of high marsh species and even glycophytes. Species distribution was caused by factors like nutrient availability, grazing intensity and soil properties (Barkowski 2003, Vegetationskundliche und paläoökologische Untersuchungen auf dem Langeooger Sommerpolder—Westteil. Unpubl. Thesis, Universität Hannover, Institut für Geobotanik, 111 p; Petersen 2003; Steffens 2003, Vegetationskundliche und paläoökologische Untersuchungen auf dem Langeooger Sommerpolder—Ostteil. Unpubl. thesis, Universität Hannover, Institut für Geobotanik. 122 p) and it was not dependent on the inundation frequency as is the case normally in common salt marshes. After the summer dike was removed the impact of the regular inundations caused an intensive die out of the former vegetation and led to new vegetation succession. Therefore flooding by seawater became the primary cause of species establishment (compare Roozen & Westhoff 1985). Now the zonation of the salt marsh is dependent on salinity. Kolditz et al. (2009) showed this on one transect (PP 60, 42, 85, 62) on Langeoog Island (Fig. 2). In Fig. 19 the salinity for PP 42 is presented as an example for low marsh and in Fig. 20 PP 85 as an example for high marsh. PP 62 situated in the Großes Schlopp showed very low salinity (0‰ to 8‰) and served as an example for the previous embanked situation before 2003. The pH results do not show much spatial variation or great amplitudes (Kolditz et al. 2009) (Figs. 21 and 22). Therefore pH is not considered to have a major influence on vegetation. The die out of the eminently fresh water related species turns out to be a direct effect of the flooding with seawater.

Dependent on the number of inundations glycophytic and high marsh species disappeared in the very low parts of the summer polder. The key species *Potentilla anserina* died out in a large part of the investigation area especially in the areas below Mean High Tide Level, because of increasing salinity after de-embankment. The same processes led to a die out of *Festuca rubra, Agrostis stolonifera* and *Juncus gerardii* in areas close to the former summer dike. The huge amount of biomass resulting from the decay of former vegetation (especially PPs of group 2 and 3) led to an increase of nutrients in the first years after de-embankment.

Principally the release of nitrogen after 2002 all over the former summer polder influenced the composition of species intensely. Nitrogen is the limiting nutrient for salt marsh plants (Adam 2002; Bakker and Piersma 2005; Cartaxana and Catarino 1997; van Wijnen and Bakker 1997; van Wijnen and Bakker 1999) so it primarily influences salt marsh succession. Data of pore water analyses from PP 42 (Fig. 23) documented a peak of TDN in spring 2005 which might be the major result of the de-embankment and additionally an effect of increased winter storm surges in 2004/05. Storm surges usually deliver a lot of biomass which serves as a nitrogen source (compare Leendertse et al. 1997). In spring 2006 TDN was at an extremely lower concentration level. Both results are

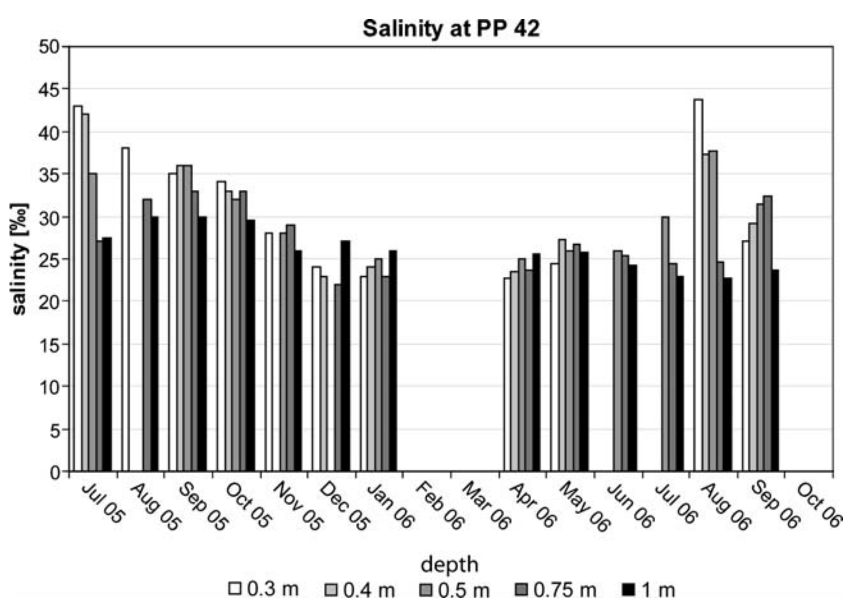

Fig. 19 Salinity at PP 42 from July 2005 to September 2006 at different depths

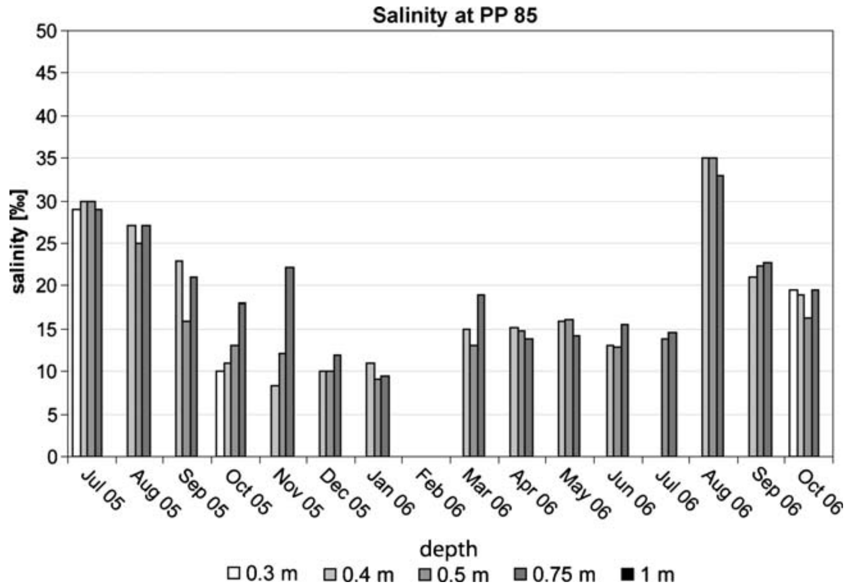

Fig. 20 Salinity at PP 85 from July 2005 to September 2006 at different depths

supported by distribution of more nitrophytic plants in 2005 than in 2006.

The expansion of three nitrophytic key species (*Suaeda maritima, Atriplex prostrata* and *Artemisia maritima*) started in 2004 after de-embankment and increased in 2005. This does not appear to be an adaptation to special salt marsh zones by the species but rather seems to be due to nutrient availability which apparently at this time is much more important as the key distribution factor than elevation (compare Roozen and Westhoff 1985). *S. maritima* had its focus of distribution in the lower and the other two species in the higher parts of the salt marsh. However, specimens of *S. maritima* were found in the high marsh in large numbers too (PP 40 in Fig. 5). Therefore nitrogen gave those three species an advantage in competition (compare Beeftink et al. 1978). Another reason was the high number of seeds these species can produce (Chang et al. 2007) and the easy dispersal by the tides of their seeds (Tessier et al. 2002). Additionally it was important that species were located in the direct surrounding of the summer polder in order to be able to colonize the investigation area this fast (Wolters et al. 2005a, b). Before de-embankment small numbers of specimens of *S. maritima, Artemisia maritima* and *Atriplex prostrata* were already present. These nitrophytic species established especially in breeding colonies of gulls with high nutrient content in the soil (Barkowski 2003, Vegetationskundliche und paläoökologische Untersuchungen auf dem Langeooger

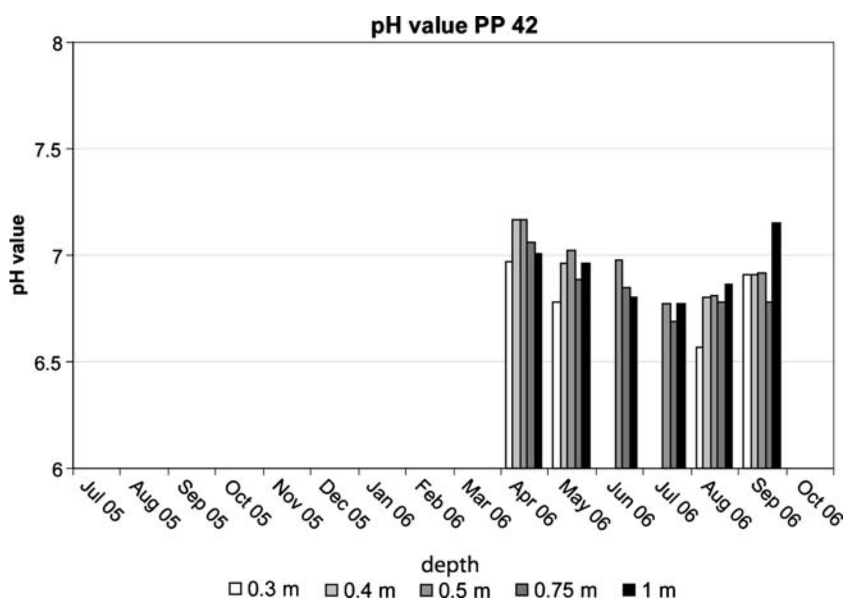

Fig. 21 pH at PP 42 from April 2006 to September 2006 at different depths

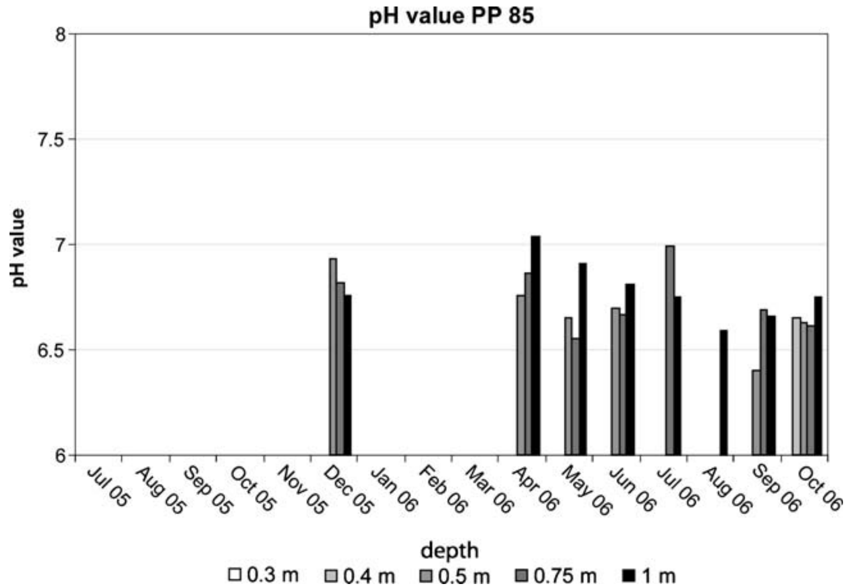

Fig. 22 pH at PP 85 from December 2005 to October 2006 at different depths

Sommerpolder—Westteil. Unpubl. Thesis, Universität Hannover, Institut für Geobotanik, 111 p) (PP 40 in Fig. 5 & PP 34 in Figs. 11 and 12).

In 2006 the huge amount of nitrogen had disappeared (Fig. 23) because of absorption by plants, washing out by pore water and additionally a result of fewer storm surges in the previous winter 2005/2006. The reduction in TDN levels increased the competitiveness and enhanced expansion of other salt marsh plants such as *Salicornia stricta, Atriplex portulacoides* or *Aster tripolium*. One reason for the much slower establishment of the key species *A. portulacoides* was its almost complete absence inside the summer polder until 2002. This species focus in 2002 was in the western part of the investigation area outside the summer polder. A still existing part of the summer dike in the west (Fig. 1) prevented direct transport of seeds to the polder by the tides. This result coincided with the definition of species pools and their influence on salt marsh succession as postulated by Wolters et al. (2005a). In 2007 *A. portulacoides* had inhabited most of the potentially available habitat in the low marsh and increased its coverage significantly. This succession is described by Wolters et al. (2005a) and Beeftink et al. (1978) as well. They predicted *A. portulacoides* as the dominant species in the low marsh and *Elymus athericus* in the high marsh. This was supported by the still existing anthropogenic ditch system, which prevents hydrodynamic activity common in a dendritic creek system. On Langeoog Island on many parts of the salt marsh this situation is given. Taking the low marsh in the west of the investigation area and the

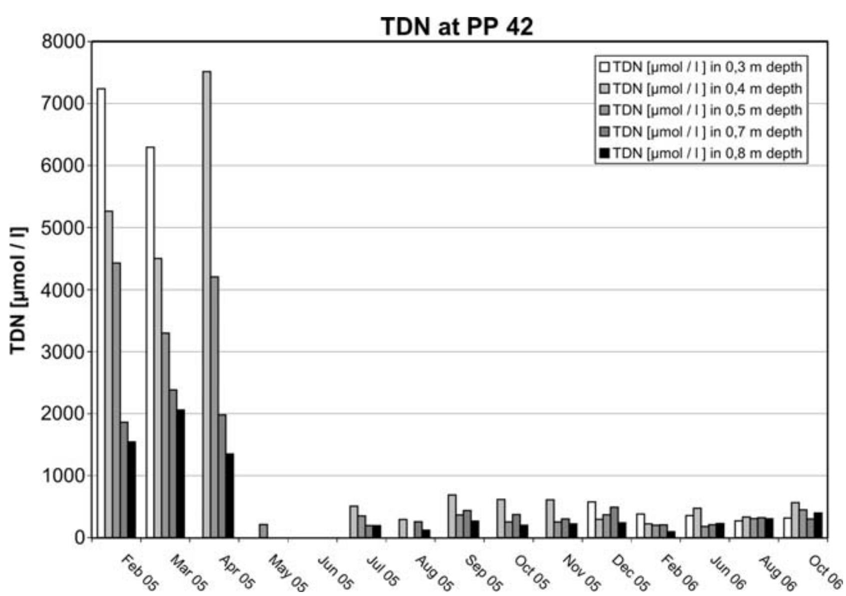

Fig. 23 Total dissolved nitrogen in pore water at PP 42 from February 2005 to October 2006 at different depths

succession from 2002 to 2007 as an example (group 8) for the future (PP 51 in Fig. 7 and PP 50 in Fig. 18) then *Atriplex portulacoides* will become the absolute dominant species in the low marsh. Species such as *Aster tripolium, Puccinellia maritima* and *Suaeda maritima* are only competitive in areas where *Atriplex portulacoides* communities are disturbed (Beeftink et al. 1978). Especially *Puccinellia maritima* needed a longer time to establish itself in the former summer polder. Additionally *A. portulacoides* was supported by the transport of fresh sediment into the investigation area after de-embankment. The accretion allowed a good aeration of the soil which resulted in an increase of *A. portulacoides* (Roozen and Westhoff 1985).

East of the former summer polder where grazing had been abandoned more than 15 years before, especially *Elymus athericus* and partly *E. repens* were able to expand and obtained absolute dominance (PPs of group 1). Other species were mostly replaced and suppressed. The effects of de-embankment were demonstrated by a decrease of *E. repens* in favour of *E. athericus* because *E. athericus* is able to tolerate a higher inundation frequency than *E. repens* (compare Esselink et al. 2002). In addition *E. athericus* reacts positively to increasing nitrogen availability (Leendertse et al. 1997; van Wijnen and Bakker 1997; van Wijnen and Bakker 2000). The highest parts of the eastern salt marsh are under the influence of fresh water coming from adjacent dunes. Under these brackish conditions *Phragmites australis* became competitive and expanded extensively (compare Bakker et al. 2003). On locations with high nitrogen availability *Cirsium arvense* expanded in the east, too. After abandoning grazing in most of the western parts of the former summer polder *Elymus athericus* established itself in more PPs in the west. Especially the PPs of group 2 were suitable. Thus, the situation of an almost complete monoculture in a large part of the summer polder is quite realistic (van Wijnen and Bakker 1999; Wolters et al. 2005a). On many parts of the mainland salt marshes this problem is found, too. To prevent this kind of succession some measures such as controlled grazing (Bakker et al. 2003; Kleyer et al. 2003) or the establishment of a more natural dendritic ditch system would help (Reise 2005). Group 6 was not so much influenced by the drainage system. The PPs in this group are as high above NN as the PPs in group 1 but they are characterised by individual factors like water logging (PP 53) or by a small mosaic of little hollows and hillocks. A greater dynamic is the result of these factors which prevents dominance by any one single species.

Another important reason for preventing monocultures is the role of salt marshes as important nature conservation areas. Especially for invertebrates and breeding birds it is necessary to provide a variety of different habitats to accommodate a larger number of species.

Comparing the investigation area with the two other salt marshes of Langeoog Island (Fig. 1) the differences between natural or anthropogenic influenced salt marshes become apparent.

Both of the potentially natural areas are quite small but show a higher species diversity. For example *Atriplex pedunculata, Carex extensa* and *Oenanthe lachenalii* are found there, yet are missing completely in the investigation area. *Juncus maritimus* covers large areas in the east and the west of Langeoog, but there are still only single specimens inside the former summer polder. A reason for this kind of species distribution could be a lack of hydrodynamics caused by the old anthropogenic persistent drainage system. Additionally the transport of seeds from the east and west to the former summer polder by the tides is more by chance. As Wolters et al. (2005a) and Dausse et al. (2008) mentioned species which belong to the regional species pool will take a long time to establish in new areas. Even *Limonium vulgare*, which is present in the investigation area, could not establish itself on many locations inside the former summer polder. Group 5 and group 7 documented a succession with salt marsh species only present in the direct surrounding after removing the former vegetation and top soil completely. Due to these facts, judging the success of a salt marsh restoration program by monitoring individual species or evaluating the number of present species has to be done carefully. The period of time after de-embankment or the location of the salt marsh with its surrounding areas must be considered as well. If species richness is the most important factor for a potential natural salt marsh, then seeds of key species must be specifically sown within the restoration area to obtain the desired results.

The opposite situation of the de-embanked summer polder is found in the Großes and Kleines Schlopp. These areas have been separated from the rest of the investigation area by a dike higher than the old summer dike, so natural flooding has become nearly impossible. The salt marsh species were replaced progressively by glycophytes (PPs of group 4). Grazing by cattle prevented the dominance of grass species like *Elymus* spec., *Phragmites australis* or *Dactylis glomerata*. Some natural and controlled inundations in winter 2006/2007 showed that salt marsh species could expand again. Therefore with little effort the Großes and Kleines Schlopp could remain salt influenced areas. The grazing activities make clear that species diversity in ditched salt marshes is increased and mono cultures are prevented.

Inundation frequency and its effect on vegetation

Before de-embankment the summer polder was flooded mostly by storm surges in winter. The average inundation rate was approximately 16 times per year. In all functional groups of PPs located in the former summer polder the inundation frequency increased after de-embankment. Group 8 is located outside the summer polder so inundation frequency remained constant. Within group 4 the inundation rate decreased dramatically because the PPs in this group are located behind the new dike. Now there is only one natural inundation per year. This explains expansion of glycophytes in this group.

The inundation frequency of group 1 rose marginally to 21 times a year. This might explain the advantage of *Elymus athericus* against *Elymus repens*. The average frequency of group 6 was nearly the same (25 times per year) but *Elymus athericus* did not establish itself within this group. Therefore other abiotic factors such as those previously mentioned must have a great influence on the extent of expansion of *E. athericus*.

There were 97 inundations per year in group 2. The increasing influence of seawater led to the die out of glycophytes like *Potentilla anserina* and benefited halophytes like *Artemisia maritima, Atriplex prostrata, Atriplex portulacoides* and *Suaeda maritima*. After adapting to the new conditions, *Juncus gerardii* and *Festuca rubra* were able to expand in this group again. The abandonment of grazing also enabled *E. athericus* to colonize PPs within group 2. The vegetation of group 3 changed more intensively than in the other groups. Inundation frequency increased up to 261 times per year. This was comparable to group 8 (276 times per year). After die out of the former vegetation of 2002 the new composition of species of group 3 was also comparable to group 8 (compare PP 46 and 50 in Fig. 18). Reestablishment of natural salt marsh zonation occurs faster if the former vegetation vanished completely and there is a more or less natural salt marsh nearby.

Group 5 and 7 showed intermediate inundation frequencies from 150 to 200 times per year. In both groups the succession started on bare soil. Therefore first pioneer annual species with high seed productivity like *Salicornia stricta* and *Suaeda maritima* were able to spread out (Wolters et al. 2005b) but until 2007 more competitive species of other salt marsh zones also were able to establish (PP 88 in Fig. 18).

Salt marshes as coastal defence

Salt marshes as a part of coastal defence became more important, thus many restoration projects all around the North Sea are being realized (Wolters et al. 2005a). The main tasks of salt marshes are to decrease wave energy and prevent eroding through is vegetation density and structure. Salt marsh vegetation is also responsible for retaining sediment from the water. This increase of salt marsh elevation accompanied by expected sea level rise is likewise an important argument for restoration projects. Wittig et al. (2004) documented that natural vegetation is more effective in coastal protection than anthropogenic influenced vegetation. Therefore it is important to start to consider the establishment of specific species early. It is necessary to break up the old drainage structure and accelerate the development of a dendritic creek system (compare Dausse et al. 2008). An anthropogenic drainage system with parallel ditches which reduces hydrodynamic processes can remain for centuries (Freund & Streif 1999). A dendritic ditch system like in natural salt marshes should be established to promote sedimentation (Reed et al. 1999). Fresh sediment allows good aeration in the soil which is important for many salt marsh species (Roozen & Westhoff 1985). On Langeoog Island natural erosion of the drainage system and creation of meandering creeks only takes place at some sites close to three big tidal channels.

Conclusion

Salt marsh restoration is a long time process. The results of this research show that only a few years after de-embankment the zonation of salt marsh is re-established but it takes mush longer for the species richness and composition of a natural salt marsh to be obtained. De-embankment is indeed an important factor for restoration however it should not be the only human measure made in the restoration process. The construction of a dendritic ditch system could accelerate succession.

Even grazing activities should not be abandoned completely to prevent mono cultures. On Langeoog Island the most successful species after de-embankment were *Atriplex portulacoides* in the low marsh and *Elymus athericus* in the high marsh. Especially in areas with low dynamics they became dominant. Due to a high nutrient availability after decay of the former vegetation temporary communities of nitrophytic plants like *Suaeda maritima, Atriplex prostrata* and *Artemisia maritima* expanded massively. After the decline of nitrogen availability other salt marsh species became more competitive. Species richness decreased after de-embankment and has not reached the level of 2002 until 2007. Monitoring vegetation succession on Langeoog Island should be continued to complete the picture.

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