Management, biodiversity and restoration potential of salt grassland vegetation of the Baltic Sea: Analyses along a complex ecological gradient

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Re: Antonia Wanner

To whom it may concern,

As a native English speaker and experienced proof-reader, I do hereby declare that the dissertation „ Management, biodiversity and restoration potential of salt grasslands of the Baltic Sea: vegetation ecological analyses along a complex ecological gradient” has been written in concise and correct English (UK).

Yours sincerely,

Tom

Tom Maxfield
English Proof-reader, TUHH

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1 Introduction

Salt grasslands are specific ecosystems along the coasts: only plant and animal species adapted to inundation with salt or brackish water survive under these extreme conditions. In the Baltic as a semi-enclosed sea, such inundations are not created by tides, but by changing wind and current conditions, and thus occur irregularly (Tyler 1969a).

Along the Baltic Sea coasts the ecological conditions change from the Kattegat via southern Denmark, the German and Polish coasts up to the Gulf of Finland and the Bothnian Bay. Salinity decreases towards the Northeast, climate becomes colder towards the North and more continental towards the East, resulting in more frequent ice cover and ice scouring in coastal areas (Cramer & Hytteborn 1987, Rheinheimer 1996).

Due to the glacial history, the land surface of the northern Baltic coasts (Finland, Northern Sweden, Estonia, parts of Northern Denmark) is still rising, causing the vegetation zones to move seaward and salt grasslands to grow on young shallow soils (Cramer 1980, Dijkema 1990). In contrast, the land surface in the Southwest (Germany, Poland) is subsiding, thereby enhancing the growth of coastal peatlands (Holz et al. 1996, Succow & Joosten 2001).

It is just this well-developed gradient in salinity and in other ecological conditions that gives the Baltic Sea salt grasslands a special interest (Dijkema 1990). Due to its isolation and low salinity, even an evolutionary significance for plant species is discussed (Russell & Thomas 1988 for aquatic plants, Jonsell & Karlsson 2004 for terrestrial plants). As sections of the gradient described above, vegetation of salt grasslands in four study regions – Northern Denmark, Schleswig-Holstein (Western Germany), Mecklenburg-Vorpommern (Eastern Germany) and Estonia – is investigated in this thesis (see part 1).

Salt grasslands along the Baltic Sea have been used for grazing or hay-making for at least the last 500 years (Schmeisky 1974, Rebassoo 1975, Jeschke 1987, Dijkema 1990). Grazing of domestic animals facilitated the development of extensive areas of salt grasslands from brackish reed beds and woodlands. Without human interference, halophytic communities would be restricted along the Baltic Sea to wave-exposed sites and early successional stages on newly created land (Jeschke 1987). Grazing or hay-making is not only essential for creating salt grasslands, but also for their maintenance. After abandonment succession to brackish reed beds, tall grasses and woodlands takes place at the cost of the halophytic vegetation (Dijkema 1990).

During the last 150 years, the area of salt grasslands has been strongly reduced due to the construction of dikes, drainage practices, intensification of agriculture and the cessation of traditional use (Dierßen et al. 1991, Härdtle & Vestergaard 1996). A further potential threat is the forecast sea level rise. After extensive diking and draining for agricultural use, e.g. in Mecklenburg-Vorpommern only 15% of former 43,400 ha salt grasslands is still affected by flooding today (Holz et al. 1996).

The cessation of traditional use increasingly threatens the remaining salt grasslands in the whole Baltic Sea region (Von Nordheim & Boedecker 1998), e.g. in Denmark (Ellemann et al. 2001) and Germany (Holz et al. 1996) as well as in Estonia (Rannap et al. 2004). The cessation of grazing and mowing is a current topic in the entire Baltic Sea region, whereas diking and drainage has occurred primarily in the south and west (due to different types of coasts and the described land-rise).

Thus, this comparative study along the salinity gradient will focus on the effects of grazing and abandonment on salt grassland vegetation.

As a consequence of the described decline and the mentioned threats, Baltic salt grasslands and their characteristic plant species are classified as threatened: today, 77% of the coastal plant species (species of salt influenced habitats, dunes and dune slacks) is listed as endangered in the Red List of vascular plants of the German Baltic coast (Berg et al. 1996). Also the Red List of marine and coastal biotopes of the Baltic Marine Environment Protection Commission (Helsinki Commission, HELCOM; Von Nordheim & Boedecker 1998) categorises lower and upper salt meadows as well as salt pioneer swards as heavily endangered in the whole Baltic Sea region. Many of the still existing salt grassland areas are today protected as nature reserves or parts of National Parks, or designated as ‘wetlands of international importance’ following the Ramsar Convention on Wetlands (1971), as ‘Sites of Community Importance’ according to the EU-Habitats Directive (European Commission 1992) and/or as ‘Special Protection Areas’ according to the EU-Birds Directive (European Commission 1979). ‘Atlantic Salt Meadows’ (*inter alia* salt grasslands in Denmark and Germany) are included in Annex I of the EU-Habitats Directive as ‘habitats of community importance’, the ‘Boreal Baltic Coastal Meadows’ occurring *inter alia* in Estonia, even as ‘priority habitat type’.

According to the Nature Conservation Laws of the Federal States Schleswig-Holstein (LNatSchG S-H 2007) and Mecklenburg-Vorpommern (LNatG M-V 2002), salt grasslands as well as brackish reed beds are listed as ‘protected habitat types’. This indicates the conflicting targets of nature conservation: If salt grasslands are preserved by grazing, the development of brackish reed beds is prevented. If succession towards brackish reed beds is allowed, salt grasslands are lost.

For reaching each of the different existing nature conservation targets for coastal areas and salt grasslands, a different management is regarded as ‘optimal’. So far, most management schemes are oriented to the habitat value for birds. But even here, different species groups differ in their habitat demands, such as roosting or wintering geese preferring extensive, open areas with a short sward (Bakker et al. 1993, Olff et al. 1997), whereas breeding birds such as redshanks prefer salt grasslands of higher vegetation and structural diversity (Norris et al. 1997). Also brackish reed beds developing after long-term abandonment provide habitat for specific bird species.

Also other animal species groups have specific demands and react differently to grazing and abandonment, such as insect species which are often highly specialised and occur only in salt grasslands (Müller-Motzfeld & Suikat 1996, Hoerschelmann et al. 1996, Meyer & Reinke 1998a,b, Heller et al. 2000, Mathiak & Müller-Motzfeld 2004, Pétillon et al. 2005). Some amphibian species, such as the natterjack toad or green toad need slightly brackish water bodies such as coastal lagoons as spawning grounds and open, short grasslands in direct vicinity (Bast & Dierking 1996, Rannap et al. 2007).

According to David Hume (1740) it is impossible to make claims ‘about what ought to be’ on the basis of statements ‘about what is’ (‘is-ought-problem’ Hume 1740/1978, ‘naturalistic fallacy’, Moore 1904/1970, see Gorke 1996, Umbricht 2003). Ecological research as part of science can only answer the question of ‘what is’, whereas answering the question of ‘what ought to be’, thus of the norms and values, is a subjective decision, which has to be taken on the basis of a community’s norms and values. These should in the ideal case be reflected in normative specifications such as laws and (international) directives and conventions. Such specifications exist in a general form, e.g. with (national) nature conservation laws, Directives of the European Union (Habitats and Birds

Directive) and the (global) Convention on Biological Diversity. However, which aspect of biodiversity, e.g. which species (group(s)), shall primarily be protected in a specific case – maybe at the cost of another species (group) – is difficult to decide.

Scientific knowledge can help to rationally and comprehensibly justify normative decisions in nature conservation and to support the utilised norms (Romahn 2002). In this thesis, the focus is to describe how grazing, abandonment and restoration of Baltic salt grasslands affect ‘botanical nature conservation targets’, such as the conservation of the characteristic salt grassland plant species, their phytodiversity and of rare and endangered plant species. In the discussion, the impact of management on other nature conservation targets will also be addressed.

Salt grasslands are not only important as a habitat for plant and animals, but do also support a number of ecosystem functions related to water balance, sedimentation and erosion processes and biogeochemical cycles. Particulate matter and nutrients can be deposited in salt grasslands by sedimentation and peat formation, and various transformation processes take place in these ecosystems. Thus, salt grasslands and salt marshes can play an important role in the nitrogen-, phosphorous- and silica balance of coastal waters (Mitsch & Gosselink 2000). This is why salt marshes and salt grasslands are meanwhile not only in the focus of nature conservation, but also of water protection. Due to the functional interactions between salt marshes and coastal waters, salt marshes can be interpreted as a part of the coastal and transitional waters according to the Water Framework Directive (WFD). Consequently, they have to be included in the classification of the ‘ecological status’ of coastal waters (see part 3).

To counteract the loss and deterioration of salt grasslands, the maintenance or re-introduction of grazing of Baltic salt grasslands has recently been financially supported by national subsidies (e.g. in Germany: Holz et al. 1996, Sweden: Larsson & Ottvall 2001, Estonia: Roosaluste 2002). At present, EU-funds to support agricultural production and implement agri-environmental policies, which became available also for e.g. Estonia with its accession to the European Union in 2004, play an increasing role. Furthermore, several European restoration projects in the Baltic Sea region support the maintenance and reintroduction of grazing regimes (e.g. Rannap et al. 2004, LIFE-project Rannametsa 2004, LIFE-project Silma 2004, Lotman et al. 2005, LIFE Baltcoast 2006).

If plant species characteristic for salt grasslands have been lost in the course of succession to brackish reed beds, these species can only re-establish if they are either dispersed into the restoration site (e.g. by wind, flooding water or animals) or have persisted in the soil seed bank of the restoration site as a ‘memory’ of the original plant community (Bakker et al. 1996a). Furthermore, conditions during or after restoration must be favourable for germination and establishment. The seed bank has to be ‘activated’, and open soil and light for germination have to be provided. Knowledge on the species composition of the soil seed banks, the relation of target versus non-target species and the longevity of seed persistence is therefore important to predict the success of restoration projects (Strykstra et al. 1998).

Aims of the thesis

This thesis aims to deliver basic knowledge concerning patterns of succession and phytodiversity of grazed and abandoned salt grasslands along the complex ecological gradient along the Baltic Sea coast. It shall also contribute to estimate the potential of grazing as a conservation and restoration measure in salt grasslands for achieving 'botanical nature conservation goals' (conservation of the characteristic salt grassland flora, especially of rare and endangered species, parts 1 and 2).

Furthermore, the impact of abandonment on the soil seed banks of Estonian salt grasslands shall be studied to assess the restoration potential from the soil seed banks (part 2).

The final chapter (part 3) will further highlight the relevance of coastal marshes of the German Baltic Sea for the ecological status of coastal waters, and propose a method for classifying coastal marshes of the German Baltic Sea for the European Water Framework Directive.

While successional processes are investigated in four study regions along the Baltic Sea gradient (part 1), the impact of restorative grazing is exemplarily studied in Estonia (part 2). The integration of coastal marshes into the classification of ecological status of coastal waters is exemplarily addressed for the German Baltic Sea.

The results of this thesis shall contribute to better understand the vegetation ecology of Baltic salt grasslands, optimise their conservation management and appreciate their ecological functions.

In this thesis, the following terms are used:

'Salt grasslands' are grassland ecosystems in the geolittoral of the Baltic Sea region. The presence of halophyte plant species in the vegetation indicates the influence of (irregular) flooding by saline or brackish water. Salt grasslands have developed due to sedimentation, peat formation or land rise, thus soil characteristics can be rather different. Salt grasslands are usually grazed or mown.

'Brackish reed beds' also occur in the geolittoral of the Baltic Sea. They are dominated by *Phragmites australis* (and/or *Bolboschoenus maritimus, Schoenoplectus tabernaemontani*) and influenced by (irregular) flooding of saline or brackish water, which is indicated by some co-occurring halophyte plant species. In most cases, they represent the terminal stage of succession after abandonment of Baltic salt grasslands.

'Salt marshes' are characterised by halophytic vegetation and occur in tidal areas. They have developed due to sedimentation and have marsh soils. Salt marshes can be grazed or ungrazed. Usually, salt marsh vegetation persists also without any use. The term 'salt marshes' is used for tidal areas to be able to distinguish between e.g. the North or Wadden Sea and the Baltic Sea.

'Coastal marshes' comprise salt grasslands and brackish reed beds of the Baltic Sea coast. This generic term is used in the chapter on the classification of ecological status for the European Water Framework Directive.

2 Study regions and sites

Four regions along the salinity gradient were selected: Northern Denmark (Northern Jutland between the Randers Fjord and Mariager Fjord and Fredrikshavn and the island of Læsø in the Kattegat) with a salinity of 22-28 psu (practical salinity unit, equivalent to ‰), the Western part of Germany (Schleswig-Holstein, salinity of 10-18 psu), the Eastern part of Germany (Mecklenburg-Vorpommern east of the Darß sill, salinity of 7-9 psu) and Western Estonia (6-7 psu).

2.1 Climate, vegetation zones

The four study regions differ in climatic conditions. The regions Denmark, Schleswig-Holstein and Mecklenburg-Vorpommern belong to the suboceanic climate zone, while Estonia belongs to the subcontinental climate zone (Troll & Paffen 1964). The general climate characteristics of temperature and precipitation distribution can be seen in the climate diagrams in fig. 2-1. For Estonia, two climate diagrams are shown: Vilsandi is located at the western tip of the Island Saaremaa, and the capital Tallinn is located further east at the North coast. The study region at the Western coast lies in between both climate stations with an intermediate climate between the more oceanic mild climate of Vilsandi and the more continental climate of Tallinn.

The mean annual temperature decreases from Schleswig-Holstein with 8.5 °C (in Kiel) to Denmark further north with 7.5 °C (in Aalborg) and to the more continental region Mecklenburg-Vorpommern with 8.0 °C (in Greifswald), and Estonia – further north and more continental – with mean temperatures between 5.1°C (in Tallinn) and 6.4 °C (in Vilsandi). Annual precipitation decreases from the more oceanic regions Denmark and Schleswig-Holstein with 612 mm/per (Aalborg) and 750 mm/year (Kiel) to the more continental eastern regions of Mecklenburg-Vorpommern with 566 mm/year (Greifswald) and Estonia between 581 mm/year (Vilsandi) and 653 mm/year (Tallinn). According to Buttenschøn (1997), the Danish Kattegat island of Læsø has an annual precipitation of 635 mm/year, with spring and summer drier and sunnier than the average of Denmark.

The number of frost days (with the lowest air temperature below 0 °C) increases from Schleswig-Holstein with 58.6 days/year (Kiel) to Mecklenburg-Vorpommern with 69.4 days/year (Greifswald) and Denmark with 75.7 days/year (Aalborg) to Estonia with 115.7 days/year (Pärnu, data of 1982-2008, except for Estonia with data of 1996-2008, data from: http://www.woeurope.eu). The length of the vegetation period (= months with a mean temperature above 5 °C) decreases from 8 months in Schleswig-Holstein to 7 months in Mecklenburg-Vorpommern and Denmark and 6 months in Estonia.

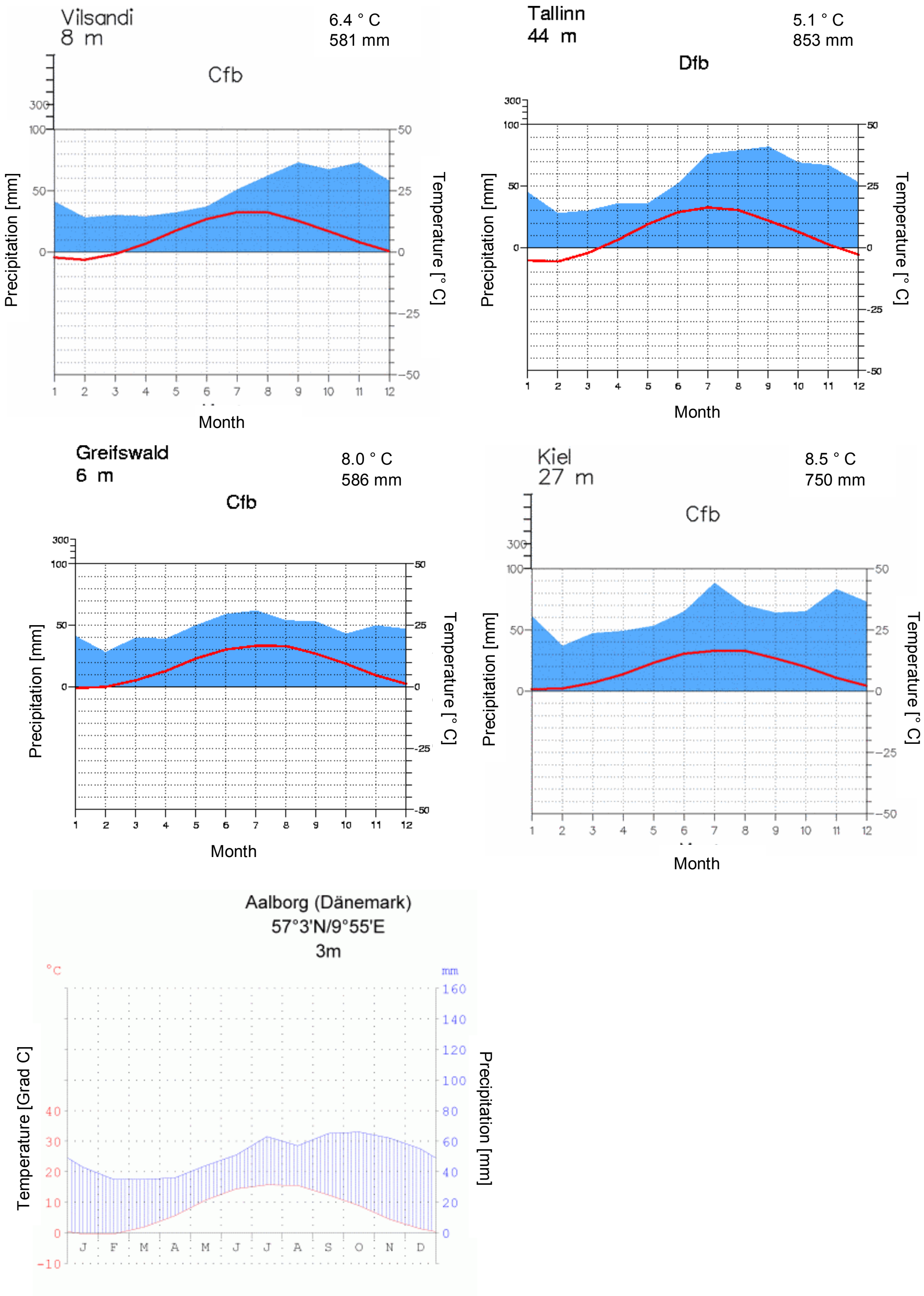


Fig. 2-1: Climate diagrams for Estonia (Vilsandi, Tallinn), Mecklenburg-Vorpommern (Greifswald), Schleswig-Holstein (Kiel) and Northern Denmark (Aalborg). (Source: klimadiagramme.de). The red lines represent mean monthly temperatures (in °C, right y-axis, except for Aalborg: left y-axis), the blue lines and areas represent the mean monthly precipitation sum (in mm, left y-axis, except for Aalborg: right y-axis). In the right upper corner, the mean annual temperature (in °C) and the mean annual precipitation sum (mm) are given (except for Aalborg). In the left corner, the climate station as well as its height above sea level are given (except for Aalborg). The x-axis represents the months from 1 (or J) for January to 12 (or D) for December.

After Dierßen (1996) Denmark, Schleswig-Holstein and Mecklenburg-Vorpommern are parts of the temperate vegetation zone, whereas Estonia is part of the hemiboreal vegetation zone.

2.2 Hydrology

2.2.1 Salinity

Salinity of the surface water of the Baltic Sea decreases from the entrance of the North Sea to the north-eastern part (fig. 2-2), where large amounts of freshwater enter the Baltic by various large and small rivers. The salinity gradient is steepest in the transition area of the Danish waters (between Kattegat, Belts and Sounds, Dijkema 1984). Fluctuations of salinity are highest in the Southern Kattegat, and can vary within 24 hours between 16.0 and 30.1 psu and monthly averages of 19.4 psu in July and 26.8 psu in April (min-max in one year: 15.6 and 32.6 psu at the Western Swedish coast, fire ship Vinga, Gillner 1960). Waters influencing the salt grasslands along the coast may have even more varying salinities, especially where freshwater influences the waters in bays, fjords or near river mouths. The strongest fluctuations occur in winter (Gillner 1960). An exemplary locality at the Swedish west coast varied between 2 and 29 psu during the year, but only between 21 and 29 psu in summer (Gillner 1960).

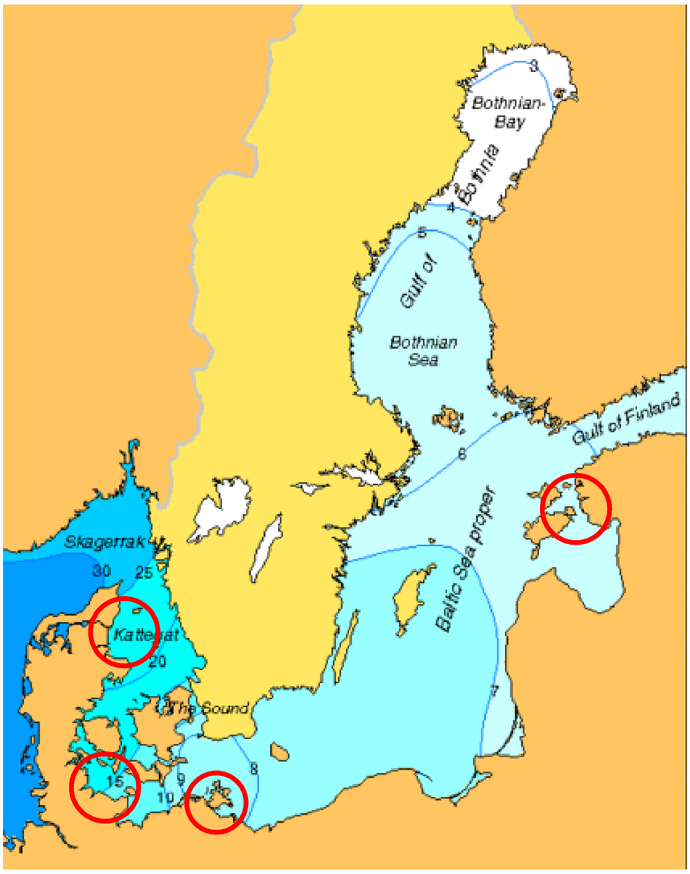


Fig. 2-2: The four study regions along the Baltic Sea salinity gradient. From the North Sea to the Inner Baltic: Northern Denmark, Schleswig-Holstein, Mecklenburg-Vorpommern, Estonia. Source: http://www.internat.naturvardsverket.se/index.php3?main=/documents/nature/nacatego/marine/marine.htm (viewed at 24.9.2004, modified).

In the Northern Danish study region between the Kattegat island Læsø and Randers Fjord, salinity ranges between 20 and 30 psu according to Dijkema (1984) or between 22-28 psu according to Jørgensen (2002). The highest monthly average is between 25 and 30 psu, whilst the lowest monthly average is 5-7 psu lower (Dietrich 1950, Vestergaard 1998). Salinity is slightly lower at a mean of 22 psu in the outer part of Randers Fjord (Udbyhøj, Århus Amt 1999, Nordjyllands Amt & Århus Amt 2004) and between 20-25 psu in the opening of the Mariager Fjord (Als Odde, Nordjyllands Amt & Århus Amt 2002), where some study sites are located. On the island of Læsø, apart from flooding by saline water, also hypersaline groundwater reaching salt concentrations of up to 150-170 psu may play a role for the vegetation (Hansen 1995, Jørgensen 2002).

Salinity in the Schleswig-Holstein study region varies between 10 and 22 psu (Härdtle 1984). The annual maximum is at about 15-18 west of Fehmarn, and between 13 and 15 east of Fehmarn, annual fluctuations are about 4 psu (Dietrich 1950). In coastal lagoons, at which some of the study sites were located, salinity is lower and strongly fluctuating, such as in the Sehlendorfer Binnensee (2.0-16.7 psu, mean of 8.5 psu, Sagert et al. 2008, LANU 2009) and Neustädter Binnenwasser (2.6-9.2 psu, mean of 6.5 psu, LANU 2006).

In the study region in Mecklenburg-Vorpommern, mean salinity ranges from 8-9 psu in the Bodden waters west of Rügen to 7-8 psu in the Greifswalder Bodden (Krisch 1992). Annual fluctuations are much lower here: they are generally below 1 psu east of the Darß sill, and around 0.5 in the Mecklenburg-Vorpommern study region (Dietrich 1950). In the coastal lagoon Neuensiener See, at which three study sites were located, salinity is only slightly lower (5.3-6.4 psu, Grunewald et al. 2001).

In Estonia, salinity of coastal waters can reach up to 6 (Dietrich 1950) or 7 psu (Puurmann & Ratas 1998). Annual fluctuations of coastal waters are low (0.5-1 psu, Dietrich 1950). Local as well as seasonal variations can be larger directly at the coast line, in particular in bays and near river mouths, such as between 0.1 and 7 psu in Matsalu Bay (Lotman 1994). The study sites are all located in the outer part of the bay with comparatively high salinities (see map, fig. 2-5d).

2.2.2 Flooding characteristics

The influence of lunar tides decreases from the entrance of the North Sea (Skagerrak, Kattegat) towards the inner Baltic. The springtide range in Skagen is approx. 30 cm (Vestergaard 1989). The mean tidal range in Kiel (Schleswig-Holstein) is between 14 (Keruss & Sennikovs 1999) and 18 cm at Kiel (FTZ 2009), 2 cm in the Odra Bay (adjacent to the study region Mecklenburg-Vorpommern, Krisch 1978), 1.0 ± 0.5 cm at the Latvian coast and 2.5 ± 0.5 cm in the Gulf of Riga (Keruss & Sennikovs 1999).

These tidal fluctuations are overlaid by aperiodical sea level fluctuations which can cause high water levels up to 1.5 m above mean sea level or even more (Vestergaard 1989), and which depend on wind and weather conditions. These irregular fluctuations are particularly apparent in autumn and winter due to a greater frequency of low-pressure areas (Tyler 1971).

Furthermore, water level changes seasonally: low water prevails in spring and early summer, but water levels rise towards summer (Tyler 1971). The average water levels between spring and summer vary by about 15 cm in the Western Baltic transition area (Gillner 1960) and 23 cm in the central Baltic Sea (Tyler1 1969a). In the Northern Baltic, snow melt also plays a role for local water level fluctuations in spring (Jerling 1999).

Differences in local and regional flooding frequencies in the four study regions, determined as flooding days/year (see 3.2), are displayed in fig. 2-3 and table 2-1. The lowest elevations of 0-25 cm above sea level are more often inundated in the western regions of Denmark and Schleswig-Holstein due to the tidal component. At higher elevations, local patterns may vary. Flooding frequency at elevations higher than 50 cm above sea level is e.g. highest in Pärnu. Pärnu has a much higher sea level amplitude than other locations in Estonia due to its geographical position: the town is located at the inner end of a bay open to southwest, in which the flooding wave – enforced by prevailing westerly winds – becomes much higher than in all other parts of the coastline due to a ‘funnel effect’ (Ivo Saaremäe, Estonian Meteorological & Hydrological Institute, pers. comm., Suursaar & Sooäär 2007).

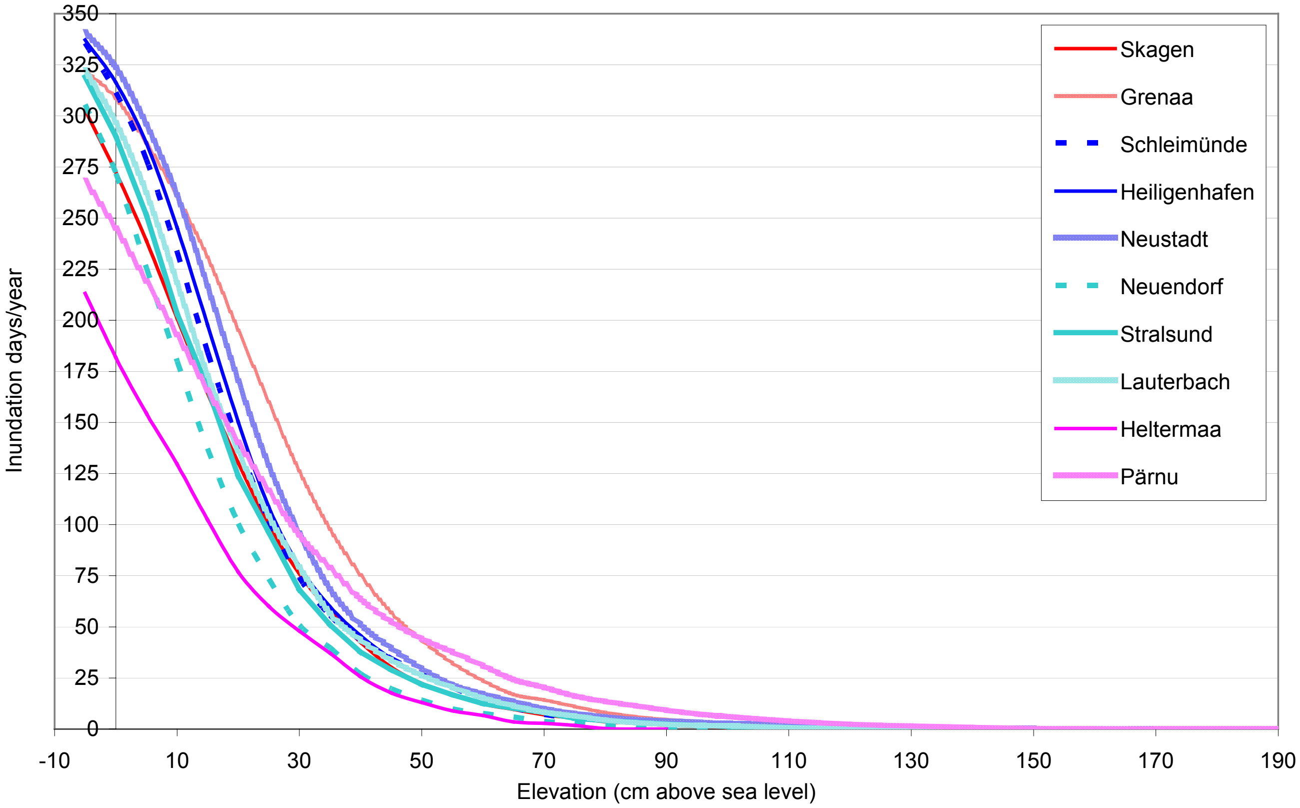


Fig. 2-3: Average number of flooding days/year in the four study regions, in relation to elevation above sea level. Sea level stations from Northwest to southwest, southeast and northeast: Northern Denmark: Skagen, Grenå; Schleswig-Holstein: Schleimünde, Heiligenhafen, Neustadt, Mecklenburg-Vorpommern: Neuendorf (Hiddensee), Stralsund, Lauterbach (southeastern Rügen); Estonia: Heltermaa (Hiiumaa, Pärnu). For the calculation of flooding days/year: see 3.2.

Table 2-1: Average number of flooding days/year at several water level stations in the four study regions, in elevations of -5 to 190 cm above sea level.

	Denmark		Schleswig-Holstein			Mecklenburg-Vorpommern			Estonia	
Elevation (cm asl)	Skagen	Grenå	Schleimünde	Heiligenhafen	Neustadt	Neuendorf	Stralsund	Lauterbach	Heltermaa	Pärnu
-5	302.7	322.5	335.6	337.1	341.0	305.6	319.1	322.4	213.2	268.4
0	272.4	308.5	311.4	316.3	323.7	271.9	290.0	296.7	181.7	245.0
5	238.9	286.8	278.6	286.7	295.9	225.6	251.4	262.4	154.5	219.1
10	200.9	260.7	233.3	245.3	261.4	179.9	203.3	218.4	129.5	193.0
15	164.4	230.9	184.3	197.9	216.7	137.3	166.9	173.0	102.4	165.9
20	130.3	195.1	139.7	150.3	170.4	100.6	123.7	135.9	76.8	140.3
25	99.9	160.0	102.0	108.6	129.0	73.6	96.1	104.1	60.1	116.8
30	76.0	126.2	74.1	79.6	96.0	50.9	68.1	79.3	48.0	94.9
35	57.7	97.7	55.6	59.9	68.4	39.7	51.0	56.6	37.1	79.0
40	42.5	75.4	43.7	45.7	51.1	27.0	37.7	43.7	25.6	63.8
45	30.3	57.0	34.4	34.4	39.7	19.7	29.0	33.7	17.7	52.6
50	22.4	43.5	27.4	26.1	29.6	14.1	21.9	26.3	13.0	44.3
55	16.9	32.3	20.3	21.0	21.7	9.9	16.7	20.4	8.9	37.8
60	12.4	23.7	15.0	15.4	17.3	7.6	12.4	15.3	6.7	31.0
65	9.6	17.0	10.4	11.4	13.6	5.9	10.1	11.4	3.6	24.3
70	7.0	14.3	7.1	7.7	10.0	3.7	8.0	8.3	2.8	20.4
75	5.4	11.1	5.6	6.0	7.6	3.0	5.3	6.4	1.8	16.3
80	3.6	8.0	4.3	4.9	6.0	1.9	4.1	4.4	0.3	13.5
85	2.8	6.0	3.1	3.9	4.7	1.3	3.3	3.1	0.0	11.4
90	1.8	4.6	2.7	3.3	4.0	0.6	2.4	2.3	0.0	9.3
95	1.4	3.7	2.0	2.6	3.4	0.6	1.9	1.9		7.4
100	0.7	3.0	1.7	2.0	2.7	0.4	1.3	1.6		6.1
110	0.5	1.4	0.9	1.4	2.3	0.1	0.6	0.7		4.0
120	0.1	0.7	0.7	1.0	0.9	0.1	0.3	0.4		2.4
130	0.0	0.3	0.6	0.6	0.4	0.0	0.1	0.1		1.5
140	0.0	0.2	0.1	0.1	0.3	0.0	0.1	0.1		0.9
150	0.0	0.0	0.0	0.0	0.3	0.0	0.1	0.1		0.4
160	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1		0.3
170	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0		0.1
180	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.1
190	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.1

2.2.3 Ice cover

Ice cover of the Baltic also differs between the four study regions, and strongly varies from year to year. It depends on climatic conditions, but also on salinity (which decreases the freezing point of water) and locally on wave action and water movement. In a 30-year period, ice was observed in Skagen (Northern Denmark) in 37% of all winters, in which ice occurred for 2-30 days (mean of 15 days). In Schleswig-Holstein (Bülk near Kiel), ice occurred in 33% of all winters for 1-78 days (mean of 31 days). The probability of ice formation and the number of days with ice increases towards the east: in Stralsund (Mecklenburg-Vorpommern), , ice was observed in 80% of all winters for 1-110 days (mean of 54 days). In Mersrags at the Gulf of Riga (Latvia), ice occurred in 83% of all winters for 1-123 days (mean of 67 days). In Hanko harbour (Southern Finland, Archipelago Sea), ice was observed in 97% of all winters for 1-124 days (mean of 71 days, Rheinheimer 1996).

The Estonian study region lies in between Mersrags (in Latvia) and Hanko (in Southern Finland) and is rather sheltered and shallow, thus it is best comparable with Hanko in the Finnish Archipelago Sea.

Ice scouring may have a severe effect on the vegetation succession (Ewanchuk & Bertness 2003), thereby preventing the dominance of reed (Siira 1970, Ericson & Wallentinus 1979, Krisch 1989, Dijkema 1990, Puurmann et al 2002).

2.3 Land rise and soils, development of salt grasslands

2.3.1 Land rise and soil development

During the last ice age, Scandinavia was covered with masses of ice, which pressed the land surface down. As the ice melted, the post-glacial isostatic rebound began. This land rise continues until today, and is strongest at the Northern tip of the Baltic Sea, the Bothnian Bay, where the land surface rises by 9 mm/year. In the northern study regions, the land rise is up to 2.8 mm/year in Estonia (Puurmann et al. 2002), 0.25 mm/year at the Northern Danish Kattegat coast (Fenger et al. 2008) and 5 mm/year at the island of Læsø (Southern part, where the study sites were located, Hansen 1995).

As a counterbalancing movement, the land surface at the Southern Baltic coast is slightly subsiding. The land subsidence rate is 0.5 mm/year at the German-Polish border increasing to up to 2.5 mm/year at the Lübeck and Wismar Bight, where it is strongest (Border Schleswig-Holstein/Mecklenburg-Vorpommern, after Bankwitz 1965, in Janke 1996). Also southeast of Rostock there is a region with subsidence of up to 2 mm/year (Möbus 1989, in Janke 1996).

As a consequence of land rise and land subsidence, soils and soil development in the four study regions strongly vary. While salt grasslands are formed on young, shallow (developing) soils in the land rise regions, land subsidence enhances the growth of coastal peatlands (Holz et al. 1996, Succow & Joosten 2001). Land rise also causes the vegetation zones to move seaward (Cramer 1980, Vestergaard 1998).

2.3.2 Development of salt grasslands

Salt grasslands and salt marshes develop in areas that are sheltered from high wave action, permitting the deposition of fine sediments and the establishment of vegetation. Such areas can be back barrier lagoons and bays, river mouths, estuaries and deltas, natural embayments and sheltered areas behind islands (Dijkema 1984, Allen & Pye 1992, Davidson-Arnott et al. 2002). Salt grasslands may also develop at open coasts where a wide, shallow nearshore dissipates wave energy (Davidson-Arnott et al. 2002).

Conditions for salt grassland formation at sedimentary shores of the Baltic Sea are more or less comparable to the salt marshes around the North Sea (in the study region of Northern Denmark, e.g. Fjords of Jutland, Aalborg Bay and on the island of Læsø, Dijkema 1990). In the (southern) Baltic Sea, primary salt grasslands develop in beach ridge systems or, more rarely, in sheltered bays following accretion of sand or silt on (wind) tidal flats (Jeschke 1987). These primary salt grasslands are usually relatively short-lived successional stages in areas of newly accreting land (Jeschke 1987). For the eastern German coast, primary salt grasslands are described as permanent plant communities only for stony beaches in front of stable cliffs at the Northern coast of Rügen Island, where they form very small-scale ‘beach meadows’ (Jeschke 1987). Other favourable conditions for salt marshes can be found on flat and skerry coasts in combination with land rise (Dijkema 1990).

Due to the lack of tides and the low salinity of the Baltic Sea, brackish reed beds and, under very low salinity conditions, also woody species can – in contrast to the North Sea – establish close to the shore. Only if growth of brackish reed beds or shrubs is prevented by grazing livestock or by mowing, may salt grasslands become more extensive (Jerling 1999).

Before the 13th to 15th century, large areas of the Baltic coasts were dominated by brackish reed beds. The land subsidence in the southwestern part of the Baltic – together with eustatic sea level rise – enhanced the development of coastal peatlands, since the growth of reed peat kept pace with the rising sea level (Holz et al. 1996, Succow & Joosten 2001). Most salt grasslands at the Southern Baltic Sea developed from these brackish reed beds secondarily by grazing, which was proven by the existence of thick layers of peat formed primarily by *Phragmites australis* (Succow & Joosten 2001). On the Graswarder spit in Schleswig-Holstein e.g., a reed peat layer of more than 50 cm depth was found only under beach ridges older than 300 years. After that, grazing was started and therefore, at younger beach ridges, salt grasslands developed directly without the precursory reed bed phase (Perschke 1974, Schmeisky 1974). According to Jeschke (1987), trampling by cattle favoured the formation of salt grassland peat (with root biomass of *Juncus gerardii* as main material for peat formation): Since the soil was compacted and soil aeration reduced, decomposition of organic matter was reduced and peat layers could grow beyond the mean water line. Coastal peatlands are built up by peat layers with intermittent layers of sandy or silty sediments deposited during stronger flood events. Their peat layers are rarely more than 1 m deep (Succow & Joosten 2001).

In the whole Baltic Sea region, salt grasslands have been used as pastures or hay-meadows for at least 500 years (Tyler 1969, Dijkema 1990), which caused the Brackish reed beds to be replaced by salt grassland vegetation (Jerling 1999). Jeschke (1987) dates the first formation of salt grasslands from brackish reed beds earliest to the 13th century.

2.3.3 Zonation

The terminology of the ‘littoral zone’ was originally developed with respect to the ‘classical’ tidal coast with up to several metres of tidal range. In this context, ‘littoral’ is the zone that falls periodically dry due to tidal fluctuations. It is difficult to transfer these terms to the Baltic Sea with only a few centimetres to decimetres of tidal range. However, to describe plant communities in the marine-terrestrial transition zone, it is important to distinguish different zones relative to the sea level (Härdtle 1984). Du Rietz (1950) has developed a topographical classification of the coastal zone for the Baltic Sea (see Gillner 1960), which will be used here. In fig. 2-4, it is compared with that used for the North Sea coast.

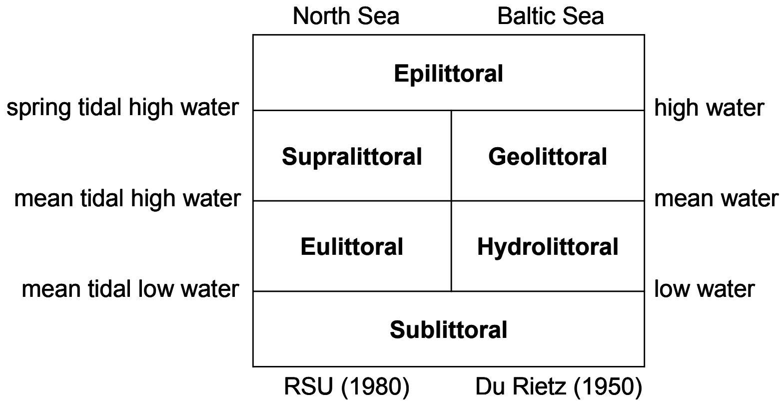


Fig. 2-4: Topographical zonation of the coastal zone of North and Baltic Sea (after Dierßen 1996). RSU (Rat von Sachverständigen für Umweltfragen, 1980): Umweltprobleme der Nordsee. Sondergutachten, Stuttgart, 503 pp. Du Rietz, G.E. (1950): Phytogeographic Excursion to the Maritime Birch Forest Zone and the Maritime Forest Limit in the Outermost Archipelago of Stockholm. 7. Intern. Bot. Congr. Stockholm. Exe. Guide B1. Uppsala.

Salt grasslands at the Baltic Sea are located in the ‘geolittoral’ (zone), which is defined as the zone between mean and high water level. In Estonia, ‘coastal meadows’ are often defined in a broader sense (especially in zoological and geographical terms). Here, we will follow the narrower botanical definition of meadows that are situated at the sea shore and to a lesser or greater extent under the influence of saline seawater (Luhamaa et al. 2001). They are divided into a ‘saline’ zone which is under the influence of sea water during wave action or high tide and a ‘suprasaline’ zone which is reached by marine influence through strong storms (Luhamaa et al. 2001, Lotman & Lepik 2004, Kaljuste 2004). Taking the plant communities of these two zones into account (Palo in Leibak & Lutsar 1996), the saline zone is equivalent to the geolittoral, while the suprasaline zone represents the (lowest part of the) epilittoral.

2.4 Salt grasslands: Distribution, decline and management (history)

The area of salt grasslands at the Baltic Sea coast has been strongly reduced due to the construction of dikes, drainage practices, intensification of agriculture (fertilisation, ploughing and seeding of highly productive grass species, transformation of drained and diked salt grasslands to arable fields) and the cessation of traditional use. These factors are of different relevance in the four study regions. Therefore, the recent decrease of salt grasslands and their current state of management will be presented for each of the four study regions separately.

2.4.1 Estonia

Human influence on Estonian salt grasslands has significantly changed during recent decades. In the 1950s, salt grasslands were overexploited in many places, whilst some others were abandoned. After Estonia regained its independence in 1991, the introduction of a market economy reduced agricultural production dramatically (Ehrlich 1996). The start of re-privatisation further enhanced abandonment of low productive semi-natural grasslands such as salt grasslands. The maintenance of salt grasslands became seriously threatened in the early 1990s (Leibak 1996).

The maximum area of coastal grasslands in Estonia was about 35,000 ha (Sammul et al. 2000, see Luhamaa et al. 2001). A strong decline in managed coastal meadows occurred mainly in the second half of the 20th century: While in the 1960s, approx. 29,000 ha of coastal meadows were still managed, 9500 ha remained in use by 1981, and the area declined further to 5100 ha in 1996 (Leibak & Lutsar 1996). In 2000, only 42% of the coastal meadows of high or moderate conservation value (5018 ha) had been managed in the last 3 years (Estonian Fund for Nature & Royal Dutch Society for Nature Conservation 2001).

2.4.2 Schleswig-Holstein

In Schleswig-Holstein, a thorough overview on the former and present state of Baltic salt grasslands is largely lacking. A rough idea can be derived from the project report by Wanner & Rudolphi (2007): In 2001, a total area of salt grasslands and brackish reed beds of 1,450 ha had been mapped at the Schleswig-Holstein Baltic coast (mapping according to the EU-Habitats Directive, data from LANU SH). 57% of these were comprised by brackish reed beds, 34% by salt grasslands and 9% by other salt influenced habitat types (such as brackish tall forb communities, brackish flood meadows etc.). Although the area of managed salt grasslands could not be determined, these numbers indicate that the majority of the presently salt influenced areas are not managed, since they have already transformed to brackish reed beds. Further areas may succeed to brackish reed beds in the future.

As the ‘potential coastal marsh area’, i.e. the area suitable for salt grassland formation if there were no dikes and drainage restricting salt water influence, the area which is located close to the Baltic shore and <1 m above mean sea level (excluding beaches, dunes and water bodies) was determined. It comprised approx. 16,000 ha. Thus, only 9% of this ‘potential area’ is currently covered by salt grasslands or brackish reed beds.

To get an indication of historic changes, for 14 areas with larger complexes of former or present coastal wetlands, historical maps from 1878/1880 (‘Preußische Landesaufnahme’) were digitised to assess the area of salt grasslands or brackish reed beds at that time. Of the total analysed area of 4,500 ha, 26% was neither influenced by diking nor drainage. 50% was already diked and a further 16% was drained by ditches (Wanner & Rudolphi 2007). This shows that diking and drainage have already had a severe impact on the majority of Baltic salt grassland areas in the 19th century. On the island of Fehmarn, 60% of the salt grasslands was lost since 1825 due to coastal protection measures (Härdtle & Vestergaard 1996).

2.4.3 Mecklenburg-Vorpommern

In Mecklenburg-Vorpommern, about 6,600 ha of salt grasslands exist today which is not diked and therefore still influenced by natural flooding dynamics (Holz et al. 1996, Herrmann & Holz 1997). This is the remains of an area between 30,400 ha (Schönfeld-Bockholt 2005) and 43,400 ha (Holz et al. 1996, Herrmann & Holz 1997) that may have been salt grassland earlier (depending on the way of calculation). About 50% of salt grasslands was already diked before 1945; a further 7,500 ha was diked between 1945 and 1985 (mostly in the 1960s, Bockholt 1985, Schönfeld-Bockholt 2005).

All of these calculations are primarily based on agricultural criteria and include areas up to 1.5 m above sea level (Bockholt 1985, Schönfeld-Bockholt 2005), which are flooded only once every few years. Thus, vegetation will not be characteristic for salt grassland on the whole area. At the southern Baltic coast, halophytic vegetation is delimited to elevations up to 0.7 m above sea level (Krisch 1990) or 1 m above sea level (Paulson & Raskin 1998, Seiberling et al. 2004, Wanner & Rudolphi 2007).

Of the remaining 6,600 ha, approx. 52% was grazed in 1985, partly with very low stocking densities and/or only late in the season (after 1st of August, Bockholt 1985, Holz et al. 1996). The other 48% was abandoned and became dominated by reed, to a large extent already since the 1960s/1970s (Bockholt 1985). About 4,200 ha of this 6,600 ha is characterised by salt water influence, whereas 2,200 ha is influenced by fresh backwater or flooding water of very low salinities (Bockholt 1985). If only coastal peatlands are taken into account, the change in area is even more drastic: of about 21,000 ha (former) coastal peatlands, only 1,800 ha (9%) is characterised by natural flooding dynamics (Succow & Joosten 2001).

To quantify the loss of salt grassland area, Held (2004) followed the approach of a historical reference: along a coastal stretch of 110 km of the mainland coast (located behind the Darß-Zingst peninsula), 98% of the salt grassland was lost between 1696 (2,100 ha) and 2001 (4 ha). 77% of the potential flood area (<1 m above sea level) is diked today, and the majority of the remaining area is covered by reed beds. Also between 1962 and 2001, a decline of salt grassland was observed: the number of mapping units (‘Messtischblattquadranten’) where *Juncus gerardii* was recorded decreased from 24 in 1962 to 17 in 1989 and 3 in 2001.*Blysmus rufus* (today a Red List species) disappeared after 1962, when it had still been found in 10 mapping units. Held (2004) explained the recent decline mainly by loss of salt grassland area due to diking and intensification of agricultural use in the 1960s and 1970s, and mentioned that the contribution of abandonment after 1989 would have to be proven in individual case studies. The youngest decline might also be caused by a time-lag in the loss of salt grassland vegetation after diking.

The particularly high numbers of losses of salt grassland mentioned by Held (2004) are representative for coastal areas without any protection status. The numbers in the balances for all of Mecklenburg-Vorpommern (see above, Holz et al. 1996, Schönfeld-Bockholt 2005) are higher due to the still existing salt grasslands in protected areas (Held 2004).

2.4.4 Northern Denmark

Vestergaard (2002b) estimates that the total area of salt grasslands in all of Denmark (including the North Sea coast) may have been reduced by 33% since the middle of the 19th century due to land reclamation. While the construction of dikes has significantly contributed to the loss of Baltic salt grasslands in southern Denmark (Ellemann et al. 2001, e.g. on Lolland, Härdtle & Vestergaard 1996), it does not play a major role in the Northern Danish land rise area (but is also relevant e.g. around Randers and Mariager fjord, Aarhus Amtskommune 1982).

For the whole of Denmark, Vestergaard (1999) indicates a present area of 8,390 ha of Baltic salt grasslands. In the area at the Kattegat coast and along the Mariager Fjord (largely corresponding to our study region ‘Northern Denmark’), 1,322 ha of salt grasslands are found, of which 62% are regularly managed and 38% are abandoned (Christiansen et al. 1991, Ellemann et al. 2001). Along the Kattegat coast, apart from the low agricultural value, the construction of summer houses along some coastal stretches was a further reason for abandonment of salt grasslands (Christiansen et al. 1991, Ellemann et al. 2001). In Aarhus Amt, where the southern part of the study region is located, salt grasslands have been reduced by nearly 80% between 1870 and 1980 (Aarhus Amtskommune 1982). 18% of the remaining areas is brackish reed beds.

On the Kattegat island of Læsø, more than 1,500 ha of salt grasslands exist (Miljøcenter Aalborg 2007), half of which is grazed. The ungrazed area is dominated by brackish reed beds, and partly by salt grassland vegetation. However, abandonment is at present not seen as a danger from a nature conservation point of view, since for the major part of the salt grasslands, a good combination of short and high vegetation is reached (caused by differential grazing pressure in dry and moist or wet areas, Miljøcenter Aalborg 2007). A part of the ungrazed salt grassland, e.g. fenced-off areas at the outer shores, can also be regarded as ‘primary salt grasslands’, since it has never been grazed since the land rose from the Sea and became vegetated (pers. obs.). Drainage, of which signs are visible on approx. 40% of the area, and coastal protection have no obvious impact on vegetation composition and zonation or dynamics (Miljøcenter Aalborg 2007).

2.5 Overview of all study sites

In each study region, grazed, early and late successional study sites were selected distributed as evenly as possible over the whole study region. In addition, restored sites were selected in Estonia (see 3, methods). Sites of the same management class were often adjacent to each other. Information on the study sites and their location can be found in table 2-2 and in the maps (fig. 2-5a-d).

Table 2-2: Overview of all study sites (see fig. 2-5). The acronyms are also used in the ordination diagram (fig. 4-8). Region: EST: Estonia, MV: Mecklenburg-Vorpommern, SH: Schleswig-Holstein, DK: Northern Denmark, management: grazed, restored, early succ.: early successional, late succ.: late successional (see 3, methods), Type: salt grassland soil type (see 3 and 4.4.5), aband. years: time since abandonment (years). Veg.height: mean canopy height (cm), indicating vegetation structure/grazing intensity, elevation: mean elevation above sea level, elev. range: range of elevation measured on 625 m² (cm) as an indicator for microrelief.

Acronym	Region	Location	Management	Type	aband. years	veg. height	eleva- tion	elev. range
KV-es	EST	Kihnu Vogelturm (bird tower) -West -es	early succ.	shallow	10	37	26	33
Msa-es	EST	Matsalu Saastna	early succ.	shallow	10	31	44	22
TN-es	EST	Silma Tahunina	early succ.	shallow	17	35	30	25
VÄ-es	EST	Värati -es	early succ.	shallow	15	33	30	36
VH-es	EST	Vormsi Hullo	early succ.	shallow	12	50	5	23
VV-es	EST	Vormsi Västurvike	early succ.	shallow	10	34	23	31
KVh-g	EST	Kihnu Vogelturm (bird tower) higher	grazed	shallow	0	41	16	55
KVt-g	EST	Kihnu Vogelturm (bird tower) lower	grazed	shallow	0	10	11	48
MN-g	EST	Matsalu Näärikivid	grazed	shallow	0	8	18	33
MP-g	EST	Matsalu Pogari	grazed	shallow	0	17	42	35
MS-g	EST	Matsalu Salmi	grazed	shallow	0	13	34	19
SL-g	EST	Saulepi	grazed	shallow	0	17	23	34
ST-g	EST	Silma Tahu	grazed	shallow	0	20	31	16
Msaa-ls	EST	Matsalu Saardu	late succ.	shallow	13	82	7	21
TN-ls	EST	Silma Tahunina -ls	late succ.	shallow	17	113	29	26
VÄ-ls	EST	Värati -ls	late succ.	shallow	15	149	23	41
VH-ls	EST	Vormsi Hullo -ls	late succ.	shallow	12	122	38	21
VV-ls	EST	Vormsi Västurvike -ls	late succ.	shallow	10	129	10	27
SN-r	EST	Karavu/Saksanina	restored	shallow	0	28	44	26
SAS-r	EST	Matsalu Sassi	restored	shallow	0	28	14	25
MT-r	EST	Matsalu Teorehe	restored	shallow	0	30	43	9
Vho-r	EST	Vormsi Hosby	restored	shallow	0	45	42	20
VR-r	EST	Vormsi Rumpo	restored	shallow	0	30	28	15
LWo-es	MV	Landower Wedde East-es	early succ.	deep	35	66	40	29
LWw-es	MV	Landower Wedde W-es	early succ.	deep	35	62	48	35
Hid-es	MV	Möwenort Hiddensee	early succ.	shallow	10	37	33	10
NeuSo-es	MV	Neuensiener See - East	early succ.	deep	10	35	40	11
NeuSw-es	MV	Neuensiener See - West	early succ.	deep	10	36	52	8
KWw-g	MV	Kooser Wiesen - West	grazed	deep	0	32	54	9
KWo-g	MV	Kooser Wiesen - East	grazed	deep	0	29	63	11
Lieb-g	MV	Liebes	grazed	deep	0	7	34	30
UmGa-g	MV	Ummanz Gahlitz	grazed	deep	0	6	42	12
UmSch-g	MV	Ummanz Schafort	grazed	deep	0	21	18	25
Baab-ls	MV	Baaber Beek	late succ.	deep	15	98	17	18
LWo-ls	MV	Landower Wedde -East -ls	late succ.	deep	35	116	37	36
LWw-ls	MV	Landower Wedde -West - ls	late succ.	shallow	35	131	30	24
NeuSo-ls	MV	Neuensiener See -ls	late succ.	deep	10	110	42	16
Sund-ls	MV	Sundische Wiese/Pramort -ls	late succ.	shallow	17	95	24	33
Hel-es	NDK	Helberskov/Als Odde -es	early succ.	deep	25	34	39	44
Ly-es	NDK	Lyngholt - southwest - es	early succ.	shallow	15	28	45	18
Ny-es	NDK	Nyland -es	early succ.	shallow	18	31	45	15
Pe-es	NDK	Pentströmsvej	early succ.	shallow	20	30	31	36
Udby-es	NDK	Udbyhoj - es	early succ.	deep	15	38	40	29
Ege-g	NDK	Egense	grazed	deep	0	7	50	30
Ly-g	NDK	Lyngholt	grazed	shallow	0	17	4	23
Ny-g	NDK	Nyland -g	grazed	shallow	0	15	41	16
Rö-g	NDK	Rönnerne	grazed	shallow	0	11	44	39
Söd-g	NDK	Södringholm	grazed	shallow	0	10	65	31
Bob-ls	NDK	Bobakker -ls	late succ.	shallow	15	81	20	22
Hel-ls	NDK	Helberskov/Als Odde - ls	late succ.	deep	25	108	39	70
Ly-ls	NDK	Lyngholt -southwest - ls	late succ.	shallow	15	83	56	18
Udby-ls	NDK	Udbyhoj	late succ.	deep	20	136	47	8
UdSee-ls	NDK	Udbyhoj Seezeichen (maritime mark)	late succ.	deep	20	146	12	22
E-es	SH	Eichholzniederung -es	early succ.	deep	15	42	30	31
G-es	SH	Graswarder -es	early succ.	deep	50	33	34	36
Ram-es	SH	Ramskamp, Fehmarn	early succ.	deep	20	26	50	24
Stm-es	SH	Schleimünde (Toter Mann) - es	early succ.	shallow	30	33	38	15
Seh-es	SH	Sehlendorfer Binnensee - es	early succ.	shallow	20	32	40	33
E-g	SH	Eichholzniederung -g	grazed	deep	0	14	27	27
G-g	SH	Graswarder -g	grazed	deep	0	6	43	50
NB-g	SH	Neustädter Binnenwasser -g	grazed	deep	0	8	71	60
Seh-g	SH	Sehlendorfer Binnensee -g	grazed	deep	0	13	17	31
Lem-g	SH	Lemkenhafen, Fehmarn	grazed	deep	0	23	60	31
Bot-ls	SH	Bottsand -ls	late succ.	deep	44	104	43	16
E-ls	SH	Eichholzniederung -ls	late succ.	deep	15	158	29	19
NB-ls	SH	Neustädter Binnenwasser -ls	late succ.	deep	20	109	60	24
Sh-ls	SH	Schleimünde Hut - ls	late succ.	deep	30	109	22	32
Stm-ls	SH	Schleimünde (Toter Mann) -ls	late succ.	shallow	30	90	44	34

Fig. 2-5a: Study sites in the study region Northern Denmark. Information on the study sites is given in table 2-2.

Fig. 2-5b: Study sites in the study region Schleswig-Holstein. Information on the study sites is given in table 2-2.

Fig. 2-5c: Study sites in the study region Mecklenburg-Vorpommern. Information on the study sites is given in table 2-2.

Fig. 2-5d: Study sites in the study region Mecklenburg-Vorpommern. Information on the study sites is given in table 2-2.

Part 1: Impact of management on Baltic salt grassland vegetation: analyses along a complex ecological gradient

Introduction

Species pool, competition, disturbance and stress – and their interactions

In general, the occurrence of plant species, their coexistence and thus the diversity of plant communities is determined by abiotic stress factors and biotic interactions, but also by the size of the regional species pool. The regional species pool results from large-scale processes such as speciation, migration and dispersal and is defined as ‘the set of species occurring in a certain region that is capable of existing in the target community’ (Zobel 1997, i.e. in a specific salt grassland community). Speciation as well as large- and small-scale migration filters which species enter the regional and local species pool. Apart from dispersal, abiotic factors and biotic interactions act as environmental filters determining which species of the local species pool actually appear in the vegetation of a target community, as part of the actual species pool (Zobel 1997).

According to Grime (1974), there are three major determinants of vegetation: competition, stress and disturbance. Plant species show different adaptations to competition, stress or disturbance (Grime 1974), which Grime used to categorise species according to three (primary) strategies.

Competition is defined by Grime (1979) as ‘the tendency of neighbouring plants to utilise the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space’. Disturbance consists of ‘the mechanisms which limit the plant biomass by causing its partial or total destruction’ (Grime 1979). Disturbances are caused by activities of grazing animals, pathogens, man (by mowing, trampling, ploughing) and by physical factors such as soil erosion (Grime 1974). Grime (1979) defined stress as ‘the external constraints which limit the rate of dry matter production of all or part of the vegetation’, such as shortage or excess of solar energy, water, and mineral nutrients. Competition, disturbance and stress interact and each plant species’ set of traits is a result of a trade-off between them.

The more extreme the abiotic conditions are (abiotic stress is), the less species – highly specialised to these harsh environmental conditions – can occur, thus the smaller the regional species pool and the lower the diversity of local communities. The less extreme the abiotic conditions are, the more species could theoretically occur (the less species are excluded by abiotic stress factors), but the stronger is also the competition between species. Strong competition may again lead to low species numbers, if it is not alleviated by disturbances, which allow more species to coexist. Following the ‘Intermediate Disturbance Hypothesis’ (Connell 1978), ecosystems are particularly species rich if regular disturbances of ‘intermediate’ intensity and frequency prevent competitive exclusion of species and thereby allow long-term coexistence of species with similar habitat requirements, but differing competitive ability.

Grime (1973a) hypothesised that species density (measured as species number per m^2) is highest in the middle of an environmental stress gradient, since towards the lowest stress intensity, many species are excluded by competition, while at the highest stress intensities, only few species are stress-tolerant enough to persist. A similar pattern is related to a gradient of increasing management intensity or disturbance frequency (in accordance with the above-mentioned intermediate-disturbance hypothesis of Connell 1978).

Ecological gradients along the Baltic Sea coast

Natural ecological gradients can be regarded as big, multi-factorial ‘experiments’ to study the interaction of abiotic stress, competition and disturbances. The systematic study of natural variation along a gradient such as that along the Baltic Sea coast as an ‘observational field experiment’ has the disadvantage of being ‘uncontrolled’ and complex, so that not all factors can be clearly distinguished from each other, but at the same time it has the advantage of being realistic (Gurevitch et al. 2006). Repeating the observational experiment in space adds confidence to the conclusions (Gurevitch et al. 2006). Since it was not possible to replicate the Baltic Sea ecological gradient, replicates here could only be placed within homogenous regions, thus representing pseudo-replicates (of the salinity ‘zone’).

In the case of Baltic salt grasslands, several abiotic stress factors, which might affect plant species distribution patterns, change along the described complex ecological gradient: salinity, flooding (connected with anoxic conditions in the soil), desiccation in periods without flooding and precipitation, and nutrient availability and limitation. These stress factors also possibly change the strength of competition. Disturbances occur naturally by flooding, erosion and ice scouring. Furthermore, livestock grazing is an essential mean of disturbance for the maintenance of Baltic salt grasslands. How plant species distribution and diversity change after abandonment, may also change along the complex ecological gradient.

These stress and disturbance factors also interact: disturbed patches of bare soil in salt marshes might become hypersaline because of a lack of plant shading, and salt-tolerant seedlings use these patches as competitive refuges from dominant plants (Bertness et al. 1992). That bare areas in less saline marshes along estuarine gradients (in New England) do not become hypersaline and thus competitive interactions between plants play a more important role in these systems, was demonstrated by Crain et al. (2004). However, this may not be true for the low salinity part of the Baltic salinity gradient: In Estonia, flooding occurs more irregularly (and less often in summer, compared to tidal areas such as the North Sea coast or the Atlantic coast) and drought periods in summer are quite common (due to the subcontinental climate). Thus, in shallow depressions in the upper salt grassland, where saline flood water remains and salt accumulates due to high evaporation rates, hypersaline ‘salty patches’ develop (with salinities of up to 9% total salt content, Puurmann & Ratas 1998). These ‘salty patches’ are typical habitats for salt-tolerant species such as *Salicornia europaea* and *Suaeda maritima* (Puurmann & Ratas 1998) – reversing the zonation known from the North Sea (Dijkema 1990). This example may show that patterns found along salinity gradients e.g. in estuarine marshes of New England may not easily be translated to the Baltic Sea complex ecological gradient.

From the perspective of nature conservation and restoration policy and practice, analyses along the complex ecological gradient of the Baltic are also highly relevant. On one hand, in the list of habitats of community importance (Annex of the Habitats Directive) the European Commission distinguished between two habitat types of salt grasslands: the ‘Atlantic salt meadows’ (Glauco-Puccinellietalia, type 1330) occurring in the South-western Baltic, and the ‘Boreal Baltic coastal meadows’ (type 1630) in the Northern part of the Baltic, which is even a priority habitat type.

On the other hand, in present LIFE-projects such as Baltcoast (2005-2011) the conservation and restoration of salt grasslands (and other coastal habitats) is regarded as a common issue for organisations and authorities in e.g. Denmark, Germany, Sweden, Lithuania and Estonia with the aim to develop common best-practice guidelines. Here, expertise gained from restoration and/or reference areas e.g. in Denmark, Germany or Southern Sweden is transferred to Estonia or the other way around. Whether these two types are similar enough regarding their ecological conditions to apply the same ‘best-practice’ to all Baltic salt grasslands, or whether the maintenance of characteristic vegetation and diversity is steered by different factors and thus needs different approaches, is still an open question.

Succession and its investigation

After the cessation of agricultural use of salt grasslands, secondary progressive succession takes place connected with changes in vegetation structure, species composition and species richness. ‘Progressive succession’ is generally described as a change from communities of low stature, low diversity and simple structure to highly diverse communities of taller plants and of complex structure (Odum 1969, Drury & Nisbet 1973). However, the expansion of highly competitive species connected with a decline in species richness in mid-successional stages has often been observed (Prach & Pyšek 1994) for example in the succession of abandoned grasslands (Schreiber & Schiefer 1985, Rosenthal 1992).

Salt grasslands represent one of the few exceptional ecosystems in temperate regions in which succession does not lead to forest. In the geolittoral of the Baltic Sea, the growth of trees is prevented by salinity and flooding (Ellenberg 1996). Thus, either some type of salt grassland or brackish reed bed represents the terminal stage of succession. Hence, structural complexity of these stages is rather low.

Different mechanisms can be involved in these successional changes, such as differing competitive abilities of plant species and different requirements for germination and establishment. Van Andel et al. (1993) assess the availability of diaspores as a key mechanism for succession. In grassland succession, the accumulation of a litter layer can be important to suppress germination and establishment (Goldberg & Werner 1983, Jensen & Gutekunst 2003) and thereby affect successional processes. Competition for light by dominant species may, together with reduced germination and establishment, lead to a decrease in population size of subordinate species and finally to their local extinction.

Successional processes can be directly studied by observing vegetation changes on permanent plots (Bakker et al. 1996b). For this approach, long-term studies are necessary. Alternatively, spatially adjacent areas of different management (history) so-called ‘chronosequences’ are often compared (indirect analysis of succession). By such a ‘space-for-time substitution’, information about the spatial neighbourhood of successional stages is indirectly transferred to a time series (Pickett 1989).

For the application of space-for-time substitution, it is important to reflect the variability between sites by using a sufficient number of replicates. If this is successful, space-for-time substitution permits general conclusions on the patterns of succession, whereas long-term studies reveal mostly more site-specific information in greater detail (Pickett 1989). A comparison of both methods by Foster & Tillman (2000) shows, that the analysis of chronosequences accurately predicted many of the observed changes in species abundance. That the chronosequence was a poor predictor of changes in species richness, is assigned to climatic fluctuations which were averaged in the chronosequences approach, but strongly affected the time series. Also Bakker et al. (1996b) point out that chronosequences can eliminate ‘climatic noise’. In general, Foster & Tillman (2000) confirm the validity of the space-for-time substitution approach to infer basic patterns of successional change.

To study effects of grazing and abandonment on the vegetation of Baltic salt grasslands, indirect succession studies have been carried out e.g. Schmeisky (1974) and Härdtle (1984) for the German coast, for Denmark by Vestergaard (2002a), for Sweden by Tyler (1969b) and Dupré & Diekmann (2001), for Finland by Kauppi (1967) and Jutila (1997, 1999, 2001) and for Estonia by Puurmann et al. (2002). Direct studies based on permanent plots were carried out e.g. by Vestergaard (1994, mowing) and Buttenschøn (1997) in Denmark, Christiansen (1937), Schmeisky (1974) and Hamann (1998) in Germany and by Kaljuste (2004a) in Estonia.

Due to the focus on general patterns and due to the limited time frame of this thesis, the approach of a ‘space-for-time substitution’ was chosen to investigate the changes of plant species composition, abundances and richness in Baltic salt grasslands during progressive succession from grazed salt grasslands towards brackish reed beds after abandonment.

Biodiversity and spatial scale

The term biological diversity summarises the diversity of living organisms on different hierarchical levels, from habitat diversity or diversity of vegetation types to species diversity and genetic diversity of populations (Hobohm 2000). It comprises on the one hand the number of habitats or species of a specific area or genes of a population, and on the other hand information on the distribution of species (or habitats, genes), such as the evenness (Hobohm 2000). Some diversity indices combine both aspects, such as the Shannon-Weaver-Index (Wilmanns 1998).

Whittaker (1972) defined the term α-diversity as ‘richness of the community in numbers of species’ (species number of a specific area = species density) and β-diversity as the ‘extent of species replacement or biotic change along environmental gradients’. γ-diversity is the ‘richness in species of a range of habitats (a landscape, a geographic area, an island, Whittaker 1972)’, which is a consequent of α-diversity (of the individual community) and β-diversity (the range of differentiation among communities). These definitions indicate that biodiversity is generally a phenomenon dependent on spatial scale (Hobohm 2000).

Succession of Baltic salt grasslands – diversity and spatial scale

It has been described previously that after abandonment of salt grasslands few species become dominant whereas many others decrease or vanish completely (Adam 1990). However, it remains unclear, how quickly these changes occur and whether they always lead to a decrease in species richness. While Bakker et al. (2003a) described that *Atriplex portulacoides* and *Elymus athericus* became dominant during primary and secondary succession in Wadden Sea salt marshes, Kiehl et al. (1996) and Schröder et al. (2002) did not observe any dominant species after more than 10 years of abandonment. For the Baltic Sea coast, many authors reported a quick spread of *Phragmites australis, Elymus repens* or *Bolboschoenus maritimus* within a few years after abandonment, e.g. Härdtle (1984) for Schleswig-Holstein, Matthes & Matthes (1996) for Mecklenburg-Vorpommern, Tyler (1969b) for Sweden, Vestergaard (1998) and Ellemann et al. (2001) for Denmark and Rebassoo (1975) and Puurmann & Ratas (1998) for Estonia. In contrast to most other studies, Jutila (1997, 1999, 2001) found less species in grazed than in abandoned coastal grasslands in Southwest Finland.

The impact of management on species number also depends largely on spatial scale. It has been shown that a coarser mosaic of dominance patches develops after abandonment (Falinska 1991). Consequently, species numbers decrease on small scales, but do not change much or even increase on larger scale (Chaneton & Facelli 1991). This was confirmed by Dupré & Diekmann (2001) for Baltic Sea salt grasslands in Sweden and by Kiehl (1997) for North Sea salt marshes in Schleswig-Holstein, but disproved by Bakker et al. (2003a) for North Sea salt marshes in the Netherlands.

How certain species traits influence the reaction of species on changes in management, has rarely been studied in salt grasslands (but see Jutila 1999, Dupré & Diekmann 2001), but may contribute to a deeper understanding of the mechanisms of successional processes.

Starting from these aspects, the following specific research questions were raised:

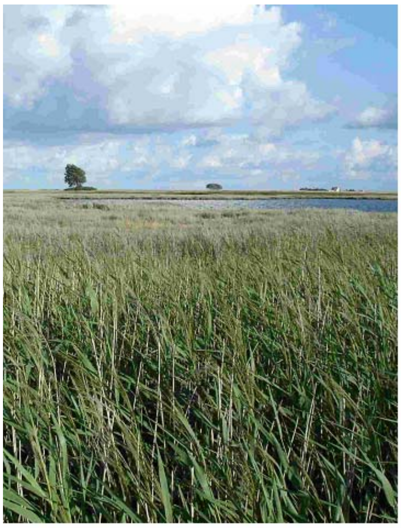
- Does species composition and richness of salt grasslands differ between the four regions (Northern Denmark, Schleswig-Holstein, Mecklenburg-Vorpommern, Estonia) along the Baltic Sea coast?
- How does management (grazing/abandonment) affect plant species composition and richness on different spatial scales?
- Do the effects of management change along the ecological gradients of the Baltic Sea coast?

3 Methods

In all four study regions (see chapter 2), continuously grazed salt grasslands were compared with early and late successional stages of abandoned salt grasslands. ‘Late successional stage’ was determined by the invasion of *Phragmites australis* with a cover of > 25%. For each region and management class, five replicate sites were selected, which should spread across the study region, as far as possible. In Estonia, seven grazed sites were investigated to better reflect the high variability in both environmental conditions as well as grazing intensities.


grazed


early successional


late successional

3.1 Vegetation analysis

Vegetation was examined between July and September in the years 2004 to 2007. At each site (see table 2-2), a representative plot of 25 m x 25 m was selected in the lower salt marsh zone, which is frequently inundated by sea water, indicated by the occurrence of species such as *Juncus gerardii, Agrostis stolonifera, Glaux maritima, Plantago maritima, Triglochin maritimum, Festuca rubra*. In a few cases, a slightly different plot shape was chosen due to geomorphological conditions (e.g. if a ditch or slope made it impossible to select a quadrate with homogenous vegetation). Species composition of vascular plants was recorded on the whole 625 m²-plot, on 5 subplots of 25 m² and 5 subplots of 1 m² (in a nested design, see fig. 3-1). The cover of each species was estimated according to the Braun-Blanquet scale (modified by Reichelt & Wilmanns 1973). Additionally, total vegetation cover was estimated (in %).

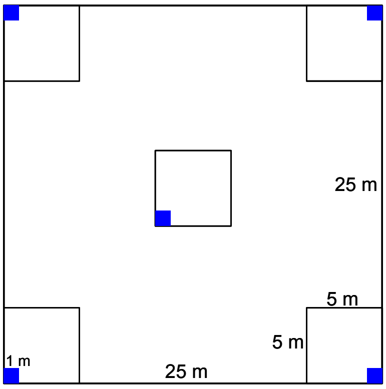


Fig. 3-1: Plot and subplots of the vegetation analysis: five 1 m²-subplots and five 5 m x 5 m subplots are nested in a 25 m x 25 m plot.

The height of the vegetation canopy was measured on each of the 1-m²-subplots. For the measurement a Styrofoam disc (diameter 50 cm, weight 29 g) was dropped. Because of its low weight (0.0148 g/cm²) it stayed on top of the vegetation canopy, while single leaves were pressed down. The distance between the disc and the soil surface was determined as the height of the canopy (see Kiehl et al. 1996). For each 1-m²-subplot, the mean of five measurements was calculated. Thickness of the litter layer was also measured with a measuring stick on the 1-m²-plots, for which the mean of 5 measurements was calculated.

3.2 Characterisation of site conditions

On all subplots and plots the **elevation** relative to the actual sea level (in cm above sea level, ASL) was measured at the four corners and in the centre. For each plot and subplot the mean of 5 measurements was calculated. The elevation was related to mean sea level using sea level data from the nearest official water level station(s). The **elevation range** (difference between highest and lowest of the 5 measuring points per 1 m²-subplot, and of the 45 measuring points per 625 m²-plot) indicated the variability in elevation on a small scale, which can either be caused by natural microtopography or by hillock structures created by grazing and trampling livestock.

The average number of **flooding days/year** was calculated from a measurement series of 7-11 years for the nearest water level station (overview in table 3-1). The reference station was generally the one with the lowest linear distance. In Estonia, differences in frequencies of water level measurements between the stations had to be considered: Water level is measured every hour in Pärnu, while it is only measured twice per day in Heltermaa, whereby short-term fluctuations were partly missed. However, the more precise data of Pärnu could not be used as the reference for all study sites, since Pärnu has a much higher sea level amplitude due to its special geographical position (funnel effect, see 2.2.2).

To correct for the loss in precision due to the lower measurement frequency, the deviation between the flooding frequencies calculated from 24 versus 2 values per day was calculated for Pärnu. This deviation (of 16-34%) was then used to extrapolate the Heltermaa data to a (higher) flooding frequency based on (hypothetical) 24 values per day. Heltermaa was used as a reference for all the sites of the Väinameri region and on Vormsi island, since water level variations in this region (e.g. Haapsalu, Virtsu and Rohuküla) were correlated to those in Heltermaa with $r^2 \geq 0.95$ (Raudsepp et al. 1999). For sites on Kihnu island and at the adjacent mainland area of Kihnu Marine Park, Pärnu was used as a reference, since Raudsepp et al. (1999) demonstrated that the variations on Kihnu were correlated to those in Pärnu with $r^2=0.95$.

In Denmark, the tidal amplitude is higher than in the other three regions, and at the same time, the distances between the investigation sites and the water level stations are larger. Thus, by comparing the water level fluctuations in Skagen, Hals and Grenå, the time lag of the tide between different localities was estimated. The actual sea level was then related to the station data with, for e.g. the island of Læsø, a time lag of 1 hour 20-30 min after Skagen and 1 hour before Hals (or of varying distances between Hals and Grenå for the mainland sites).

Table 3-1: Database for relating plot and subplot elevation of the study sites to mean sea level, and for calculating flooding frequencies: Sources of the data, the water level stations used, frequency of water level measurements, years of the used datasets as well as treatment of data are described.

Region	Data source	Water level station	Frequency of measurements	Years of continuous data	Treatment of data
Estonia	Estonian Meteorological and Hydrological Institute	Pärnu	hourly measurements	1998-2005 (8 years)	
		Heltermaa	6 and 18 h (twice a day)	1995-96, 1998-2005 (10 years)	Extrapolation to hourly measurements (with % deviation of Pärnu)
		Rohuküla, Virtsu	6 and 18 h (twice a day)	July/ August 2004 and 2006	
Mecklenburg-Vorpommern	Water and Shipping Authority Stralsund	Barhöft, Neuendorf, Kloster, Stralsund, Greifswald, Lauterbach, Thiessow	Daily maxima (of measurements every few minutes) 1999-2006, hourly measurements for summers 2004, 2006, 2007	November 1999 – October 2006 (7 years)	
Schleswig-Holstein	Water and Shipping Authority Lübeck	Schleimünde, Kiel Lighthouse, Heiligenhafen, Neustadt	hourly measurements	November 1997 – October 2004 (7 years)	
Denmark	Danish Maritime Safety Administration (Farvandsvæsenet)	Skagen, Grenå	Measurements every 10/15 minutes	1996-2005, 2007 (11 years)	For relation to actual sea level: time lag of the tide between station(s) and measuring location interpolated
	DHI Water & Environment (havmodellen.dk)	Hals	Measurements every 10 minutes	Summers of 2005, 2007	

Data or estimates on the management history (**time since abandonment** in years) were derived from written or oral information by tenants or land owners, local authorities or nature conservation organisations responsible for nature reserves. In many cases, the values are estimates including an error of about ± 2-3 years.

Habitat use by geese, rabbits, hares, deer or moose was recorded on each site by observing geese and rabbit/hare or deer/moose droppings on all plots. Three classes indicating **degrees of 'natural grazing'** were differentiated (Table 3-2), assuming that animals staying on the site also feed there (signs of grazing on the leaves were also observed, but could not be distinguished from cattle grazing if cattle were present). That dropping density is a good estimate of the amount of grazing has been stated by Owen (1971) for geese and by Langbein et al. (1999) for hares (Kuijper & Bakker 2005).

Table 3-2: Scale of measuring the degree of 'natural grazing' by geese, rabbits, hares, deer or moose.

Degree of 'natural grazing'	Code	Droppings on 25 m^2-plots	
No	0	0 plots	anywhere on the 625 m^2-plot
Little	1	less than 3	
Strong	2	at least 3	

Soil characteristics

At all 1-m²-subplots, a pooled soil sample of 3-4 soil cores (diameter 2.5 cm) down to 30 cm was taken. At each core, the depth of the upper 'organic layer' was measured in cm. In the case of an organic, peaty layer of at least 30 cm, the organic layer measurement was set to '30 cm'. Afterwards, the core was divided into two horizons: either the upper organic layer and the sandy or loamy subsoil or, if the whole core consisted of organic, peaty material, in 0-15 and 15-30 cm layers. The samples of each horizon of all five 1-m²-subplots were dried and later pooled per site. Due to financial limitations only the pooled samples from the upper horizon could be analysed for soil chemistry parameters.

The pH-value and the content of phosphate (P_2O_5), potassium (K_2O) and magnesium were measured in the soil samples with the standard methods described in VDLUFA A 5.1.1 (pH measurement in $CaCl_2$), A 6.2.1.2DL and A 6.2.4.2DL (VDLUFA 1991/1997). The content of organic carbon and nitrogen (in %) were determined after dry combustion (elementary analysis, DIN ISO 10694). The content of organic matter was calculated from the carbon content multiplied by the factor 1.72. The C/N-ratio was also calculated as an additional measure of nutrient availability. Salinity in relation to dry soil matter was measured as electric conductivity (g KCl/100g) and recalculated to practical salinity unit (psu, the SI 'unit' which is comparable to the old unit ‰) by multiplication with the factor 10.79. The content of inorganic carbon was determined for all samples with a pH ≥ 6 by gas chromotography, whereby the CO_2 that developed after addition of phosphoric acid and 2 hours of heating to 80°C was measured.

In retrospect, sites were separated in two groups of differing soil types: the 'shallow soil type' with up to 15 cm organic layer, and the 'deep soil type' with an organic layer of more than 15 cm (in most cases a peat horizon of 30 cm or more).

3.3 Data analysis

For statistical analysis, the class values of the modified Braun-Blanquet scale were transformed to a metric scale of % cover class means as follows:

Table 3-3: Transformation of modified Braun-Blanquet-scale (Reichelt & Wilmanns 1973) to a metric scale of percentage cover class means for statistical analyses.

Braun-Blanquet-class	cover (%)	no. of individuals	metric scale (class mean)
r	< 5	1	1
+	< 5	2-5	2
1	< 5	6-50	3
2m	< 5	>50	4
2a	5-15		10
2b	16-25		20
3	26-50		38
4	51-75		63
5	76-100		88

Nomenclature followed Wisskirchen & Haeupler (1998). *Lotus tenuis* and *Lotus corniculatus* could not be safely distinguished in non-flowering state and were thus pooled in the analysis (*Lotus tenuis/corniculatus*). Taxa that were determined only to genus level were counted as a separate ‘species’/taxon e.g. for species richness only if it was clear that they did not belong to a species already present in the respective relevé.

To allow for a comparison of species groups in the vegetation relevés independent of the total species richness and total cover, data was transformed to relative species number (species number of group A/total species number) and relative abundance (cover of species (group) A/cover sum of all species) in each relevé.

3.3.1 Different measures of diversity

The number of species/taxa per (sub)plot is regarded as **species richness** (=species density) on the three investigated spatial scales of 1, 25 and 625 m². The total number of species/taxa per region and/or management class is taken as an indicator for the size of the regional **species pool** of salt grasslands (see above, Zobel 1997). Furthermore, the **evenness** was calculated for the vegetation of 1-, 25- and 625-m²-(sub)plots (Hobohm 2000).

Species-area-curves were calculated separately for each site as linear regressions (y=ax+b) in log-log space (species number and spatial scale log-transformed) with data of all individual relevés on 1, 25 and 625 m².

3.3.2 Species traits

Plant species were categorised according to their **life cycle** (Grime et al. 1988, Schubert & Vent 1994). Because only very few biennial species occurred in the study sites, annuals and biennials were summed to one group as a counterpart to perennial species. Furthermore, species were assigned to **socio-ecological species groups**. These groups each comprise one or several phytosociological classes belonging to one ‘class group’ after Ellenberg et al. (1992). By combining phytosociological classes with few species in the dataset, seven species groups were obtained comprising between four and 44 species (see Table 3-4).

Table 3-4: Socio-ecological classification of all species in the vegetation data set (including restored sites in Estonia for part 2) according to Ellenberg et al. (1992).

		Number of species	
Species group	Phytosociological class(es)	in vegetation of all 4 regions	In seed bank + vegetation in Estonia
Reed bed	Phragmitetea australis	15	17
Fen	Scheuchzerio-Caricetea nigrae, Montio-Cardaminetea, Oxycocco-Sphagnetea	11	12
Salt marsh	Asteretea, Thero-Salicornietea, Saginetea, Cakiletea	26	15
Ruderal	Bidentetea, Artemisietea vulgaris, Isoeto-Nanojuncetea, Plantaginetea, Chenopodietea, Agropyretea	21	23
Flood meadow	Agrostietea stoloniferae	15	11
Grassland	Molinio-Arrhenatheretea, Sedo-Scleranthetea, Festuco-Brometea	44	44
Forest (edge)	Querco-Fagetea, Trifolio-Geranietea, Betulo-Adenostyletea, Alnetea glutinosae	4	6
Indifferent		17	16
Others*		15	15
*: with low frequencies, most determined on genus level		168	159

Ellenberg indicator values were used as integral, long-term indicators for abiotic site conditions. Unweighted mean Ellenberg values were calculated for 1- and 625-m²-relevés as the average indicator value of all species with Ellenberg values given, including those classified as 'indifferent' (but excluding the taxa not listed by Ellenberg et al. 1992, or not determined to species level). Unweighted mean Ellenberg values were preferred to cover-weighted mean Ellenberg values, since otherwise dominant species such as *Phragmites australis* strongly affected the results. Especially in the reed dominated late successional stages of salt grasslands, a moisture value of *Phragmites australis* of 10 does not reflect the situation of these 'terrestrial reed beds' well. According to Ellenberg et al. (1992), qualitative (unweighted) values are in most cases the best choice, and in species rich vegetation stands, weighted and unweighted values differ only very little.

The salt value of Ellenberg et al. (1992) was combined with the salt indicator value of Scherfose (1990) since the latter refers more directly to species from salt and brackish marshes of the North and Baltic Sea coasts. Species like *Phragmites australis* do not indicate pure freshwater conditions at the coast which are implied by an Ellenberg salt value of zero. To combine both salt indicators, the Ellenberg salt values were transformed (see Table 3-5) to a scale from 0 (salt intolerant) to 6 (high salt tolerance) to match the scale of Scherfose (1990). Then, for species whose indicator values in both systems deviated by 1 or more units, priority was given to the classification by Scherfose (1990). Otherwise, the (transformed) Ellenberg salt value was used. The combined indicator value was denoted as 'salt indicator value'.

Table 3-5: Indicator values of salinity tolerance by Ellenberg et al. (1992) and Scherfose (1990). The Ellenberg indicator value was transformed to a scale from 0 to 6, corresponding to the scale by Scherfose (1990). The range of the chloride content of the soil (%), as given by Scherfose (1990), was recalculated to salinity (psu) to enable a comparison with the values measured in this study.

		Ellenberg		Scherfose		
Salinity level	Description (Ellenberg et al. 1992)	indicator value	transformed	indicator value	Chloride content (%)	Salinity (psu)
not salt-tolerant	only on soils without salt	0				
salt-tolerant	mostly on soils poor in salt or free of salt, occasionally on slightly saline soils (0-0.1 % Cl$^-$)	1	1	**I**	0-0.3	0-5.4
oligohaline	often on soils of very low chloride content (0.05-0.3 % Cl$^-$)	2	1	**I**	0-0.3	0-5.4
β-mesohaline	mostly on soils of low chloride content (0.3-0.5 % Cl$^-$)	3	2	**II**	0.3-0.6	5.4-10.8
α/β-mesohaline	mostly on soils of low to moderate chloride content (0.5-0.7 % Cl$^-$)	4	2.5	**II/III**		
α-mesohaline	mostly on soils of moderate chloride content (0.7-0.9 % Cl$^-$)	5	3	**III**	0.6-0.95	10.8-17.2
α-meso-/ polyhaline	on soils of moderate to high chloride content (0.9-1.2 % Cl$^-$)	6	4	**IV**	0.95-1.6	17.2-28.9
polyhaline	on soils of high chloride content (1.2-1.6 % Cl$^-$)	7	4	**IV**	0.95-1.6	17.2-28.9
euhaline	on soils of very high chloride content (> 1.6-2.3 % Cl$^-$)	8	5	**V**	1.6-2.3	28.9-41.6
euhaline to hypersaline	on soils of very high, in dry periods extreme chloride content (> 2.3 % Cl$^-$)	9	6	**VI**	>2.3	> 41.6

Ellenberg indicator values which were developed for Germany can only be transferred with caution to other study regions (as regarded here from Northern Denmark to Estonia). *Inter alia*, some taxa may not be included in the Ellenberg list at all. However, in the 625-m²-relevés of the presented dataset, only between 0% and max. 9.1% of the taxa are not included in the Ellenberg list (the mean varies from 0.7% in Denmark to 3.35% in Estonia), and these are largely specimen determined only to genus level and occurring only with a low cover.

Nevertheless, for some indicator values, the percentage of 'indifferent' species was very high, making interpretation of results difficult. This was the case especially for 1-m²-relevés, where for example, the mean continentality value was determined by only one or two species (or totally lacking in a number of 1-m²-relevés). Thus the continentality value with a mean percentage of indifferent species of 43-63% per region (up to 86% in 625-m²-relevés), the temperature value with an increase from 10-15% of indifferent species in Denmark, Schleswig-Holstein, and Mecklenburg-Vorpommern to 30% in Estonia, and the reaction value with 27-35% of indifferent species were not included into the analyses.

The (unweighted) percentage of flooding indicators ('Überschwemmungszeiger') and water level fluctuation (WLF, 'Wechselfeuchtezeiger') indicator species according to Ellenberg et al. (1992) was also calculated for the 625 m²-relevés.

Using the data base of Frank & Klotz (1990), 95.4% of all species could be classified in **CSR-strategy types after Grime** (1979). The relative cover of each strategy type was calculated for 625-m²-relevés (percentage of all classified species, weighted by species' cover). The components of C-, S- and R-strategies of each 625 m²-relevé were also calculated (weighted by cover). For species with secondary strategies, i.e. strategies that were midway between two (or three) primary strategies, the sum of the scores was set to 1. For example, a species with a CS-strategy, i.e. possessing a strategy between that of a competitor and of a stress-tolerant, had a score of 0.5 as a competitor and 0.5 as a stress-tolerant, and a CSR-strategist had a score of 0.33 in all three components.

Nature conservation perspective

To estimate the relevance of management and abandonment with respect to nature conservation targets, two approaches were followed:

'Characteristic plant species' of the Natura 2000 habitat types '*Salicornia* and other annuals colonising mud and sand (1310)', 'Atlantic Salt Meadows (Glauco-Puccinellietalia maritimae, 1330)' and 'Boreal Baltic Coastal Meadows (BBCM, 1630)' were derived from the Interpretation Manual of European Union habitats (European Commission 2007). In addition, *Angelica palustris*, the only species listed in annex II that occurred in the vegetation dataset, was added to these species. With this combined list of 35 species (see Annex), the relative species number and relative abundance of 'characteristic species' of EU-Habitat types was calculated for the four regions, enabling a consistent comparison.

For the Estonian dataset (vegetation and seed bank) in part 2, only 'characteristic plant species' of the Natura 2000 priority habitat type 'Boreal Baltic Coastal Meadows' (BBCM) were used in the analysis.

Red Lists evaluate rarity and the degree of threat of individual species on a national or regional scale. Thus, as a more qualitative indicator for rare and endangered species, the number of **Red List**

species was also calculated. For the two German regions, the ‘Red List of vascular plants of the German Baltic coast’ (Berg et al. 1996) was selected, because it referred most explicitly to the situation at the Baltic coast. The national Red Lists of Denmark (Stoltze & Pihl 1998) and Estonia (Nature Conservation Committee 1998) included only very few of the species of the presented dataset, which made any statistical analysis impossible.

3.3.3 Statistical analysis

Because in most cases ‘sites’ were significantly different (in a nested ANOVA design with site as a random factor nested in management), but differences between sites were not of primary interest, the mean of the five 1- or 25-m²-subplots was calculated and used in subsequent statistical tests. Individual subplots were only used for multiple regression analyses and for calculating species-area-curves and subplot similarities.

The impact of management and region on the following variables was tested with two-factorial ANOVAs: abiotic site conditions (elevation range, flooding days/year, phosphate and magnesium content of the soil), vegetation structure parameters (vegetation cover, thickness of the litter layer), slope of the species-area-curves, mean Ellenberg values, percentage of flooding indicators and of water level fluctuation indicators, relative species numbers (RS) and relative cover (RC) of annual/biennial species, of different socio-ecological species groups (RS: reed, salt marsh, ruderal and grassland species, RC: salt marsh and flood meadows species), relative cover of S-, SR- and CSR-strategists, and cover or frequency of individual species.

The impact of management, region and spatial scale on species richness and evenness was tested with three-factorial (within-subjects-)ANOVAs with scale as a within-(subjects-)factor and management and region as between-(subjects-)factors.

If necessary, data was log-, root- or arcsin-transformed to meet ANOVA assumptions. If ANOVA assumptions were still not fulfilled after data transformation, Kruskal-Wallis-tests were carried out. First, two separate Kruskal-Wallis-tests for region and management class were carried out. If visual inspection of median (and mean) values in regions and management classes separately (or the interaction plot of the ANOVA) led to the suspicion that the effect might differ in the regions (or management classes), separate Kruskal-Wallis-tests for selected regions/management classes were performed in addition. To minimise the number of additional tests (and maximise the power of the test), regions/management classes with similar patterns were merged. This means that, e.g. all regions where a certain species occurred frequently were merged, while another region, where the respective species was missing, was therefore excluded. In case of two or more separate Kruskal-Wallis-tests on the same variable, the significance levels for the p-value of these tests was adapted with the Bonferroni-correction (p divided by the number of tests). If different numbers of tests were applied for results presented in the same table, the number of analyses is also given in the table.

Two Kruskal-Wallis-tests were used to test the impact of management and region on abiotic site conditions (elevation, depth of organic layer, pH, soil content of potassium, nitrogen, organic matter and inorganic carbon, salinity of soil and inundating water, C/N-ratio), intercept of the species-area-curve, vegetation height, and time since abandonment. Between two and six separate Kruskal-Wallis-tests were applied to test the impact of management and region on the degree of natural grazing, relative species number (RS) and relative cover (RC) of socio-ecological species groups

(RS: fen, flood meadow and forest species, RC: reed, fen, ruderal, grassland and forest species), relative cover of C-, CR-, CS- and R-strategists and cover or frequency of individual species.

Differences between the four regions or three management classes were tested with Post-Hoc-Tests (Tukeys HSD, HSD for unequal n, or multiple comparisons in case of a Kruskal-Wallis-Test).

Similarities and differences in vegetation composition between regions and management classes were visualised by a detrended correspondence analysis (DCA). In this analysis all sites with %-cover data of all 128 taxa present in more than one of the 625 m^2-plots were used. Rare species were down weighted. The ordination plot was overlaid and the first two axes correlated with environmental variables such as vegetation structure (vegetation height, thickness of litter layer, vegetation cover), abiotic site conditions (elevation, elevation range, flooding days/year, depth of organic layer, pH, soil content of phosphate, potassium, magnesium, nitrogen, organic matter, inorganic carbon, salinity of soil, C/N-ratio), natural grazing, time since abandonment, mean Ellenberg values (moisture, salt, light and nitrogen) and percentage of flooding and water level fluctuation indicators. Only environmental variables with correlations of $r^2>0.15$ were shown. Management categories and regions were included as dummy variables and were displayed as centroids (symbols, irrespective of the r^2-values). Since the first axis had a gradient length of >3, both DCA and principal component analysis (PCA) are appropriate (Lepš & Šmilauer 2003, Leyer & Wesche 2007), and the DCA revealed a more balanced distribution of vegetation relevés.

Single linear regression analyses were carried out to investigate the relationship between cover of *Phragmites australis* and species richness of late successional 1-m^2-subplots. Only subplots with at least 20% cover of *Phragmites* were included, since a lower cover of *Phragmites* was not assessed as being characteristic for the ‘late successional’ stage. The relationship between elevation and the logarithm of flooding frequency was also analysed with a single regression analysis, as well as the relationship between salinity related to soil dry matter and salinity related to soil solution (linear and power function).

The impact of various parameters of site conditions and vegetation structure on species richness of 1-m^2-subplots was investigated with multiple linear regression models. These were calculated for the complete dataset (or all regions and management classes) as well as for regions and management classes separately to compare which factors differentially affect local and regional patterns of species richness.

Parameters were selected avoiding to combine parameters with high intercorrelations. However, no fixed upper limit for the r-level was set. Parameters that are ecologically correlated (such as elevation and flooding frequency, cover of *Phragmites australis* and vegetation height, potassium/magnesium and soil salinity) were not combined in multiple regressions. In contrast, other parameters are confounded in certain regions and thus are correlated in the whole dataset, but not in regional subsets (e.g. soil salinity and organic layer/organic matter/pH, organic layer and organic matter). Consequently such parameters representing different ecological properties were nevertheless included in the same model. For all regression models (for the whole data set and subsets) the same 9 or 10 (indirect/direct approach, respectively, see below) variables were included in the stepwise forward selection procedure.

Two alternative approaches for the multiple regressions were pursued: the first included vegetation structure parameters, elevation characteristics and some soil chemical parameters (organic layer, pH, soil salinity, organic matter, P). These soil parameters were directly measured, but – except for organic layer – only for one pooled sample per site. Thus, they did not reflect small-scale variations within the 625-m²-plots. For the second approach, these measured soil parameters were replaced by the mean Ellenberg values for nitrogen, salt, moisture and light. These indirect indicators for site conditions have two advantages: firstly, they integrate over longer time periods in contrast to the measured values that may strongly vary such as e.g. the soil salinity depending on flooding, rainfall and temperature in the time before measuring; and secondly, they reflect small-scale variations within the investigation sites.

Because the two 'salt grassland soil types' which were designated in hindsight did not occur in all regions and management classes with the same frequency, the dataset had to be reduced for statistical comparison between the two types. To still allow for checking interactions between the factors type, region, management class and scale, 4-factorial ANOVAs were carried out, but Estonian sites (since they all belonged to the 'shallow soil type') and grazed sites were excluded (since grazed sites in Schleswig-Holstein and Mecklenburg-Vorpommern all belonged to the 'deep soil type'). 4-factorial ANOVAs with scale as within-factor were carried out to investigate the impact of region, type, management and scale on species richness and evenness of the vegetation. The slope and intercept of the species area curves of the two soil types in Denmark, Schleswig-Holstein and Mecklenburg-Vorpommern were compared with two-factorial ANOVAs.

To check whether the separation of the two soil types is justified, correlation analyses were carried out on the relationships between depth of organic layer and site conditions such as vegetation structure (vegetation cover, vegetation height, thickness of litter layer), elevation range, elevation, soil parameters (pH, soil content of phosphate, potassium, magnesium, nitrogen, organic matter, inorganic carbon, salinity of soil and inundating water, C/N-ratio) and mean indicator values (moisture, salinity, nitrogen) were carried out, as well as between species richness and the same site conditions.

Statistics were performed with the software package Statistica 8.1 (StatSoft 2007), except for the DCA which was performed with Pc-Ord version 4 (MjM software design 2002). Similarity indices and evenness were calculated with PAST (Hammer et al. 2001).

Although non-parametric tests were applied in many cases, the mean (and not the median) is generally displayed in tables and figures to allow for an easier comparison of the results. Untransformed values are displayed in all figures and tables, irrespective of the statistical test. In figures and tables, the following abbreviations are used for the regions and management classes: Estonia: EST, Schleswig-Holstein: SH, Mecklenburg-Vorpommern: MV, Northern Denmark: DK, grazed: G, early successional: ES or early succ., late successional: LS or late succ.

4 Results

4.1 Abiotic site conditions

The investigation sites in the four regions differed in various abiotic characteristics (see table 4-1): Estonian sites were located at significantly lower elevations than sites in Schleswig-Holstein and Northern Denmark, while sites in Mecklenburg-Vorpommern were at intermediate elevations (see also fig. 4-1). The logarithm of flooding frequency was significantly correlated to the elevation with $r^2=0.91$. However, the number of flooding days per year was not significantly different between the regions.

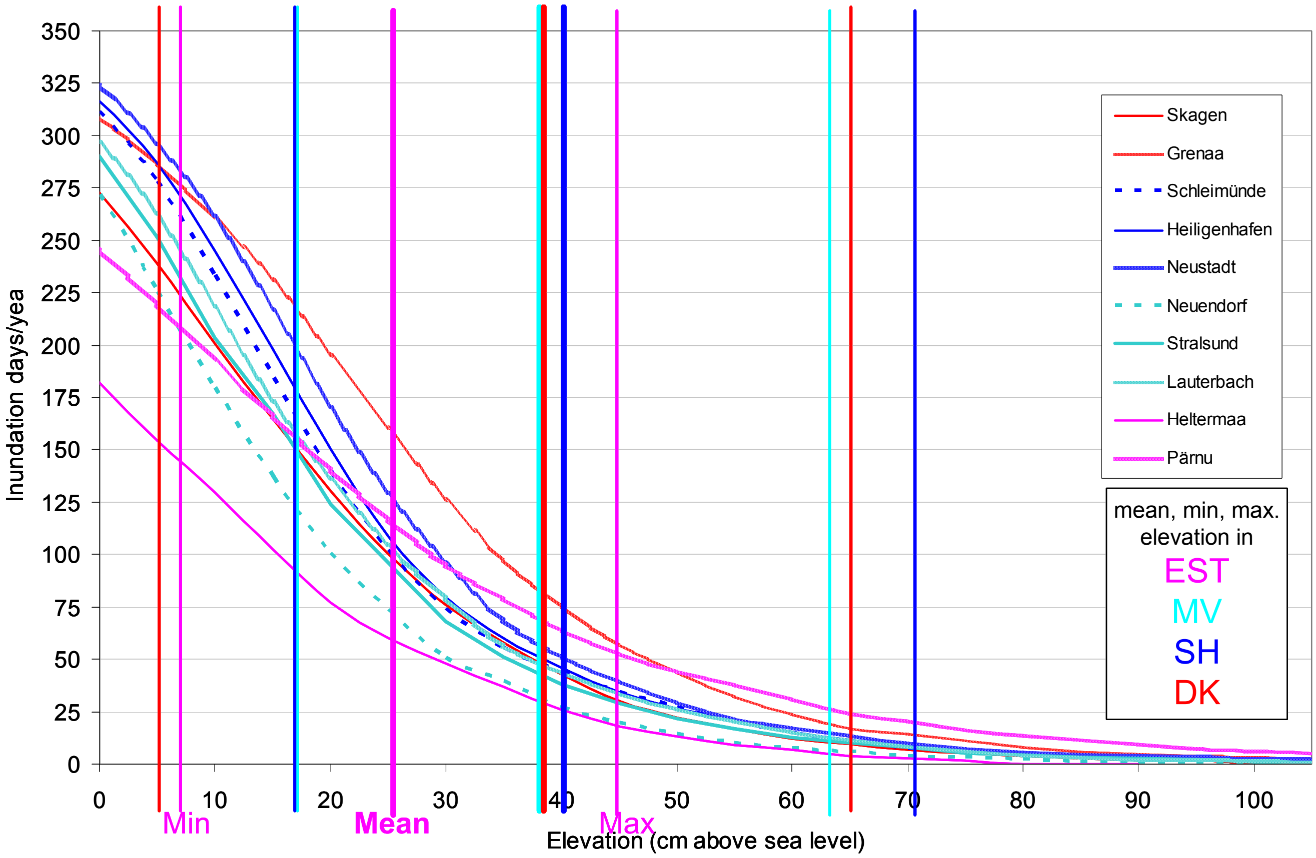


Fig. 4-1: Mean number of flooding days/year in Denmark (Skagen, Grenå), Schleswig-Holstein (Schleimünde, Heiligenhafen, Neustadt), Mecklenburg-Vorpommern (Neuendorf, Stralsund, Lauterbach) and Estonia (Heltermaa, Pärnu). The vertical lines indicate mean (bold line), minimum and maximum (slim line) elevation of 625 m²-plots in the four regions (marked with colours, see legend).

Soil salinity was significantly lower in Estonia than in the other three regions. Potassium (K) content was significantly higher in Denmark than in Estonia, while Mecklenburg-Vorpommern and Schleswig-Holstein were intermediate. The organic layer in Mecklenburg-Vorpommern (26.2 cm) was significantly thicker than that in Estonia (9.6 cm) and Northern Denmark (15 cm), while Schleswig-Holstein (20.3 cm) had intermediate values. Soils in Mecklenburg-Vorpommern contained more organic matter (31.5%) than in Estonia (15.8%) and Denmark (17%), Schleswig-Holstein was intermediate with 22.3%. The same relations were observed for total nitrogen content, whereas the C/N-ratio did not differ. Phosphate content was lower in Estonia and Mecklenburg-Vorpommern than in Denmark, and intermediate in Schleswig-Holstein.

Values for pH were significantly lower in Mecklenburg-Vorpommern than in all other regions and higher in Estonia (6.3) than in Mecklenburg-Vorpommern and Denmark, while Schleswig-Holstein was intermediate between Estonia and Denmark. The content of inorganic carbon was higher in Estonia than in Mecklenburg-Vorpommern and Denmark, while Schleswig-Holstein was intermediate.

Table 4-1: Differences of abiotic characteristics (elevation, soil parameters) between regions and/or management classes. Results of 2-factorial ANOVAs (F, p) or 2 separate Kruskal-Wallis-Tests (H, p). *: $p<0.05$, **:$p<0.01$, ***: $p<0.001$. In cases where 2 separate Kruskal-Wallis-Tests were carried out, The significance level of the p-values is Bonferroni-corrected: *:$p<0.025$, **: $p<0.005$, ***: $p<0.0005$. A, b, c: significant differences according to Post-Hoc-Tests (HSD for unequal N/multiple comparisons test). Last 4 columns: means of all regions. Soil parameters: one bulk sample per 625 m²-plot. Elevation, elevation range: mean of all measurements per 625 m²-plot. trans: data-transformation (log).

	Region				Post-Hoc-test				Management			Interaction		Mean			
parameter	F	H	p	trans.	EST	MV	SH	DK	F	H	p	F	p	EST	MV	SH	DK
Elevation (cm a. sl.)		11.5	*		a	ab	b	b		2.24	0.33			25.5	38.4	40.4	38.6
Elevation range	2.33		0.09						0.61		0.55	0.86	0.53	30.8	20.5	30.9	28.1
Flooding days/year	0.94		0.43	log					1.19		0.31	0.34	0.91	72.4	51.3	59.7	65.1
Organic layer (cm)		29.45	***		a	b	ab	a		0.17	0.92			9.6	26.2	23.6	15.0
pH		32.8	***		a	b	ac	c		0.52	0.77			6.25	5.14	5.97	5.67
P (mg P_2O_5/100g)	5.47		**	log	a	a	ab	b	0.21		0.81	1.48	0.20	5.65	5.27	8.13	9.73
K (mg K_2O /100g)		9.5	*		a	ab	ab	b		2.98	0.23			37.5	49.1	72.2	71.9
Mg (mg/100g)	0.14		0.94	log					2.90		0.06	0.28	0.94	226	170	203	195
Soil salinity (psu)*		20.3	***		a	b	b	b		0.52	0.77			9.6	33.6	39.4	28.3
Organic matter (%)		19.3	***		a	b	ab	a		1.75	0.42			15.8	31.5	22.3	17.0
Total N (%)		19.4	***		a	b	ab	a		1.18	0.55			0.70	1.34	1.03	0.75
C/N		5.49	0.14							2.90	0.23			13.2	13.5	12.6	12.9
C inorganic (%)		23.7	***		a	b	ab	b		0.45	0.80			0.65	0.00	0.03	0.03

* The given soil salinity values are related to soil dry matter, salinity values related to soil solution are much lower (approx. 30% of these) and significantly correlated (see 5.1).

4.2 Management history, ‚natural' grazing

The length of the abandonment period did not significantly differ between 'early' and 'late' successional sites (H=0.40, p=0.53), but between regions (H=12.29, $p<0.025$): Salt grassland sites in Schleswig-Holstein were abandoned for a significantly longer period (mean of 27 years) than sites in Estonia (mean of 13 years). Sites in Mecklenburg-Vorpommern and Denmark were abandoned for intermediate periods of 21 (Mecklenburg-Vorpommern) and 19 (Denmark) years, respectively (table 4-2).

Table 4-2: Period of abandonment (in years) of ‚early' (ES) and ‚late' successional (LS) sites in the four regions. Mean, minimum and maximum are given. Results of two separate Kruskal-Wallis-Tests (H, p). The significance level of the p-values is Bonferroni-corrected: *:$p<0.025$, **: $p<0.005$, ***:$p<0.0005$. A, b: significant differences according to Post-Hoc-Test (multiple comparisons test).

		Management				Region					
		H	p	ES	LS	H	p	EST	MV	SH	DK
	Mean	0.40	0.53	20	21	12.29	*	13	21	27	19
	Min-Max			(10-50)	(10-44)			(10-17)	(10-35)	(15-50)	(15-25)
								a	ab	b	ab
early succ.	Mean							12	20	27	19
	Min-Max							(10-17)	(10-35)	(15-50)	(15-25)
late succ.	Mean							13	22	28	19
	Min-Max							(10-17)	(10-35)	(15-44)	(15-25)

The degree of 'natural' grazing did not differ significantly between the four regions (see table 4-3), although natural grazing of grazed sites was slightly lower in Denmark. Grazed sites showed a significantly higher degree of 'natural' grazing by geese, rabbits, hares, deer or moose than early and late successional sites, in the latter no habitat use by geese, rabbits etc. was detected at all. The degree of 'natural' grazing of early successional sites differed between the regions: In Mecklenburg-Vorpommern, early successional sites were not used as habitat at all, while the habitat use in Denmark was as intensive as that of grazed sites. In Estonia and Schleswig-Holstein, where habitat use of grazed sites was most intensive, the habitat use of early successional sites was intermediate.

Table 4-3: Degree of 'natural' grazing by geese, rabbits, hares, deer or moose on a scale from 0 (no) to 2 (strong, see 3.2). Mean, minimum and maximum are given. Results of six separate Kruskal-Wallis-Tests (H, p). P-values are Bonferroni-corrected: *:p<0.0083, **: p<0.0017, ***:p<0.00017. A, b: significant differences according to Post-Hoc-Test (multiple comparisons test). (*): P-values just above the Bonferroni-corrected significance level are interpreted as trends.

		Management					Region					
Region		H	p	G	ES	LS	H	p	EST	MV	SH	DK
all	Mean	33.34	***	1.5	0.5	0	2.25	0.52	0.8	0.5	0.9	0.4
	Min-Max			(0-2)	(0-2)	0			(0-2)	(0-2)	(0-2)	(0-1)
				a	b	b						
EST	Mean	9.56	0.0084(*)	1.7	0.4	0						
				(a	ab	b)						
	Min-Max			(0-2)	(0-2)	0						
MV	Mean	13.46	**	1.6	0.0	0						
				a	b	b						
	Min-Max			(1-2)	0	0						
SH	Mean	9.5	0.0087(*)	2.0	0.8	0						
				(a	ab	b)						
	Min-Max			2	(0-2)	0						
DK	Mean	4.67	0.097	0.6	0.6	0						
	Min-Max			(0-1)	(0-1)	0						

4.3 Vegetation structure

Vegetation structure was strongly affected by management (see table 4-4): vegetation was significantly higher in early successional sites than in grazed sites, and late successional sites had significantly higher vegetation than early successional sites (H=51.2, p<0.0005). Vegetation cover was higher in early and late successional sites than in grazed sites (F=10.2, p<0.001).

Litter layer was thicker in early and late successional sites than in grazed sites (F=162.4, p<0.001). Also regions differed (F=4.8, p<0.01): in Estonian sites a thicker litter layer was found than in Denmark, but this was only significant for the grazed sites. Late successional sites in Schleswig-Holstein had a significantly thicker litter layer than in Denmark. The significant interaction showed further that, only in Schleswig-Holstein, the litter layer of late successional sites was thicker than that of early successional sites (interaction management* region: F=4.4, p<0.01, fig. 4-2).

Table 4-4: Differences of vegetation structure characteristics: Vegetation height (cm), cover (%), thickness of litter layer (cm) between management classes and/or regions. Results of 2-factorial ANOVAs (F, p): *: p<0.05, **:p<0.01, ***: p<0.001. Results of 2 separate Kruskal-Wallis-Tests (H, p) with Bonferroni-corrected p-levels: *:p<0.025, **: p<0.005, ***:p<0.0005. A, b, c: significant differences according to Post-Hoc-Tests (HSD for unequal N/multiple comparisons test). Means of all regions/management classes are also given, for litter also separately for all regions, to reveal the significant interaction term. Values are means of the measurements on each of the five 1-m²-subplots per 625 m²-plot.

	Management						Region			Interaction						
	F	H	p	G	ES	LS	F	H	p	F	p	transf.	EST	MV	SH	DK
n				22	20	20							17	15	15	15
Vegetation height (cm)		51.2	***	15.8	36.7	113.4		0.75	0.86				52.5	58.8	53.4	51.7
				a	b	c										
Cover (%)	10.2		***	93.7	97.4	98.6	1.6		0.19	2.19	0.06	arcsin	97.9	97.8	98.4	95.9
				a	b	b										
Thickness of litter (cm)	162.4		***	0.38	3.79	6.97	4.8		**	4.4	**	loglog	3.57	3.68	4.51	2.67
				a	b	c							a	ab	ab	b

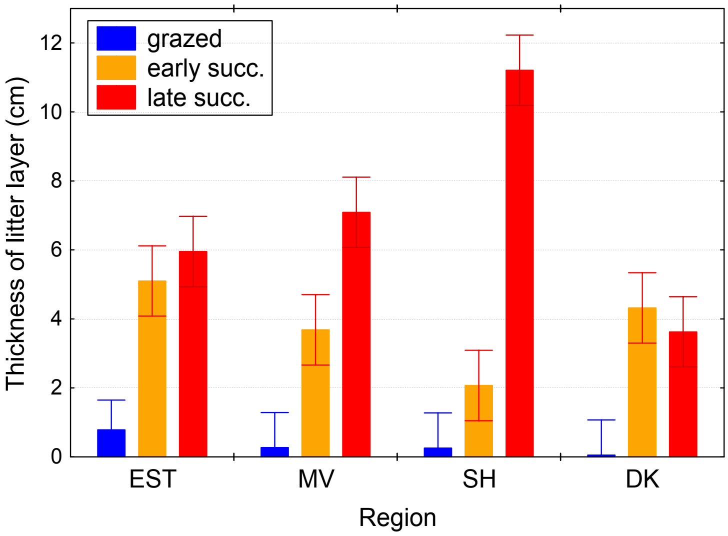


Fig. 4-2: Mean thickness of the litter layer in cm (± SE) in grazed, early and late successional sites in Estonia, Mecklenburg-Vorpommern, Schleswig-Holstein and Denmark. Results of 2-factorial ANOVA (data loglog-transformed): Management: F=162.4, p<0.001, Region: F=4.8, p<0.01, interaction management* region: F=4.4, p<0.01.

4.4 Species richness and diversity

4.4.1 Species richness and spatial scale: impact of management and region

In total, 149 species were found in the vegetation of all study sites (plus 9 taxa determined only to genus level). Estonian study sites had by far the largest species pool with 106 species, whereas 57 species were identified in Mecklenburg-Vorpommern, 59 in SH and 67 in Denmark. 25 species were common to all four regions, 19 species occurred in three regions, 27 species in two regions and more than half of all species (78) occurred in only one region. Of these, 50 were found only in Estonia, 5 only in Mecklenburg-Vorpommern, 11 only in Schleswig-Holstein and 12 only in Denmark (see Annex 3).

Total species number in grazed (97) and early successional sites (96) was slightly lower than in late successional sites (118, table 4-5). This effect was not consistent in the four regions: in Estonia, species number was lower in early successional sites than in grazed and late successional sites, while it increased steadily in Mecklenburg-Vorpommern from 25 in grazed to 35 in early successional and 46 in late successional sites. In Schleswig-Holstein, the number of species in grazed and early successional was quite similar (38 vs. 41) and decreased to 34 in late successional sites. In Denmark, species number was also similar in grazed and early successional sites (42 vs. 44), but increased to 57 in late successional sites.

Table 4-5: Total number of species in regions and management classes. EST: Estonia, MV: Mecklenburg-Vorpommern, SH: Schleswig-Holstein, DK: Northern Denmark.

	EST		MV		SH		DK		total	
	n	species no.	n	species no.	n	species no.	n	species no.	n	species no.
grazed	7	77	5	25	5	38	5	42	22	97
early successional	5	60	5	35	5	41	5	44	20	96
late successional	5	73	5	46	5	34	5	57	20	118
total	17	106	15	57	15	59	15	67	62	149

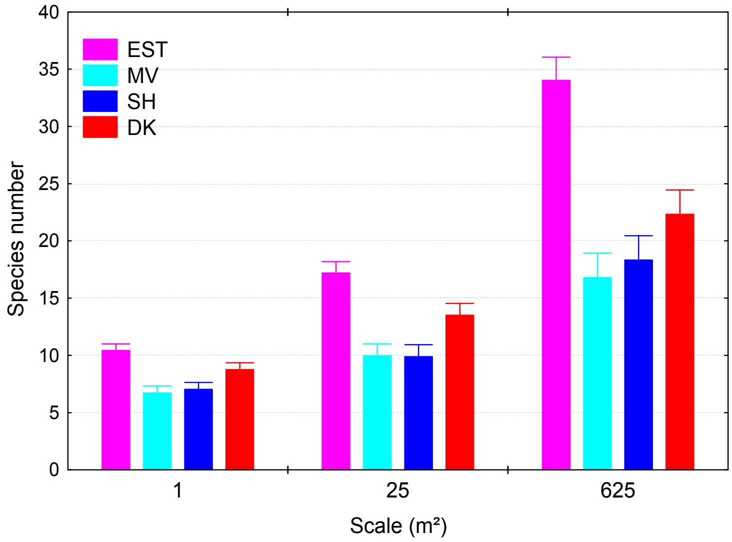
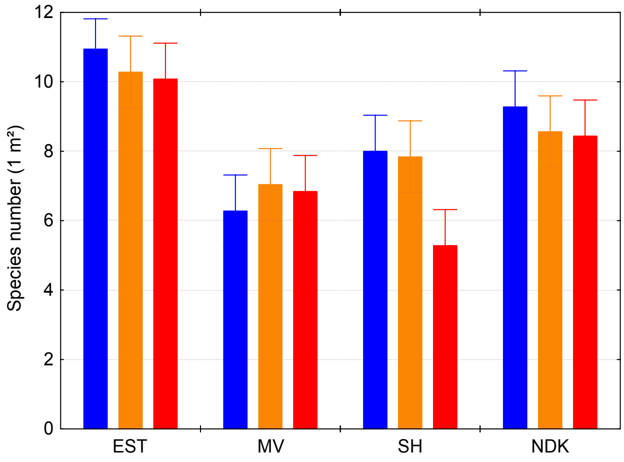


Fig. 4-3: Species number in the four regions on 1, 25 and 625 m² (mean ± SE). Results of the 3-factorial ANOVA (data sqrt-transformed, scale as within-factor): Region: F=14.1, p<0.001, Scale: F=541.9, p<0.001, Interaction Scale * Region: F=11.4, p<0.001.

Overall, species numbers strongly varied between individual sites (see table 4-6). Species number per plot/subplot was strongly affected by spatial scale: it increased with increasing scale, and all three scales (1 m², 25 m², 625 m²) were significantly different from each other in species number (F=541.9, p<0.001). Species richness was significantly higher in Estonia than in Schleswig-Holstein, Mecklenburg-Vorpommern and Denmark (F=14.1, p<0.001). A significant interaction revealed that this difference was more pronounced on larger scales (F=11.4, p<0.001, table 4-6, fig. 4-3).

Management had no significant impact on species number (F=0.15, p=0.86). Only in Schleswig-Holstein, species number was significantly lower in late successional sites than in grazed and early successional sites on 1 m², and also showed a trend to decrease in late successional compared to grazed sites on 25 m². On 625 m², management had no significant impact (fig. 4-4 b, 1-factorial ANOVAs with square-root transformed data: 1 m²: F=6.96, p<0.017, 25 m²: F=5.52, p=0.023, 625 m²: F=0.51, p=0.61, significance levels for p were Bonferroni-corrected.).



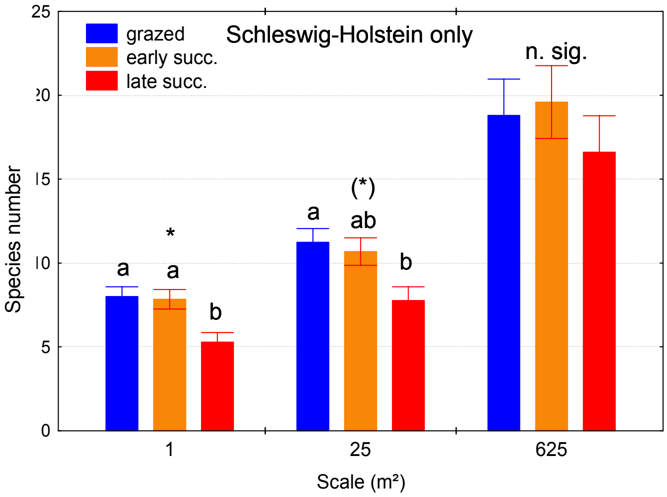


Fig. 4-4a: Impact of management on the species number in the four regions on 1 m² scale (mean ± SE). Results of the 3-factorial ANOVA (data sqrt-transformed, scale as within-factor): Region: F=14.1, p<0.001.

Fig. 4-4b: Impact of management on species richness in Schleswig-Holstein on 1, 25 and 625 m² (mean ± SE). 1-factorial ANOVAs with Schleswig-Holstein data only: 1 m²: F=6.96, p<0.017, 25 m²: F=5.25, p=0.023, 625 m²: F=0.51, p=0.61.

Table 4-6: Results of a 3-factorial ANOVA. Impact of region, management and spatial scale on species number (data sqrt-transformed, scale as within-factor). A, b, c: significant differences according to Post-Hoc-Tests (HSD for unequal N/Tukeys HSD). ***: p<0.001.

	SQ	FG	MQ	F	p	EST	MV	SH	DK	1 m²	25 m²	625 m²
Constant	2481.4	1	2481.4	2724.4	***							
Region	38.6	3	12.9	14.1	***	a	b	b	b			
Management	0.3	2	0.1	0.2	0.86							
Region*Management	2.6	6	0.4	0.5	0.82							
Error	45.5	50	0.9									
Scale	106.6	2	53.3	541.9	***					a	b	c
Scale*Region	6.7	6	1.1	11.4	***							
Scale*Management	0.7	4	0.2	1.9	0.12							
Scale*Region*Management	0.3	12	0.0	0.3	1.00							
Error	9.8	100	0.1									

Table 4-7: Species numbers of the vegetation on 1, 25, 625 m² in the four regions and the management classes (mean, minimum and maximum, on 1 m² and 25 m² the mean of 5 relevés per site was calculated).

Species number on		1 m²			25 m²			625 m²		
		mean	min	max	mean	min	max	mean	min	max
EST		10.5	6.4	16.2	17.3	12.0	28.4	34.1	22.0	54.0
MV		6.7	4.2	10.4	10.0	5.6	15.4	16.8	7.0	33.0
SH		7.0	3.4	9.2	9.9	5.2	14.0	18.3	11.0	28.0
NDK		8.8	4.0	13.6	13.5	7.0	26.8	22.3	13.0	47.0
	grazed	8.8	4.8	16.2	13.5	5.6	28.4	23.5	7.0	54.0
	early succ.	8.4	4.6	13.6	12.9	6.4	21.6	22.7	8.0	39.0
	late succ.	7.7	3.4	13.6	12.0	5.2	26.8	23.6	11.0	47.0
EST	grazed	10.9	6.4	16.2	17.9	12.0	28.4	34.3	22.0	54.0
EST	early succ.	10.3	7.6	12.4	17.8	13.2	21.0	34.2	27.0	39.0
EST	late succ.	10.1	7.4	12.2	15.9	13.4	18.8	33.6	24.0	47.0
MV	grazed	6.3	4.8	7.0	9.4	5.6	12.0	14.8	7.0	17.0
MV	early succ.	7.0	4.6	8.6	10.2	6.4	14.8	15.8	8.0	28.0
MV	late succ.	6.8	4.2	10.4	10.3	6.4	15.4	19.8	11.0	33.0
SH	grazed	8.0	7.2	9.2	11.2	10.0	14.0	18.8	14.0	28.0
SH	early succ.	7.8	7.0	8.6	10.7	9.4	12.4	19.6	16.0	27.0
SH	late succ.	5.3	3.4	8.0	7.8	5.2	10.6	16.6	11.0	20.0
DK	grazed	9.3	7.6	10.6	13.7	11.4	17.4	21.6	13.0	32.0
DK	early succ.	8.6	6.4	13.6	12.8	9.4	21.6	21.0	13.0	38.0
DK	late succ.	8.4	4.0	13.6	14.0	7.0	26.8	24.4	14.0	47.0

4.4.2 Species richness and cover of *Phragmites australis*

Species richness in late successional sites (1 m²) was significantly negatively correlated to the cover of *Phragmites australis.* The linear regression explained 30% for all regions, and between 11% and 41% of the variation in species richness in the separate regions (see table 4-8).

Table 4-8: Linear regressions between the cover of *Phragmites australis* and species richness of late successional 1-m²-subplots in all regions and the four regions separately, subplots with less than 20% cover of *Phragmites australis* excluded.

Region(s)	n	r	r²	p
All	95	-0.55	0.30	***
Estonia	24	-0.44	0.20	*
Mecklenburg-Vorpommern	25	-0.49	0.24	*
Schleswig-Holstein	24	-0.33	0.11	0.12
Northern Denmark	22	-0.64	0.41	**

4.4.3 Species-area-curves

The slope of the species-area-curve was significantly higher in Estonia than in Schleswig-Holstein and Mecklenburg-Vorpommern (F=3.94, p<0.05). It was also significantly different between management classes (F=3.53, p<0.05), and showed a trend to be higher in late successional sites than in grazed sites (the Post-Host-Test was marginally non significant with p=0.077). Thus, in late successional sites, species number increased more strongly with increasing plot size than in grazed sites, and in Estonia, the increase was stronger than in the other three regions. The intercept of the species-area-curve was not affected by management (H=1.50, p=0.47), but was significantly higher in Estonia than in Mecklenburg-Vorpommern and Schleswig-Holstein (H=21.45, p<0.0005, table 4-9).

Table 4-9: Differences in the characteristics of the species-area-curves (slope and intercept) between management classes and/or regions. Results of 2-factorial ANOVAs (F, p) or 2 separate Kruskal-Wallis-Tests (H, p). *: $p<0.05$, **:$p<0.01$, ***: $p<0.001$. If 2 separate Kruskal-Wallis-Tests were carried out, the significance level of the p-values was Bonferroni-corrected: *:$p<0.025$, **: $p<0.005$, ***: $p<0.0005$. A, b, c: significant differences according to Post-Hoc-Tests (HSD for unequal N/multiple comparisons test). Means of all regions/management classes. Species-area-curves were calculated for individual sites separately as linear regressions in log-log space with data of all relevés.

	Effect of region			EST	MV	SH	DK	Effect of management			G	ES	LS
n	F	H	p	17	15	15	15	F	H	p	22	20	20
slope	3.94		*	0.17	0.14	0.14	0.14	3.53		*	0.14	0.14	0.17
				a	b	b	ab				(a	ab	b)
intercept		21.45	***	2.28	1.82	1.85	2.09		1.50	0.47	2.11	2.05	1.88
				a	b	b	ab						

4.4.4 Evenness

Evenness of the vegetation was significantly higher in Estonia (0.80) than in the other three regions (Mecklenburg-Vorpommern: 0.71, Schleswig-Holstein: 0.70, Denmark: 0.73, F=7.71, $p<0.001$, fig. 4-5). It was lower in late successional sites (0.66) than in grazed and early successional sites (0.77 each, F=7.73, $p<0.01$)). Evenness increased with increasing spatial scale from 0.55 at 1 m^2 to 0.74 at 25 m^2 and 0.79 at 625 m^2 (F=425.47, $p<0.001$). The effect of management was scale-dependent, visible in a significant interaction scale*management (F=4.29, $p<0.01$) indicating that management had no effect on evenness on the 1-m^2-scale, but that evenness decreased in late successional sites on the 25- and the 625-m^2-scale (fig. 4-5).

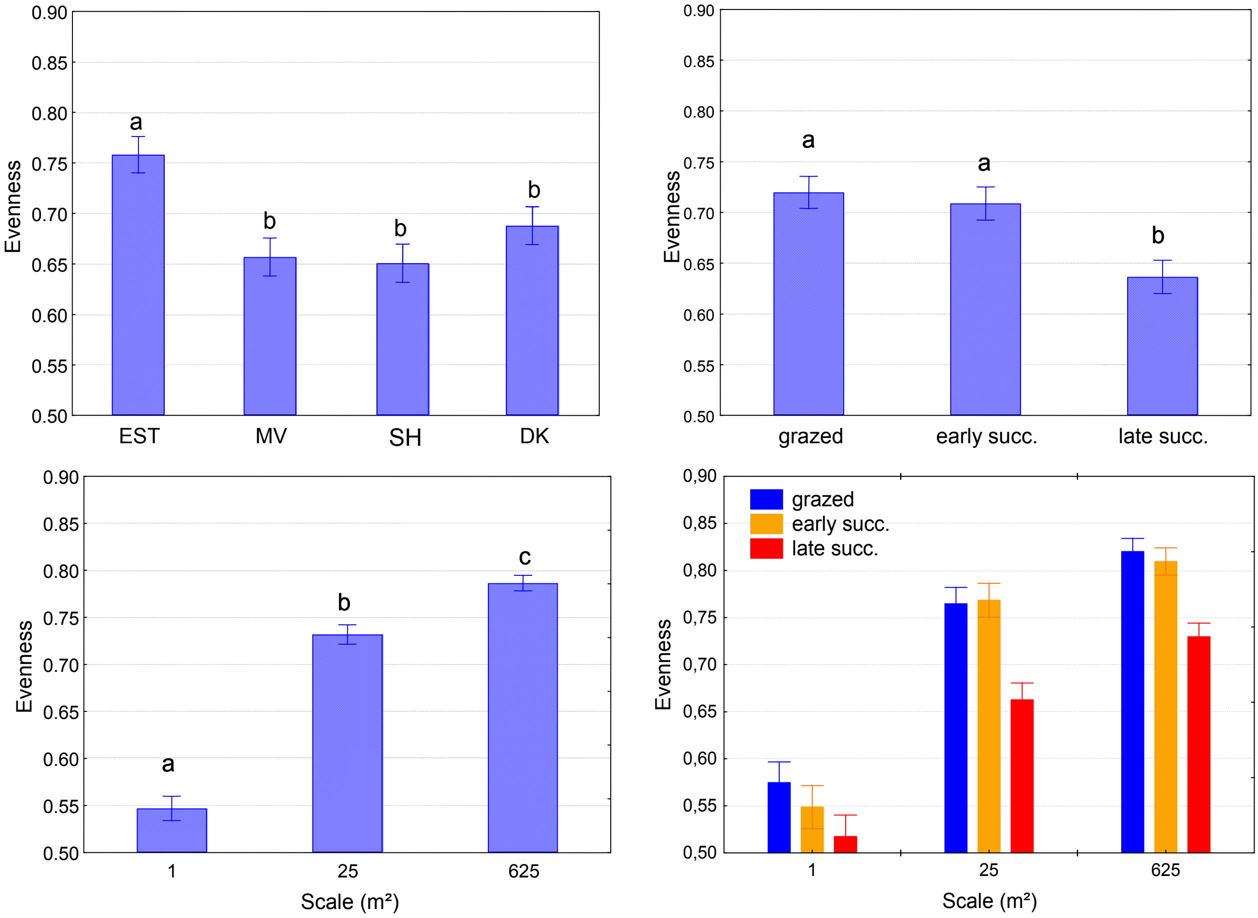


Fig. 4-5: Impact of region, management and spatial scale on evenness of the vegetation (Mean ± SE). Results of a 3-factorial ANOVA with scale as a within-factor (arcsin-transformed, on 1- and 25-m²-scale: mean of 5 subplots per site used). Region: F=7.71, p<0.001, Management: F=7.73, p<0.01, Scale F=425.47, p<0.001, Scale *Management: F=4.29, p<0.01, indicating that management has an impact only on 25- and 625-m²-scale. a, b, c: significant differences according to Post-Hoc-Tests (Tukeys HSD/HSD for unequal N).

4.4.5 Diversity and salt grassland soil types

The depth of the organic layer was significantly positively correlated to a number of abiotic site condition parameters such as elevation, potassium content, soil salinity, organic matter, total nitrogen, and significantly negatively correlated to the pH value (table 4-10). Furthermore, depth of the organic layer was significantly correlated to mean Ellenberg nitrogen and salt indicator value, and to total species number. The strongest correlations, explaining more than a third (33%) of the variation in organic layer depth, were (in order of decreasing magnitude): total nitrogen content, organic matter content, mean Ellenberg nitrogen value, species number and soil salinity. Furthermore, mostly the same variables were significantly correlated to species number (see table 4-10).

Thus, it can be assumed that by classifying the salt grassland sites by the depth of the organic layer, a syndrome of various parameters is described, and that consequently, it is justified to separate two ‘salt grassland soil types’.

Table 4-10: Correlations of vegetation structure parameters, abiotic site conditions and mean Ellenberg values with depth of the organic layer and species number. Significant correlations are marked in red. (mF: mean Ellenberg moisture value, mN: mean Ellenberg nitrogen value, mS: salt indicator value combined of Ellenberg et al. (1992) and Scherfose (1990) on a scale from 0 (salt intolerant) to 6.

	organic layer		species number	
	r	r^2	r	r^2
Elevation range (cm)	-0.11	0.01	0.31	0.10
Elevation (cm ASL)	0.32	0.10	-0.21	0.05
Vegetation cover (%)	0.11	0.01	0.12	0.01
Vegetation height (cm)	0.10	0.01	-0.01	0.00
Thickness of litter layer (cm)	-0.05	0.00	0.00	0.00
pH	-0.42	0.18	0.45	0.20
P (mg P_2O_5/100g)	0.22	0.05	-0.18	0.03
K (mg K_2O /100g)	0.27	0.07	-0.42	0.18
Mg (mg/100g)	0.06	0.00	-0.05	0.00
Soil salinity (psu)	0.58	0.34	-0.61	0.37
Organic matter (%)	0.70	0.48	-0.48	0.23
Ntot (%)	0.73	0.53	-0.48	0.23
C/N-ratio	-0.03	0.00	-0.04	0.00
Cinorganic (%)	-0.24	0.06	0.34	0.11
mN	0.68	0.46	-0.71	0.51
mF	0.24	0.06	-0.25	0.06
mS	0.52	0.27	-0.79	0.62
Organic layer (cm)	1.00	1.00	-0.66	0.44
Species number (625 m²)	-0.66	0.44	1.00	1.00

In the following, only results connected with the salt grassland soil type will be highlighted. Effects of region, management or scale that are consistent with the results of the complete data set (see 4.4.1-4.4.5) are listed in the tables, but not extensively described to avoid redundancies.

Species richness was significantly higher in sites of the 'shallow soil type' than in sites of the 'deep soil type', in particular in Mecklenburg-Vorpommern (shallow: 25.7 species/625 m² versus deep: 14.6 species/625 m²) and Denmark (shallow: 26.4 species/625 m² versus deep: 16.2 species/625 m²), and less pronounced in Schleswig-Holstein (shallow: 21 species/625 m² versus deep: 17.7 species/625 m², F=10.11, $p<0.01$, see fig. 4-6 and table 4-11). There was a trend of decreasing species richness from early to late successional sites of the deep soil type, while species richness slightly increased in sites of the shallow soil type (interaction type*management: F=3.30, p=0.09, fig. 4-6 b). Species richness increased with increasing scale (F=247.98, $p<0.001$), and a significant interaction scale*management showed that this increase was steeper in late successional sites (F=3.49, $p<0.05$).

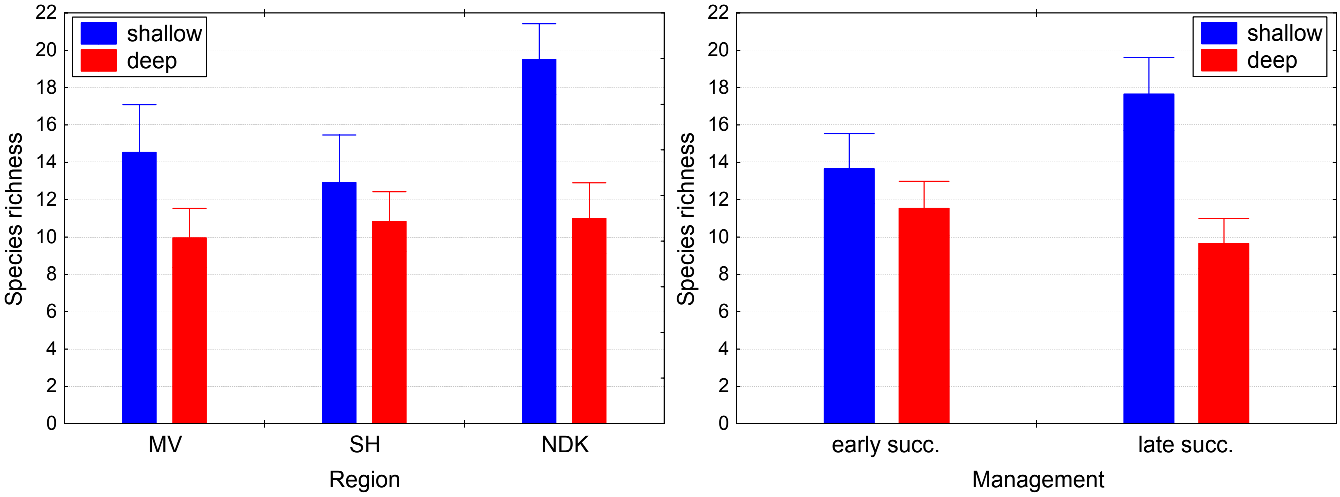


Fig. 4-6: Species richness (Mean ± SE) of early and late successional sites of the shallow and deep soil types in Mecklenburg-Vorpommern (MV), Schleswig-Holstein (SH) and Denmark (DK). Results of 4-factorial ANOVA (with scale as within-factor) see table 4-11. Type: F=10.11, p<0.01, Interaction Type*Region: F=0.72, p=0.50 ns, Interaction Management*Type: F=3.30, p=0.09 (trend). Be aware that all Estonian and all grazed sites were excluded for methodological reasons (only one soil type represented).

Table 4-11: Impact of Region, management, type and scale on species richness. Results of 4-factorial ANOVA with log-transformed data of all regions except for Estonia (since there, only the shallow soil type was found) and for early and late successional sites (since grazed were all of the shallow type in SH and MV).

	SSq	df	MS	F	p	Effect
Region	0.71	2	0.35	1.43	0.26	
Management	0.00	1	0.00	0.00	0.98	
Type	2.49	1	2.49	10.11	**	shallow>deep
Region*Management	0.35	2	0.18	0.72	0.50	
Region*Type	0.34	2	0.17	0.70	0.51	
Management*Type	0.81	1	0.81	3.30	0.09 (*)	(ES>LS in deep, s>d only in LS)
Region*Management*Type	0.01	2	0.00	0.01	0.99	
Error	4.44	18	0.25			
Scale	11.46	2	5.73	247.98	***	625>25>1
Scale*Region	0.07	4	0.02	0.76	0.56	
Scale*Management	0.16	2	0.08	3.49	*	stronger increase in LS
Scale*Type	0.02	2	0.01	0.42	0.66	
Scale*Region*Management	0.02	4	0.01	0.22	0.92	
Scale*Region*Type	0.07	4	0.02	0.79	0.54	
Scale*Management*Type	0.01	2	0.00	0.14	0.87	
Scale*Region*Management*Type	0.15	4	0.04	1.64	0.19	
Error	0.83	36	0.02			

The slope of the species-area-curve did not differ between the two types (2-factorial ANOVA with data of Denmark, Mecklenburg-Vorpommern and Schleswig-Holstein, factor type: F=0.27. p=0.60, factor region: F=0.25, p=0.78, type*region: F=1.46, p=0.24). The intercept was significantly higher for sites of the shallow soil type (mean of 2.16) than for sites of the deep soil type (mean of 1.80, 2-factorial ANOVA with data of Denmark, Mecklenburg-Vorpommern and Schleswig-Holstein, factor type: F=6.69. p<0.05, factor region: F=1.04, p=0.36, type*region: F=1.38, p=0.26).

Evenness was significantly higher in sites of the shallow soil type than in those of the deep soil type (F=8.93, p<0.01, see fig. 4-7 and table 4-12). A significant interaction management *type revealed that management had no impact on the evenness of sites of the shallow soil type, but that evenness decreased in late successional sites of the deep soil type (F=5.38, p<0.05, see fig. 4-7 b).

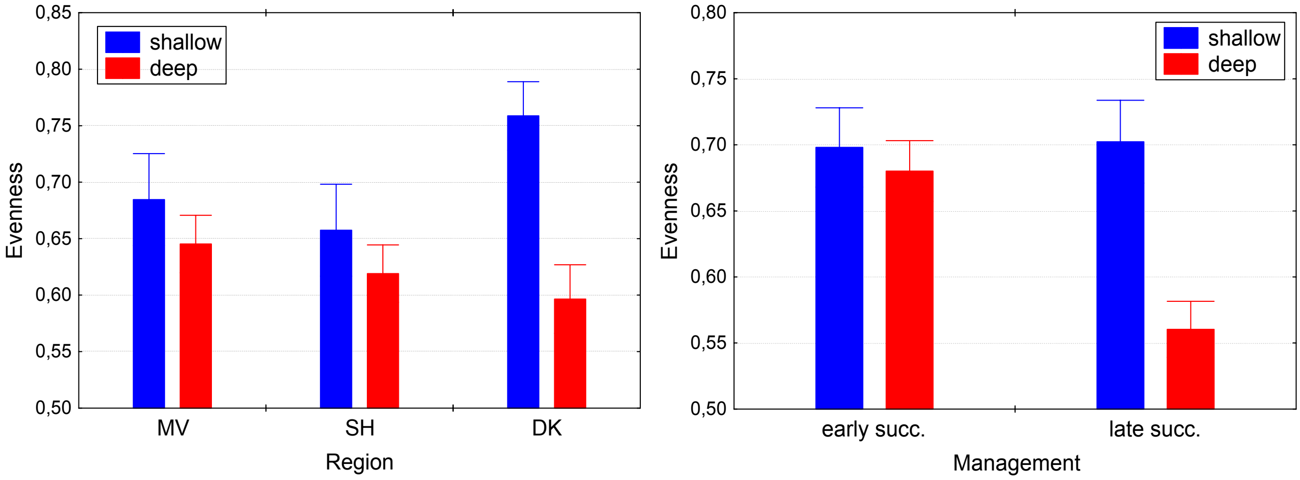


Fig. 4-7: Evenness (Mean ± SE) of early and late successional sites of the shallow and deep soil types (in MV, SH and DK). Results of 4-factorial ANOVA (with scale as within-factor) see table 4-12. Type: F=8.93, p<0.01, Region: ns, interaction Region*Type: F=2.54, p=0.11, management: F=4.65, p<0.05, interaction management*type: F=5.38, p<0.05: evenness decreased only in late successional sites of the deep soil type. Be aware that all Estonian and all grazed sites were excluded for methodological reasons (only one soil type represented).

Table 4-12: Impact of region, management, type and scale on the evenness of the vegetation. Results of 4-factorial ANOVA with data of all regions except for Estonia (since there, only the shallow soil type was found) and for early and late successional sites (since grazed were all of the shallow type in SH and MV).

	SSq	df	MS	F	p	Effect
Region	0.02	2	0.01	0.76	0.48	
Management	0.06	1	0.06	4.65	*	ES>LS
Type	0.12	1	0.12	8.93	**	s>d
Region*Management	0.03	2	0.02	1.23	0.32	
Region*Type	0.07	2	0.03	2.54	0.11	
Management*Type	0.07	1	0.07	5.38	*	ES>LS only in deep
Region*Management*Type	0.02	2	0.01	0.75	0.49	
Error	0.24	18	0.01			
Scale	0.82	2	0.41	128.88	***	625>25>1
Scale*Region	0.01	4	0.00	0.85	0.50	
Scale*Management	0.02	2	0.01	2.59	0.09 (*)	(Management not sig. on 1 m^2)
Scale*Type	0.00	2	0.00	0.21	0.81	
Scale*Region*Management	0.01	4	0.00	0.58	0.68	
Scale*Region*Type	0.01	4	0.00	0.59	0.67	
Scale*Management*Type	0.01	2	0.01	1.97	0.15	
Scale*Region*Management*Type	0.02	4	0.00	1.23	0.31	
Error	0.11	36	0.00			

4.4.6 Impact on species richness: site conditions and vegetation structure

With the direct approach, multiple linear regression models of all 1-m²-subplots and separately for each region and management class explained between 20.0% and 56.1% of the variation of species richness, if up to 9 vegetation structure parameters and abiotic site conditions were included (table 4-13a). In the model for all subplots, 9 variables explained together 35.3% of the variation. Separate models for the regions or management classes mostly had higher power with 3 to 9 variables: the highest explained variation was obtained for all grazed subplots with 56.1%, for Schleswig-Holstein with 50.6% and for Estonia with 50.0%. The lowest proportion was explained for Mecklenburg-Vorpommern with only 20.0%. Variables of importance differed between the models: organic layer was the first variable most often, explaining alone up to 30.5% (in Denmark). Vegetation height was the variable explaining the highest percentage of variance alone, with 43.4% in Schleswig-Holstein. No variable was included in all models. Elevation range was included in all but one of the models (all except for that for late successional sites), and was also the first or second most important variable in several models. Soil salinity was the second most important variable in two models, and pH, organic matter and elevation were among the first or second most important variable(s) each in one of the models. Phosphate and thickness of the litter layer consistently explained low percentages of variation.

Multiple regression models based on vegetation structure, elevation parameters and mean Ellenberg values instead of directly measured chemical parameters (indirect approach, table 4-13 b) explained in general higher proportions of variance of species richness (between 45.1% for early successional and 70.9% for late successional sites). The firstly selected variable in nearly all models was either the Ellenberg nitrogen value, explaining up to 48.9% (in late successional sites), or the mean salt indicator value, explaining up to 47.4% (in grazed sites). These two or the mean Ellenberg moisture value were the first two, except for the model for Schleswig-Holstein with vegetation height as the firstly selected variable, and the model for the grazed subplots with elevation range as the second variable. Elevation range was the only variable included in all models.

Table 4-13: Multiple linear regression models with a) elevation and vegetation structure parameters and abiotic site conditions (**direct approach**), b) elevation and vegetation structure parameters and mean indicator values (**indirect approach**) explaining the variation of species richness on 1 m², in all subplots (n=309/310) and separately for the four regions and three management classes. n: number of subplots included in the regression model. % v: % of total variation explained by one factor in the respective step of the forward stepwise regression, calculated from corrected cumulative r² after each step. p: significance level of the ANOVA-model for inclusion/exclusion of each factor, *: $p<0.05$, **:$p<0.01$, ***: $p<0.001$. st: step of the stepwise regression procedure. Parameters included in the models: in a+b): Elevation: elevation above mean sea level (cm), Elev. range: elevation range of each subplot (cm), Veg. height: vegetation height (cm), cover: total vegetation cover (%), Litter: thickness of the litter layer (cm), in a): Org. layer: depth of the organic layer (cm), Soil salinity: salinity in the upper soil layer (psu), P: Phosphate content of the soil (mg P_2O_5/100g), Org. matter: organic matter content of the upper soil layer (%), pH: soil pH-value, b): mN: mean Ellenberg value for nitrogen, mS: mean salt indicator value combined after Ellenberg et al. (1992) and Scherfose (1990), mF: mean Ellenberg value for moisture, mL: mean Ellenberg value for light, Variables: number of variables in each regression model. Total var. explained: Total variance of species richness explained by each of the multiple regression models. The first parameter of each regression model is marked with grey.

Region	all			EST			MV			SH			DK			all			all			all		
Management	all						all			all			all			G			ES			LS		
	% v.	p	st.	% v.	p	st.	% v.	p	st.	% v.	p	st.	% v.	p	st.	% v.	p	st.	% v.	p	st.	% v.	p	st.
a) direct approach																								
n	309			85			74			75			75			110			100			99		
Org. layer	22.9	***	1										30.5	***	1	2.4	*	4	11.8	***	1	36.1	***	1
Elev. range	6.9	***	2	29.1	***	1	0.6	0.05	4	1.1	0.11	4	2.0	0.06	4	17.0	***	2	4.4	*	2			
Veg. height	2.6	***	3				5.0	0.05	2	43.4	***	1				0.4	0.16	8	2.7	0.04	5	5.6	**	2
Soil salinity	1.8	**	4	10.5	***	3				4.7	**	2	8.4	***	2				2.2	0.06	3			
Cover	0.5	0.06	5	1.4	0.08	5		0.22	5	0.6	0.18	3				6.1	***	3						
Litter	0.1	0.26	6	0.8	0.13	6				0.8	0.16	5				0.1	0.29	7	0.9	0.15	6	1.7	0.05	3
pH	0.1	0.22	7	2.8	*	4										29.3	***	1	1.1	0.13	8			
P	0.3	0.14	8													0.7	0.11	5	0.5	0.20	9			
Elevation	0.1	0.19	9	5.4	**	2	3.4	0.02	3				2.9	*	3	0.1	0.25	6	0.2	0.26	7			
Org. matter							11.0	0.01	1				0.2	0.28	5				2.0	0.07	4			
variables	9			6			5			5			5			8			9			3		
total var. explained	35.3			50.0			20.0			50.6			44.0			56.1			25.8			43.4		
b) indirect approach																								
n	310			85			75			75			75			110			100			100		
mN	29.9	***	1	0.3	0.22	6				0.9	0.12	3	44.1	***	1				10.7	***	2	48.9	***	1
mS	13.9	***	2	33.9	***	1	12.8	***	1				12.7	***	2	47.4	***	1	26.1	***	1	0.9	0.06	4
mF	4.9	***	3	18.4	***	2	15.3	***	2	6.9	**	2	0.8	0.13	4	0.4	0.13	5				14.4	***	2
Elev. range	4.9	***	4	3.6	**	3	1.9	0.07	5	0.5	0.20	4	1.8	*	3	9.6	***	2	5.0	**	3	0.9	*	6
mL	1.4	**	5	2.6	*	4										2.2	**	4	1.1	0.09	5	0.7	0.09	5
Elevation	0.5	*	6				9.2	**	3															
Litter	0.4	*	7				7.8	**	4										2.2	0.03	4	5.1	***	3
Veg. height	0.4	0.07	8	1.6	0.04	5				43.4	***	1	1.2	0.08	5	5.0	***	3						
Cover				0.2	0.25	7	1.2	0.11	6	1.3	0.09	5				0.5	0.13	6						
variables	8			7			6			5			5			6			5			6		
total var. explained	56.3			60.6			48.2			53.0			60.6			65.1			45.1			70.9		

4.5 Species composition

4.5.1 Ordination

The detrended correspondence analysis (DCA) showed that grazed sites were found at the right, early successional sites in the middle and late successional sites at the left side of the ordination diagram (fig. 4-8). Estonian sites were found at the upper part, while the sites of the other three regions strongly overlapped. The first axis, thus representing grazing/abandonment, was correlated with (the dummy variables) late successional (negatively) and grazing (positively), and with vegetation height, litter and cover (all negatively). 'Natural grazing' (by geese, hares etc.) was also (positively) correlated to the first axis.

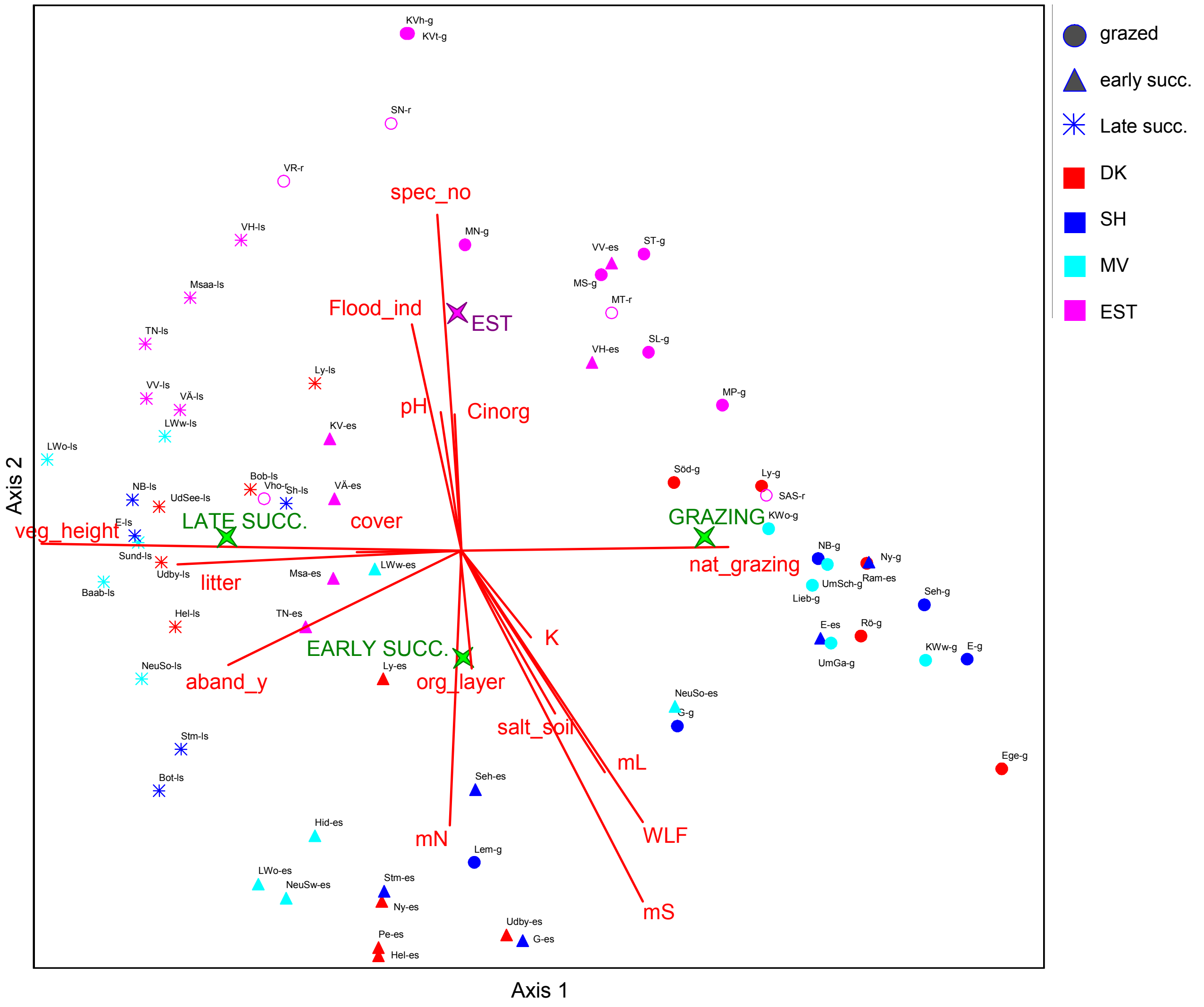


Fig. 4-8: Detrended correspondence analysis (DCA) of the species composition of the 625-m²-plots with %-cover data of all 128 taxa occurring at more than one site (rare species were downweighted). Correlations with environmental variables are shown if $r^2>0.15$. Management categories (dummy variables) are displayed as centroids (symbols, presented also if r^2 was below 0.15). First and second axis eigenvalues: 0.46 and 0.29, respectively, first and second axis length of gradient: 3.17 and 2.81, respectively. Spec_no: Species number (625 m²), Cinorg: soil content of inorganic carbon (%), nat-grazing: Degree of 'natural' grazing by geese, rabbits, hares, deer or moose on a scale from 0 (no) to 2, K: soil potassium content (mg K_2O /100g), salt_soil: salinity in the upper soil layer (psu), mS: mean salt indicator value combined after Ellenberg et al. (1992) and Scherfose (1990), mN: mean Ellenberg value for nitrogen, mL: mean Ellenberg value for light, WLF: percentage of water level fluctuation indicator species and flood_ind: percentage of flooding indicator species according to Ellenberg et al. (1992), Org. layer: depth of the organic layer (cm), aband_y: time since abandonment (years), Litter: thickness of the litter layer (cm), Veg. height: vegetation height (cm), cover: total vegetation cover (%),pH: soil pH-value. The acronyms for all sites can be found in table 2-2 (chapter 2).

The second axis, related to the regional gradient, was positively correlated to (the dummy variable) Estonia, to total species number, percentage of WLF indicators (= indicators of water level fluctuations), pH and inorganic carbon. It was negatively correlated to mean salt, light and nitrogen (N) value, soil salinity and percentage of flooding indicators and (less strongly) also to the depth of the organic layer and potassium (K) content.

4.5.2 Mean Ellenberg values

Differences in species composition were also reflected in mean Ellenberg indicator values for regions and management classes (see table 4-14). Estonia and Mecklenburg-Vorpommern had lower light values than Schleswig-Holstein and Denmark. Estonia had lower nitrogen and salt indicator values, a lower percentage of flooding indicator species and a higher percentage of water level fluctuation (WLF) indicator species than the other three regions. Moisture values did not differ between regions.

Late successional sites had lower light and salt, but higher nitrogen values than grazed and early successional sites, and a lower percentage of flooding indicator species than grazed sites. Moisture values as well as water level fluctuation indicator percentages did not differ between management classes.

Table 4-14: Mean (unweighted) Ellenberg indicator values (mL: light, mF: moisture, mN: nitrogen) and percentage of flooding and water level fluctuation (WLF) indicators (% of all species, unweighted) of all management classes and regions (calculated per 625-relevé). mS: salt indicator value combined of Ellenberg et al. (1992) and Scherfose (1990) on a scale from 0 (salt intolerant) to 6. Results of 2-factorial ANOVAs (F, p). *: p<0.05, **:p<0.01, ***: p<0.001. A, b: significant differences according to Post-Hoc-Tests (HSD for unequal N). N=5 for each region and management class, except for grazed in Estonia n=7.

	Factor Region							Factor Management					Interaction	
	F	p	transf.	EST	MV	SH	NDK	F	p	G	ES	LS	F	p
mL	24.5	***		7.5	7.6	7.8	7.9	9.3	***	7.7	7.7	7.6	1.9	0.10
				a	a	b	b			a	a	b		
mF	1.3	0.30		7.1	7.0	7.0	6.9	2.6	0.08	7.0	6.9	7.2	0.3	0.95
mN	27.3	***		4.5	5.7	5.8	5.5	6.7	**	5.1	5.3	5.7	0.6	0.75
				a	b	b	b			a	a	b		
mS	27.7	***		2.2	3.4	3.7	3.6	11.1	***	3.4	3.3	2.8	1.2	0.31
				a	b	b	b			a	a	b		
Flooding indicators (%)	18.9	***	log	35.3	60.1	60.9	69.4	5.4	**	61.6	57.7	47.4	1.0	0.42
				a	b	b	b			a	ab	b		
WLF indicators (%)	25.5	***		23.7	8.4	9.6	8.0	0.1	0.89	13.2	12.7	12.4	1.1	0.37
				a	b	b	b							

4.5.3 Species groups

Annual and biennial species

Annual and biennial species represented a higher percentage of all species in grazed than in early and late successional sites. Their relative species number was also higher in Denmark than in Estonia and Mecklenburg-Vorpommern, Schleswig-Holstein was still significantly higher than Estonia (see Table 4-15). The cover of annual and biennial species was higher in grazed than in late successional sites. It was also higher in Denmark than in Estonia, while Mecklenburg-Vorpommern and Schleswig-Holstein were intermediate.

Table 4-15: Mean of relative species number and relative cover of annual and biennial species in management classes and regions (625 m² scale). Results of 2-factorial ANOVAs (F, p). *: p<0.05, **:p<0.01, ***: p<0.001. A, b, c: significant differences according to Post-Hoc-Tests (HSD for unequal N). N=5 for each region and management class, except for grazed in Estonia n=7.

	Factor Region						Factor Management					Interaction	
	F	p	EST	MV	SH	NDK	F	p	G	ES	LS	F	p
Percentage of annual + biennial species (%)	13.4	***	13.2	17.3	24.2	27.4	7.1	**	24.5	18.1	17.9	0.5	0.83
			a	ab	bc	c			a	b	b		
Relative cover of annuals + biennials (%)	5.2	**	7.4	7.1	10.5	12.4	4.6	*	11.5	8.6	7.5	1.1	0.37
			a	ab	ab	b			a	ab	b		

Socio-ecological species groups

The percentages of sociological-ecological species groups differed both between management classes and between regions: The relative species number of salt marsh species declined in late successional sites, while reed bed species and ruderal species increased (see fig. 4-9, table 4-16). With respect to relative cover, these three groups showed the same pattern (fig. 4-10). In addition, the relative cover of flood meadow species declined in late successional sites. However, this effect was only observed in Mecklenburg-Vorpommern (significant interaction, see table 4-16).

With increasing salinity, salt marsh species increased in Schleswig-Holstein and especially in Denmark both in relative species numbers and in relative cover. Flood meadow species declined in relative species number in Schleswig-Holstein and Denmark, but their cover increased in Mecklenburg-Vorpommern and declined only in Denmark. Grassland species had a higher percentage in species number and cover in Estonia than in the other three regions. Relative species number of ruderal species increased in Mecklenburg-Vorpommern and Schleswig-Holstein and were intermediate in Denmark, but they did not change in cover. Reed bed species declined in relative species number in Denmark and Schleswig-Holstein, but also not in cover.

Some effects were specific for one region: the relative cover of flood meadow species was only higher in grazed sites in Mecklenburg-Vorpommern, while in other regions management had no impact on flood meadow species' relative cover or relative species number. The increase of relative species number of ruderals in late successional sites occurred only in Schleswig-Holstein.

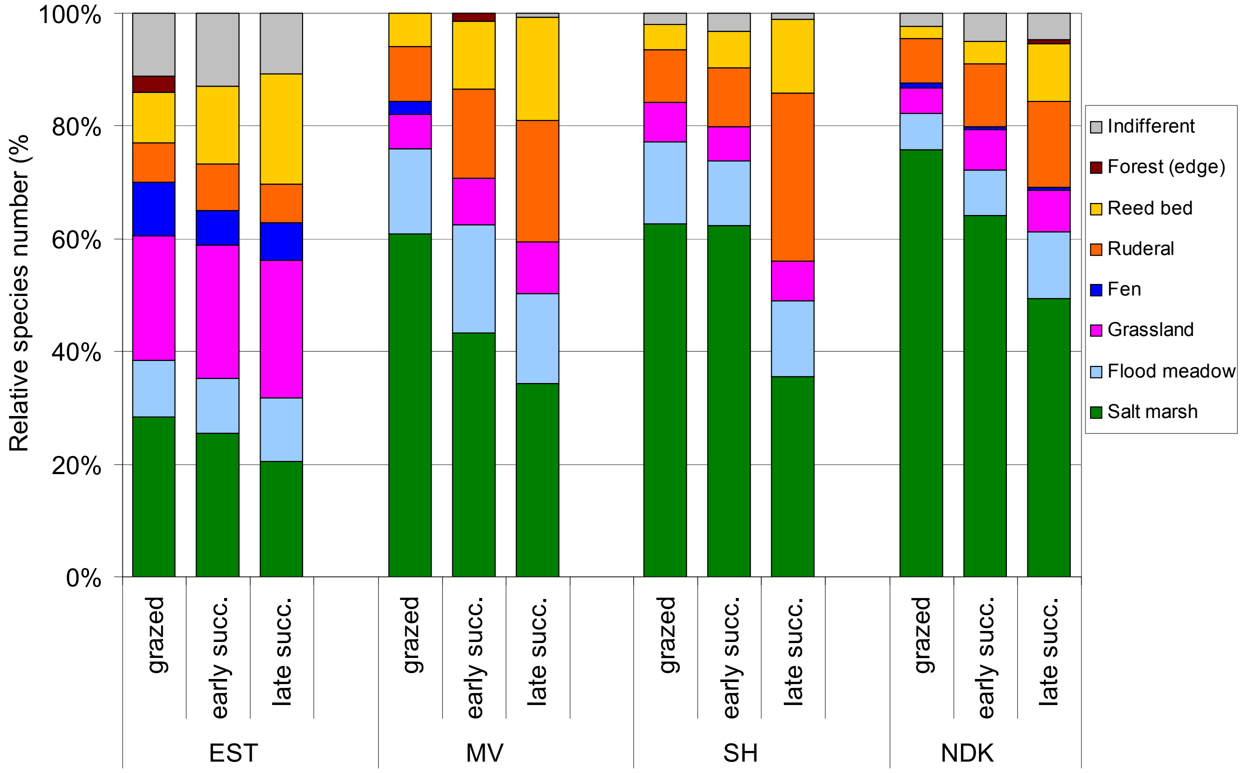


Fig. 4-9: Relative species number (%) of socio-ecological species groups in grazed, early (early succ.) and late successional (late succ.) sites in the four regions (on 625 m²-plots).

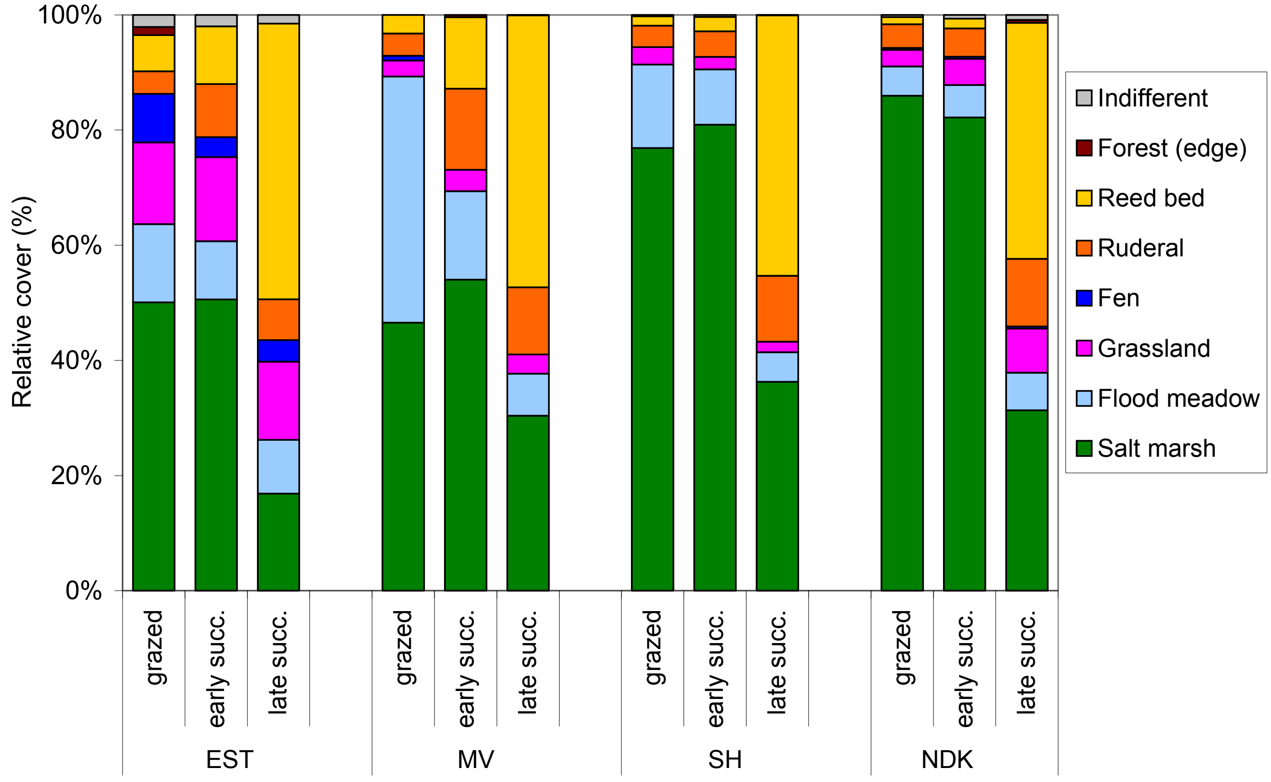


Fig. 4-10: Relative cover (%) of socio-ecological species groups in grazed, early (early succ.) and late successional (late succ.) sites in the four regions (on 625 m²-plots).

Table 4-16: Mean of relative species number and relative cover of socio-ecological species groups according to Ellenberg et al. (1992) in management classes and regions (625 m^2 scale). Results of 2-factorial ANOVAs (F, p): *: p<0.05, **:p<0.01, ***: p<0.001, or results of 2 separate Kruskal-Wallis-Tests (H, p) with Bonferroni-corrected p-levels: *:p<0.025, **: p<0.005, ***:p<0.0005. A, b, c: significant differences according to Post-Hoc-Tests (HSD for unequal N/multiple comparisons test). Data of relative cover of flood meadow species was log-transformed.

	Management						Region							Interaction		
	F	H	p	G	ES	LS	F	H	p	EST	MV	SH	DK	F	p	effect
Relative species number																
Reed bed	17.4		***	5.7 a	9.1 a	15.3 b	8.0		***	13.5 a	12.0 ab	8.0 bc	5.4 c	0.3	0.96	
Fen		2.2	0.34	3.8	1.6	1.7		38.2	***	7.6 a	0.8 b	0.0 b	0.6 b			
Salt marsh	13.8		***	54.4 a	48.8 a	34.9 b	22.7		***	25.2 a	46.2 b	53.5 bc	63.1 c			
Flood meadow		2.6	0.28	11.4	12.1	13.1		20.9	***	10.3 a	16.8 b	13.2 ab	8.8 a			
Ruderal	10.0		***	8.4 a	11.4 a	18.4 b	5.3		**	7.3 a	15.7 b	16.5 b	11.5 ab	2.6	*	max LS only SH
Grassland	0.3		0.77	11.0	11.3	12.0	11.5		***	23.3 a	7.8 b	6.6 b	6.4 b	0.0	0.99	
Forest (edge)		4.0	0.13	0.9	0.4	0.2		7.5	0.06	1.2	0.5	0.0	0.3			
indifferent				4.6	5.3	4.3				11.6	0.2	2.1	4.0			
Relative cover																
Reed bed		41.0	***	3.4 a	6.6 a	45.3 b		5.0	0.17	19.6	20.9	16.4	14.6			
Fen		1.8	0.41	2.9	1.0	1.0		40.0	***	5.6 a	0.3 b	0.0 b	0.4 b			
Salt marsh	44.2		***	63.5 a	66.9 a	28.7 b	14.6		***	40.4 a	43.7 a	64.7 b	66.5 b	1.7	0.15	
Flood meadow	5.2		**	18.5 a	10.2 ab	7.1 b	8.4		***	11.3 ab	21.8 a	9.7 bc	5.8 c	2.8	*	man sig only MV
Ruderal		14.6	**	3.9 a	8.2 ab	10.5 b		0.5	0.92	6.4	9.9	6.5	6.9			
Grassland		0.0	1.00	6.5	6.3	6.6		24.3	***	14.1 a	3.3 b	2.3 b	5.0 b			
Forest (edge)		4.0	0.13	0.5	0.1	0.1		7.5	0.06	0.6	0.1	0.0	0.2			
indifferent				0.8	0.7	0.6				1.9	0.0	0.2	0.6			

Strategy types after Grime (1979)

Management had an impact on the relative cover of CR-, C-, CSR-, CS-, S- and SR-strategists (see fig. 4-11, table 4-17). CR-strategists had a higher relative cover in late successional sites than in grazed sites (H=11.3, p<0.01). The relative cover of C-strategists increased already in early (and late) successional sites (H=26.5, p<0.001). CS-strategists increased in relative cover only in late successional sites (H=40.7, p<0.001). In contrast, SR- and CSR-strategists had a higher share in grazed and early successional sites than in late successional sites (SR: F=19.3, p<0.001, CSR: F=10.5, p<0.001). However, a significant interaction revealed that the effect of management on CSR-strategists was only significant in Mecklenburg-Vorpommern (F=3.9, p<0.01). S-strategists had a significantly lower relative cover in early successional than in grazed sites, and relative cover decreased again in late successional sites (F=37.4, p<0.001).

The relative cover of CSR-, S-and SR-strategists also differed significantly between the four regions (table 4-17). CSR-strategists had a significantly higher relative cover in Estonia and Mecklenburg-Vorpommern than in Schleswig-Holstein and Denmark (F=13.8, p<0.001). A significant interaction demonstrated that this effect occurred only in grazed sites, in which relative cover of CSR-strategists was significantly higher in Mecklenburg-Vorpommern than in Estonia and Schleswig-Holstein, whereas values in Denmark were still significantly lower (F=3.9, p<0.01). In contrast, cover of S- and SR-strategists significantly increased towards the more saline western regions: S-strategists had a lower relative cover in Mecklenburg-Vorpommern than in Denmark (F=17.5, p<0.001). SR-strategists had a significantly higher relative cover in Denmark than in the other three regions (F=14.2, p<0.001).

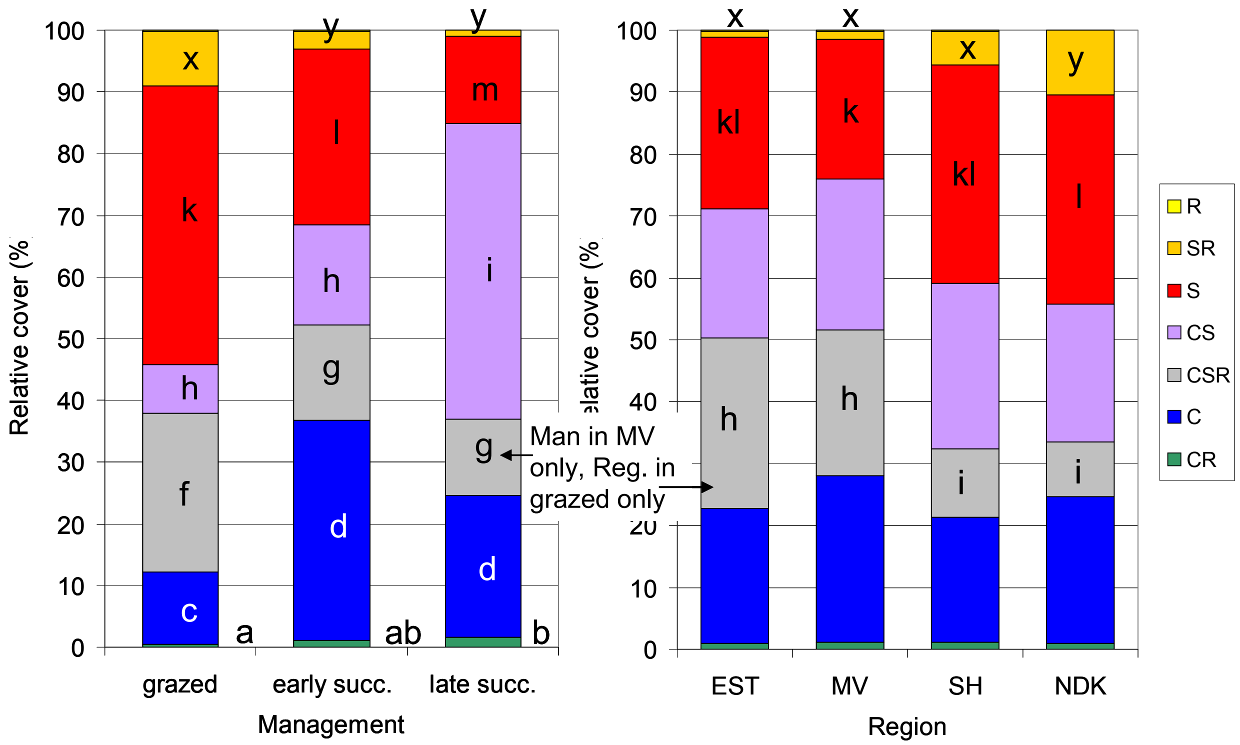


Fig. 4-11: Impact of management and region on mean relative cover of CSR-strategy types after Grime (1979) on 625 m²-plots (percentage of cover of all species with CSR-category assigned by Frank & Klotz 1990). Ab, cd, fg, hi, klm, xy: Significant differences according to 2-factorial ANOVAs or 2 separate Kruskal-Wallis-Tests for each strategy type are indicated with different letters. Statistical results: see table 4-17. C: competitive strategy, S: stress-tolerance strategy, R: ruderal strategy (adapted to disturbance) and four secondary strategies (CR, CS, SR, CSR).

Table 4-17: Impact of management and region on mean relative cover of CSR-strategy types after Grime (1979) on 625 m²-plots (percentage of cover of all species with CSR-category assigned by Frank & Klotz 1990). Results of 2-factorial ANOVAs (F, p): *: p<0.05, **:p<0.01, ***: p<0.001. Results of 2 separate Kruskal-Wallis-Tests (H, p) with Bonferroni-corrected p-levels: *:p<0.025, **: p<0.005, ***:p<0.0005. Effect: Direction of difference is indicated with > (larger than). C: competitive strategy, S: stress-tolerance strategy, R: ruderal strategy (adapted to disturbance) and four secondary strategies (CR, CS, SR, CSR).

	Management				Region				Interaction			
	F	H	p	Effect	F	H	p	Effect	F	p	Effect	transf.
C		26.5	***	ES/LS>G		1.2	0.8					
CR		11.3	**	LS>G		0.2	1					
CS		40.7	***	LS>G/ES		0.6	0.9					
CSR	10.5		***	G>ES/LS	13.8		***	EST/MV>SH/DK	3.9	**	Man. only in MV, Reg. only in G (MV>EST/SH>DK)	
R		3.1	0.21			1.9	0.6					
S	37.4		***	G>ES>LS	3.8		*	DK>MV	0.3	0.95		log
SR	19.3		***	G>ES/LS	14.2		***	DK>others	1.6	0.2		loglog

The triangular graph of all 625-m² plots (fig. 4-12) illustrated that vegetation succession as well as vegetation changes along the Baltic Sea ecological gradient were primarily reflected in a shift between C- and S-strategy components, but that grazing also slightly affected the R-strategy component. Grazed sites had a significantly lower C-component and a higher R- and S-component than early and late successional sites (C: $F=44.01$, $p<0.001$, R: $H=24.26$, $p<0.0005$, S: $F=21.12$, $p<0.001$).

The four regions only differed significantly in the S-component, which was significantly higher in Denmark than in Mecklenburg-Vorpommern, whereas Estonia and Schleswig-Holstein were intermediate ($F=3.55$, $p<0.05$). The C-component was inversely proportional to the S-component, but differences were marginally insignificant ($F=2.77$, $p=0.051$).

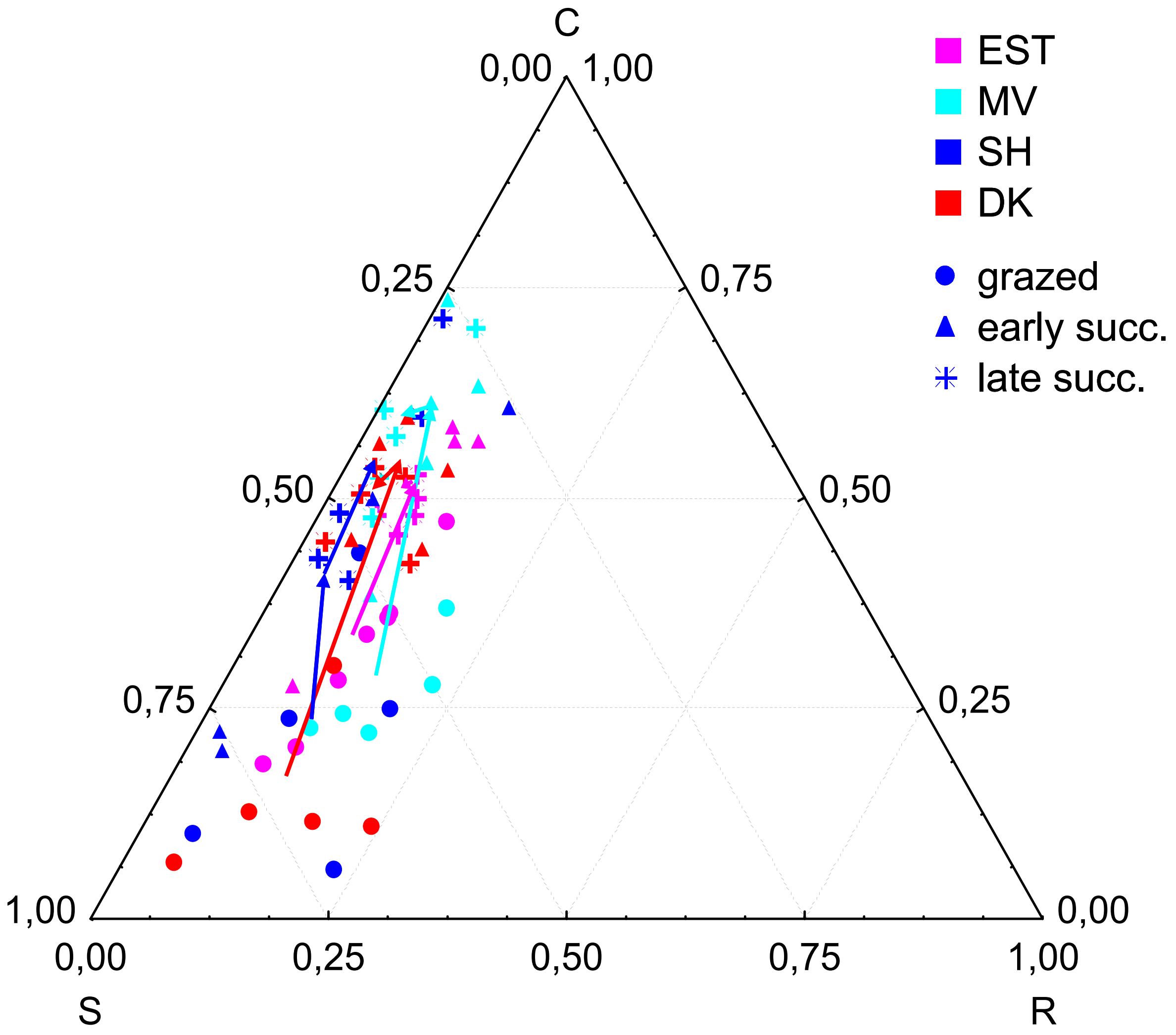


Fig. 4-12: Triangular graph of all 625-m² relevés with C-, R- and S-components (weighted by species' cover). The arrows indicate the successional pathways from grazed to early and late successional sites in the four regions (marked by colours) by connecting the (group) mean of all sites per region and management class.

4.6 Individual species

The impact of management and region on the cover (table 4-18) and frequency (table 4-19) of individual species was also visible. For some species, the impact of management was only significant in the region(s) where the species occurred most frequently, as indicated in the tables.

Table 4-18: Impact of management and region on mean cover (%) of individual species (25-m^2 scale, means of regions and management classes are given in Annex 4). Species are grouped according to their reaction to abandonment and/or distribution between regions. Results of 2-factorial ANOVAs (F, p) or 2 separate Kruskal-Wallis-Tests (H, p). For ANOVAS: *: p<0.05, **:p<0.01, ***: p<0.001. p-levels were Bonferroni-corrected (number of Bonferroni-corrections is given in column 'b-c'). P-levels for 2 analyses: *: p<0.025, **:p<0.005, ***: p<0.0005, for 3 analyses: *: p<0.017, **:p<0.003, ***: p<0.0003, for 6 analyses: *:p<0.0083, **: p<0.0017, ***:p<0.00017. 'Effect': direction of differences between management classes. tr: transformation: lg: log, sq: square-root. Trends are given in brackets if Post-Hoc-test was insignificant, or p-level was slightly above significance-level. The impact of management and region was tested for the most frequent species, but only species with significant effects or trends are listed here.

	Management				Region				Interaction		interaction/		
	F	H	p	effect	F	H	p	effect	F	p	effect in region(s)	tr.	b-c
max in grazed													
Juncus gerardii	11.0		***	G>ES/LS	0.6		0.63		0.3	0.95		lg	
Agrostis stolonifera	8.2		***	G>LS	9.0		***	MV>DK/SH, EST>DK	4.2	**	only in MV: G>ES/LS, MV-G > all others	lg	
Puccinellia maritima		15.0	***	G>LS		12.5	*	SH>EST					3
Glaux maritima		6.0	(0.05)	(G>LS)		5.2	0.16						2
Plantago maritima		13.2	**	G/ES>LS		5.5	0.14						2
Triglochin maritimum	5.8		**	G/ES>LS	1.4		0.25		0.4	0.87		sq	
max in early succ.													
Bolboschoenus maritimus		8.5	*	ES>G		3.8	0.28						2
Festuca rubra		19.2	***	ES>G/LS		0.5	0.91						2
Artemisia maritima		6.7	(0.04)	(ES>G)		20.8	***	DK>MV/EST			(DK+SH:*ES>G)		3
Limonium vulgare		3.2	0.20			26.7	***	DK>MV/EST			(DK+SH:ES>LS)		3
Festuca arundinacea		4.8	0.09			12.7	*	(EST>DK/SH)			EST+MV:(ES>G)		3
Elymus repens		15.6	**	ES/LS>G		3.9	0.27				EST: *ES/LS>G, DK(*): LS>G, SH, MV: ns		6
max in late succ.													
Phragmites australis		43.9	***	LS>G/ES		1.0	0.80						2
Galium palustre		9.1	*	LS>G		29.5	***				EST+MV+DK: ** LS>G/ES		3
Eleocharis uniglumis		1.6	0.46			35.5	***	EST>others			EST: **LS>G, others ns		6
max (or only) in EST													
Carex panicea		2.3	0.31			38.2	***	only EST					
Leontodon autumnalis	0.3		0.75		9.9		***	EST>others	0.2	0.98		lg	
Carex nigra		1.8	0.41			20.5	***	(EST>others)					
Angelica palustris		1.7	0.42			23.8	***	(EST>others)					
Carex distans		1.2	0.54			19.4	***	EST>MV			EST:(ES>LS)		
Vicia cracca		2.7	0.26			9.1	0.03	(EST>SH)					
max in DK													
Aster tripolium		3.2	0.21			11.5	*	DK>EST					2

The impact of management or region on the cover of 22 species is shown in table 4-18. Six species had a higher cover in grazed sites (*Juncus gerardii, Agrostis stolonifera, Puccinellia maritima, Glaux maritima, Plantago maritima* and *Triglochin maritimum).* Six species had their maximum cover in early successional sites *(Bolboschoenus maritimus, Festuca rubra, Artemisia maritima, Limonium vulgare, Festuca arundinacea* and *Elymus repens),* whereas three species increased in cover in late successional sites *(Phragmites australis, Galium palustre* and *Eleocharis uniglumis*).

Five species had a higher cover in Estonia than in the other regions (*Leontodon autumnalis, Carex nigra, Angelica palustris, Carex distans and Vicia cracca*), and *Carex panicea* occurred only in Estonia. In contrast, *Aster tripolium* had a higher cover in Denmark than in Estonia (table 4-18).

For some more species, an effect of management or region on their frequencies was detected (table 4-19). 14 species were more frequent in grazed sites *(Spergularia salina, Puccinellia maritima, Juncus gerardii, Trifolium fragiferum, Agrostis stolonifera, Centaurium littorale, Spergularia media, Triglochin maritimum, Plantago maritima, Glaux maritima, Odontites litoralis, Leontodon autumnalis, Salicornia europaea, Suaeda maritima*). Four species were most frequent in early successional sites *(Festuca rubra* agg., *Artemisia maritima, Festuca arundinacea, Elymus repens*). Six species increased in frequency in late successional sites (*Phragmites australis, Sonchus asper, Oenanthe lachenalii, Bolboschoenus maritimus, Galium palustre, Eleocharis uniglumis*).

Of the species included in the statistical analysis, seven occurred only in Estonia, further 17 species were more frequent in Estonia than in the other regions. Five species were most frequent in Schleswig-Holstein and/or Mecklenburg-Vorpommern, six in Denmark, one in Denmark and Estonia and one in Denmark and Schleswig-Holstein.

Table 4-19: Impact of management and region on mean frequency (%) of individual species (25-m² scale, means of regions and management classes are given in Annex 5). Species are grouped according to their reaction to abandonment and/or distribution between regions. Results of 2-factorial ANOVAs (F, p) or 2 separate Kruskal-Wallis-Tests (H, p). For ANOVAs: *: p<0.05, **:p<0.01, ***: p<0.001. p-levels were Bonferroni-corrected (number of Bonferroni-corrections is given in column 'b-c'). P-levels for 2 analyses: *: p<0.025, **:p<0.005, ***: p<0.0005, for 3 analyses: *: p<0.017, **:p<0.003, ***: p<0.0003, for 6 analyses: *:p<0.0083, **: p<0.0017, ***:p<0.00017. 'Effect': direction of differences between management classes. tr: transformation: lg: log, sq: square-root. Trends are given in brackets if Post-Hoc-test was insignificant, or p-level was slightly above significance-level. The impact of management and region was tested for the most frequent species, but only species with significant effects or trends are listed here.

	Management				Region				Interaction		Effect management in region(s)	
	F	H	p	Effect M.	F	H	p	Effect Region	F	p		b-c
max in grazed												
Spergularia salina		24.0	***	G>ES/LS		7.7	(0.05)	(SH>EST)				2
Puccinellia maritima		16.2	***	G>LS		11.6	*	(SH>EST)				2
Juncus gerardii		14.0	**	G>LS		1.5	0.69					2
Trifolium fragiferum		8.6	*	(G>LS)		5.1	0.17					2
Agrostis stolonifera		6.9	(0.03)	(G>LS)		8.3	(0.04)	(EST>DK)				2
Centaurium littorale		8.1	(0.02)	(G>LS)		24.0	***	EST>MV/SH			EST: * G>LS	3
Spergularia media		9.1	*	(G>LS)		15.4	**	DK>EST			DK+SH+MV: ** G>ES/LS	3
Triglochin maritimum		16.5	**	G/ES>LS		12.0	*	(EST>SH)			MV: *G>LS, others ns	6
Plantago maritima		28.5	***	G/ES>LS		3.8	0.28					2
Glaux maritima	5.3		**	G/ES>LS	0.6		0.60		0.5	0.79		
Odontites litoralis		3.0	0.22			27.6	***	EST>MV/SH			EST:*G> LS	3
Leontodon autumnalis	0.1		0.91		14.4		***	EST>others	0.5	0.82	EST: *G/ES>LS	lg
Salicornia europaea		6.4	*			14.1	**	(DK/SH>EST/MV)			DK+SH: *G>LS	3
Suaeda maritima		9.1	*			4.4	0.11				DK+SH:**(G>LS)	3
max in early succ.												
Festuca rubra agg.		8.6	*	(ES>LS)		0.8	0.86					2
Artemisia maritima		5.3	0.07	(ES>G)		22.4	***	DK>MV/EST				2
Festuca arundinacea		4.7	0.09			14.4	**	(EST>SH)			(EST+MV: peak in ES)	3
Elymus repens		14.2	**	ES/LS>G		3.5	0.32					2
max in late succ.												
Phragmites australis		43.6	***	LS>G/ES		1.3	0.72					2
Sonchus asper		10.5	*	(LS>G)		7.9	(0.05)					2
Oenanthe lachenalii		10.5	*	(LS>G)		7.5	0.06	(MV>others)				2
Bolboschoenus maritimus		7.3	(0.03)	(LS>G)		2.8	0.43					2
Galium palustre		5.9	0.05			33.5	***	EST>others			EST+MV+SH: *(LS>G)	3
Eleocharis uniglumis		0.8	0.66			36.6	***	EST>others			(EST: LS>G)	3
max (or only) in Estonia												
Carex panicea		2.3	0.32			38.2	***	only EST				2
Molinia caerulea		1.3	0.51			34.5	***	only EST				2
Rhinanthus angustifolius		1.4	0.51			20.5	***	(only EST)				2
Blysmus rufus		4.4	0.11			27.2	***	(only EST)				2
Carex nigra		2.0	0.37			20.5	***	(only EST)				2
Angelica palustris		1.7	0.42			23.8	***	(only EST)				2
Selinum carvifolia		0.3	0.85			14.1	**	(only EST)				2
Trifolium pratense		0.9	0.65			27.6	***	EST>others				2
Potentilla anserina	0.1		0.89		5.1		**	EST>others	0.4	0.89		
Carex distans		1.1	0.58			22.3	***	EST>MV/SH				2
Juncus articulatus		0.5	0.77			14.1	**	(EST>MV/SH)				2
Taraxacum officinale		0.2	0.93			13.8	**	(EST>MV/SH)				2
Trifolium repens		1.0	0.60			6.8	0.08	(EST>others)				2
Schoenoplectus tabernaemontani		2.0	0.36			22.3	***	(EST>SH/DK)				2
Centaurea jacea		2.8	0.25			8.2	(0.04)					2
Lotus corniculatus/tenuis		3.8	0.15			7.3	0.06	(EST>DK)				2
max in SH and/or MV												
Cirsium arvense		5.1	0.08			8.4	(0.04)	(SH>DK)				2
Atriplex prostrata		5.1	0.08			12.0	*	MV/SH>EST				2
max (or only) in DK												
Limonium vulgare		2.9	0.24			29.1	***	DK>MV/EST				2
Armeria maritima		2.6	0.28			23.0	***	DK>MV/EST				2
Aster tripolium	0.1		0.95		4.1		*	DK>EST	0.6	0.75		
Cochlearia officinalis		3.6	0.16			20.4	***	(only DK)				2
max in DK and EST												
Centaurium pulchellum		4.5	0.11			8.5	(0.04)	(DK/EST>MV/SH)			(EST:G/R>ES/LS)	2

4.7 Conservation perspective

4.7.1 Characteristic species

The ‘characteristic species’ according to the EU Habitats Directive (1992) were present at a significantly lower percentage in late successional sites (61.6%) than in grazed (86.1%) and early successional sites (82.9%, F=17.54, $p<0.001$, fig. 4-13). The relative number of ‘characteristic species’ decreased with increasing scale (F=63.09, $p<0.001$). The significant interaction scale*management (fig. 4-13 a) revealed that the decrease with increasing scale was most pronounced in grazed sites and not significant in late successional sites (F=4.96, $p<0.01$). In Estonia, ‘characteristic species’ had a lower share than in the other three regions (F=8.35, $p<0.001$), although a significant interaction scale*region showed that this effect occurred only on 25 m^2- and 625 m^2-scale and that the effect of scale was most pronounced in Estonia, and not significant in Denmark (fig. 4-13 b, F=5.79, $p<0.001$, 3-factorial ANOVA with scale as within-factor, data arcsin-transformed).

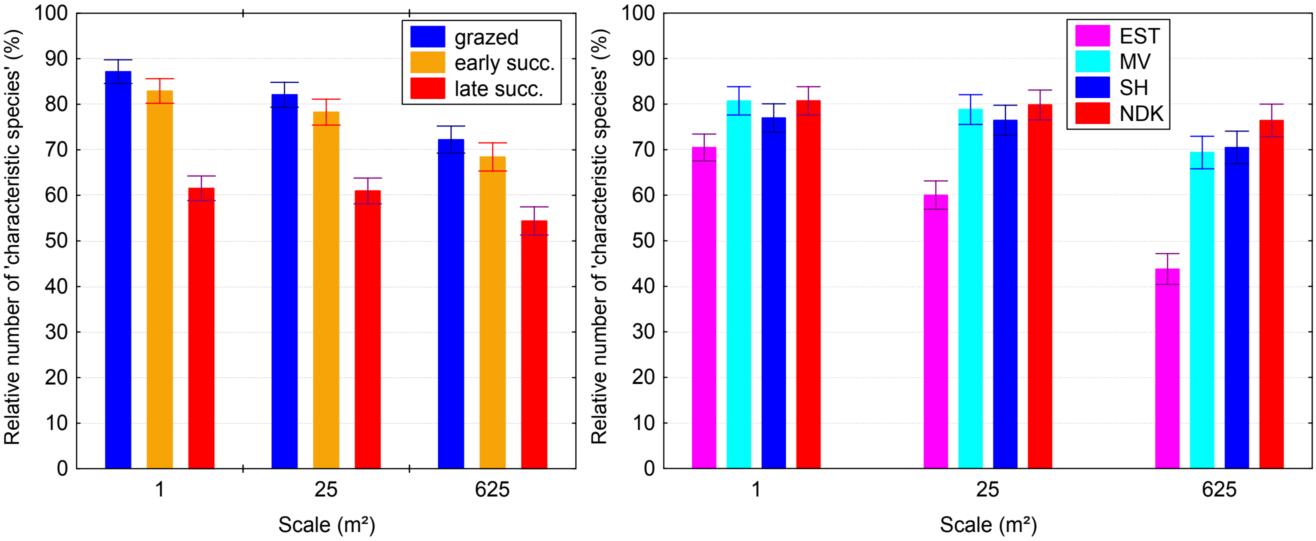


Fig. 4-13: Impact of region and management on mean relative number (± SE) of ‘characteristic species’ of the habitat types ‘*Salicornia* and other annuals colonising mud and sand (1310)’, ‘Atlantic Salt meadows (1330)’ and ‘Boreal Baltic Coastal Meadows (1630)’ according to the EU Habitats Directive (listed in EC 1992, EU Interpretation Manual, plus *Angelica palustris* as a priority species of Annex II) on 1, 25 and 625 m^2. Results of 3-factorial ANOVA with scale as within-factor (data arcsin-transformed): Management: F=17.54, $p<0.001$, Scale: F=63.09, $p<0.001$, Interaction Scale*Management: F=4.96, $p<0.01$, Region: F=8.35, $p<0.001$, Scale*Region: F=5.79, $p<0.001$.

The relative cover of ‘characteristic species’ was also significantly lower in late successional sites than in grazed and early successional sites, with a much stronger decrease than for relative species number (from 93.0% in grazed and 91.4% in early successional to 44.5% in late successional sites, F=93.69, $p<0.001$, fig. 4-14). The relative cover of ‘characteristic species’ decreased with increasing scale (F=53.08, $p<0.001$). The effect of scale was only significant in grazed and early successional sites (fig. 4-14a, interaction scale*management: F=7.63, $p<0.001$). The relative cover of ‘characteristic species’ was significantly higher in Mecklenburg-Vorpommern than in Estonia, while Schleswig-Holstein and Denmark showed intermediate values (F=4.17, $p<0.05$). The regions differed only on 625 m^2-scale, and differences in scale were only significant in Mecklenburg-Vorpommern and – more pronounced – in Estonia (fig. 4-14b, interaction scale*region: F=6.68, $p<0.001$, 3-factorial ANOVA with scale as within-factor, data arcsin-transformed).

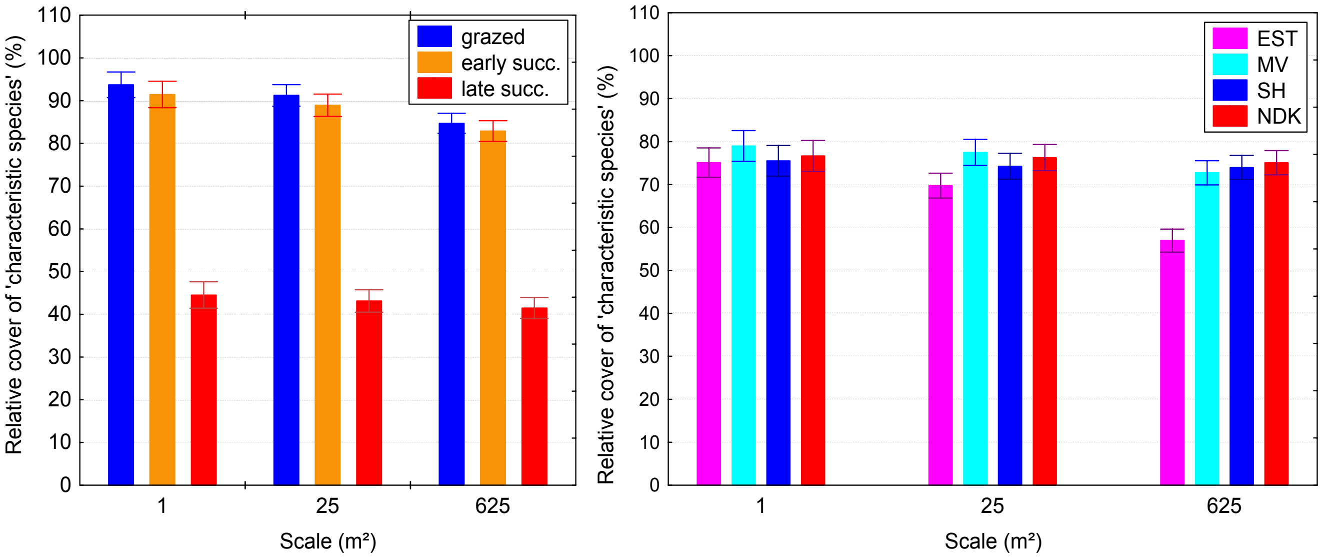


Fig. 4-14: Impact of region and management on mean relative cover (± SE) of 'characteristic species' of the habitat types '*Salicornia* and other annuals colonising mud and sand (1310)', 'Atlantic Salt meadows (1330)' and 'Boreal Baltic Coastal Meadows (1630)' according to the EU Habitats Directive (listed in EC 1992, EU Interpretation Manual, plus *Angelica palustris* as a priority species of Annex II) on 1, 25 and 625 m². Results of 3-factorial ANOVA with scale as within-factor (data arcsin-transformed): Management: F=93.69, $p<0.001$, Scale: F=53.08, $p<0.001$, Interaction Scale*Management: F=7.63, $p<0.001$, Region: F=4.17, $p<0.05$, Scale*Region: F=6.68, $p<0.001$.

4.7.2 Red List species

In total, 25 species of the 'Red List of vascular plants of the German Baltic coastal area' (Berg et al. 1996) were found in the German study sites. 22 Red List species occurred in the study sites in Schleswig-Holstein (14 in grazed, 16 in early successional and 9 in late successional sites), and 15 in those in Mecklenburg-Vorpommern (7 each in grazed and early successional, and 8 in late successional sites). 12 species occurred in both regions (*Juncus gerardii, Triglochin maritimum, Aster tripolium, Puccinellia maritima, Oenanthe lachenalii, Salicornia europaea, Artemisia maritima, Armeria maritima, Centaurium pulchellum, Trifolium fragiferum, Plantago major ssp. winteri, Carex viridula* var. *viridula).* Ten species occurred only in Schleswig-Holstein *(Limonium vulgare, Carex distans, Suaeda maritima, Cochlearia anglica, Ophioglossum vulgatum, Sagina maritima, Carex extensa, Althaea officinalis, Plantago coronopus, Apium graveolens).* Three Red List species occurred only in Mecklenburg-Vorpommern *(Odontites litoralis, Triglochin palustre, Inula britannica).*

The percentage of Red List species was higher in Schleswig-Holstein than in Mecklenburg-Vorpommern (F=8.43, $p<0.01$), and was significantly lower in late successional sites than in early successional and grazed sites (F=5.97, $p<0.01$). However, the impact of management differed between the two regions, as the significant interaction showed (fig. 4-15, region*management: F=3.86, $p<0.05$): In Schleswig-Holstein, the percentage of Red List species initially increased from 39.2% in grazed to 48.5% in early successional sites and then significantly decreased to 23.4% in late successional sites. In contrast, the percentage of Red List species did not differ significantly in Mecklenburg-Vorpommern and only slightly (and steadily) decreased from 32.5% in grazed to 24.7% in early successional and 23.0% in late successional sites.

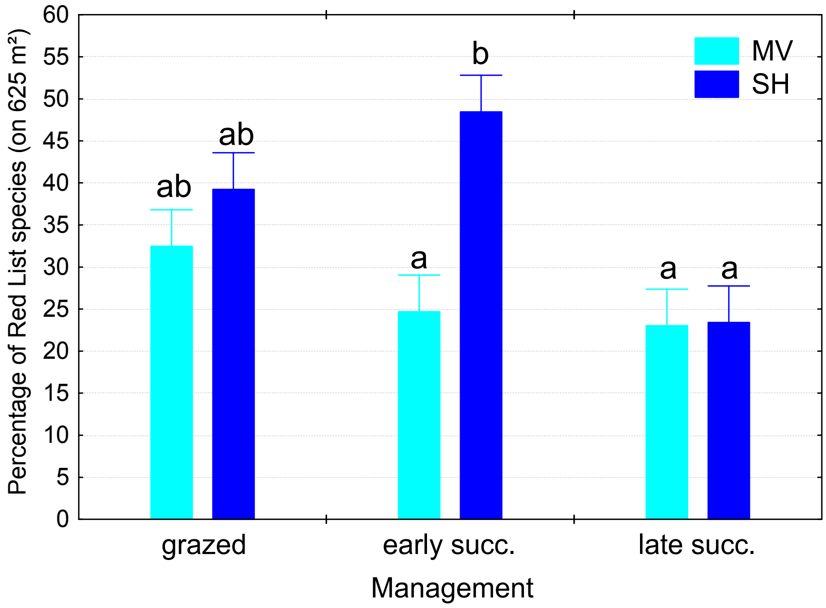


Fig. 4-15: Percentage of Red List species (Mean ± SE) in Schleswig-Holstein and Mecklenburg-Vorpommern on 625-m²-plots (after Berg et al. 1996). Results of a 2-factorial ANOVA: Region: F=8.43, p<0.01, Management: F=5.97, p<0.01, Interaction region*management: F=3.86, p<0.05. A, b: significant differences according to Post-Hoc-Test (Tukeys HSD).

5 Discussion

5.1 Discussion of methods

Soil salinity

Soil salinity was measured related to dry matter. However, for conclusions on the physiological effectiveness of salt, chloride or salinity, measurements related to % of dry soil have to be referred to the soil solution (Schmeisky 1974). Unfortunately, the water content could not be determined for all samples properly under field conditions due to technical reasons.

For 33 sites where the water content was determined, a linear correlation with salinity related to dry matter (in psu) and salinity related to soil solution (in psu) explained 78% of the variation. A regression fitted with a power function even explained 96% of the variation (Fig. 5-1). This illustrates that salinity related to dry matter can be used as an indicator for soil salinity. The absolute values related to soil solution are about 30% of the values related to dry matter, which are given in the text, and are in the same range as those measured by Schmeisky (1974: 5.4-28.9 psu at the same location, 1.8-39.7 psu under different plant communities).

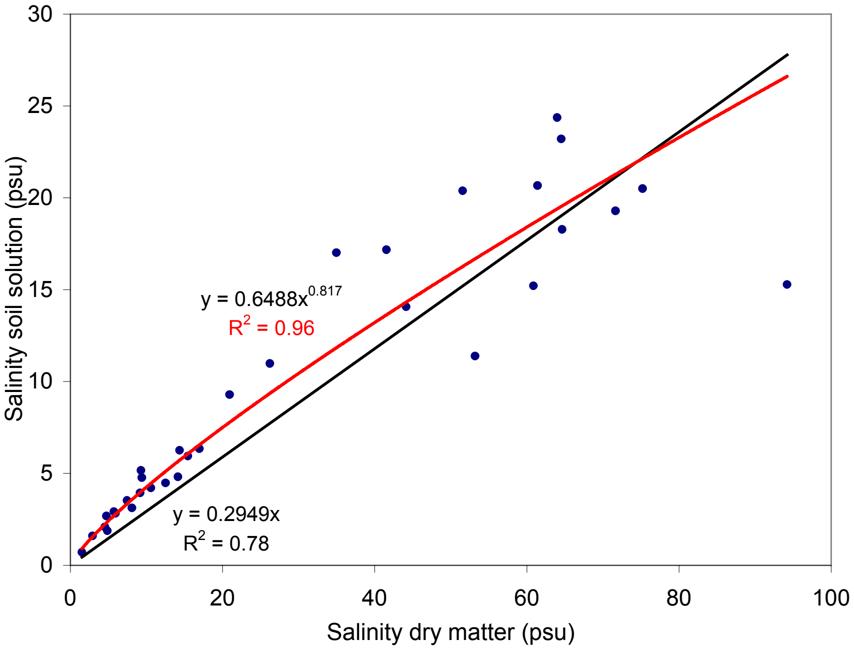


Fig. 5-1: Correlation between salinity related to dry matter (psu, as listed in results chapter) and salinity related to soil solution (psu). Linear correlation: $r^2 = 0.78$, regression following a power function: $r^2 = 0.96$.

However, the water content also varied strongly between sites, from 44% to 84%. Thus salinity of the soil solution may vary up to the factor of 3.5 depending on the water content of individual samples. The water content was significantly correlated to organic matter content ($r^2=0.53$), indicating that one factor influencing soil water content is the soil type and that peaty soils contain more water than mineral soils.

Both water content (Tyler 1971a, Vestergaard 1998) and salinity itself are strongly influenced by weather conditions such as precipitation, evaporation and inundation, which cause strong spatial variation and fluctuations throughout the year and also within the season primarily in the upper soil layer (Tyler 1971a, Schmeisky 1974). In Mecklenburg-Vorpommern as well as in Schleswig-Holstein, salinities between the investigation years differed significantly (Mecklenburg-

Vorpommern: F=8.24, p<0.01, 2004 (Mean of 56.4 psu) > 2006 (21.3 psu)/2007 (27.5 psu), Schleswig-Holstein: F=10.93, p<0.01, 2005 (mean of 56.5 psu) > 2006 (19.8 psu)). This may demonstrate that weather conditions strongly influenced the salinity values. For a more precise determination of soil salinity, a series of measurements at each location would be necessary. Since this was not the main aim of the study and not possible for practical reasons, the measured salinity values as 'snapshots' can only serve as rough relative measurements.

A significant correlation of the measured soil salinity with the mean salt indicator value explaining 47% of the variation (in single regions: 29% in Mecklenburg-Vorpommern and Schleswig-Holstein, 53% in Estonia and 55% in Denmark) proposes that the values can be used for a comparison, but also that they are influenced by various factors (which were not measured).

Elevation and inundation frequency

Due to different measurement frequencies of water levels in the four study regions, the number of days that a site was flooded was calculated, instead of the number of floodings (as is usually calculated for the North Sea coast). The latter would be higher in particular where lunar tides are the most important cause for water level fluctuations. For the study sites in this report, the highest deviation would be for the lowest elevations in Northern Denmark (approx. 20 cm above and below mean sea level).

Since the elevation measurements were taken relative to sea level at the time of measuring and then referred to the measurement of the nearest water level station – across a distance of up to 45 km –, the calculation of the elevation and hence the inundation days includes an error. For Estonian sites, the extrapolation of the Heltermaa data with the relative deviation between 2 and 24 values per day from Pärnu may have added further uncertainty to the calculated inundation frequencies.

Bockelmann et al. (2002) demonstrated that local inundation frequency of different sites at the same elevation can deviate up to 300% already at a distance of 2.5-5 km. Thus, measured and estimated inundation frequencies were only reliably correlated within tens of metres, but not within hundreds of metres or kilometres. However, since inundation in the Baltic is not caused by tides, but occurs irregularly depending on wind directions and forces, major changes of water level occur less often (not twice a day like in lunar tides) but for longer time periods. Furthermore, the salt grassland sites are much smaller than the North Sea salt marshes and do not have an extensive tidal creek system, which should cause a smaller time-lag between water fluctuations in coastal waters and in salt grassland stands (except for local depressions which retain the water after inundation). Thus, the error may be somewhat smaller than in tidal marshes. Nonetheless, the specified elevation and inundation frequency can only be a rough estimate to compare individual study sites.

5.2 Environmental gradients

The four study regions do not only differ in salinity of the Baltic Sea, but represent sections of a complex ecological gradient. In the following, these aspects which characterise salt grassland vegetation will be discussed.

Elevation and inundation frequency

In Estonia, the investigation sites were located at slightly lower elevations than in the other three regions. Inundation frequency was slightly higher, but differences were – in contrast to those of the elevation – not significant, since the same elevation is less often flooded in Estonia than in the other regions. In particular in Denmark and Schleswig-Holstein, higher inundation frequencies in the lowest 20-25 cm (except for Skagen) indicate a somewhat higher relevance of the tidal component. At elevations above 50 cm, inundation frequency was highest in Pärnu due to the described local 'funnel effect', where also the highest absolute flood (in the years 1995-2007 for which sea level data was analysed) of 275 cm ASL occurred (January 2005, Suursaar & Sooäär 2007). The study sites were located between 4 and 71 cm above sea level, which corresponds to the extension of the geolittoral specified as 60-75 cm by Vestergaard (1998) in south-eastern Denmark, and also to the extension of the 'seashore meadow proper' of 45 to 52 cm by Tyler (1971a).

Lower sites of e.g. 15 cm elevation above sea level were flooded between 102 days/year (near Pärnu in Estonia) and 230 days/year (near Grenå in Denmark), which is comparable to the lower salt marsh at the North Sea coast being flooded 250 times/year (between -20 and +25 cm above mean high tide, Dierßen 1988). The middle geolittoral zone (40 cm ASL) is flooded 26-64 days/year in Estonia, 27-44 days/year in Mecklenburg-Vorpommern, 44-51 days/year in Schleswig-Holstein and 43-75 days/year in Denmark. This is about equivalent to the upper salt marsh of the North Sea (above 25 cm ASL) with 40-70 inundations/year (Dierßen 1988), and to the *Juncetosum gerardii* at the Swedish Baltic coast (5-6 days/month in July and 6-10 days/month in autumn and winter, Tyler 1971a). Thus, the flooding frequency of the lower and middle geolittoral at the Baltic Sea coast is comparable to that of North Sea salt marshes, although the tidal range – and therefore the extension of the salt marshes – is higher at the North Sea than the inundation range and extension of salt grasslands at the Baltic.

The mean high water level in high-tidal areas ecologically corresponds to the mean water level in low-tidal areas, both being indicated by the lower limit of continuous vegetation (Beeftink 1977, Ellenberg 1996, Vestergaard 1998). An exponential relation of the flooding frequency to elevation as in the presented data set was also found by Vestergaard (1998) for south-eastern Denmark and by Jerling (1984) for the inner Baltic. A similar pattern is also found in tidal areas (Ranwell 1972, Jensen 1974), in spite of the differences in hydrography between Baltic and North Sea.

Salinity gradient

Soil salinity values strongly varied, which was partly due to methodological reasons (see above). Soil salinity values were in some cases lower than the salinity of the adjacent sea water because of dilution by rainfall, in other sites soil salinity was higher than the salinity of sea water due to evaporation and subsequent salt accumulation. Also upward salt transport from the groundwater is possible (Schmeisky 1974).

It is not clear why soil salinity did not differ significantly between Denmark, Schleswig-Holstein and Mecklenburg-Vorpommern, although the salinity gradient of the Baltic Sea water is steepest in this part of the Baltic Sea. The strongest decrease of sea water salinity can be observed from Northern Denmark to Schleswig-Holstein (about 50%), and – somewhat less pronounced in absolute values – again by about a third from Schleswig-Holstein to Mecklenburg-Vorpommern. That salinity values in Denmark were found to be slightly lower than those in Schleswig-Holstein and Mecklenburg-Vorpommern, whereas relevant site conditions did not differ in other respects (such as elevation and inundation frequency), does not seem to have a 'real' ecological background. This might be caused by the mentioned methodological reasons and because the measurements only represent a 'snapshot' of highly variable salinity conditions, which also causes the large differences between sites in particular in Schleswig-Holstein and Mecklenburg-Vorpommern.

Dijkema (1990) pointed out that the middle and upper geolittoral of different localities along the Baltic are less different in soil salinities than the salinity of the flooding water, because they are comparatively rarely flooded and because soil salinity is strongly determined by climatic and hydrological factors (evaporation, precipitation, drainage). During the growing season, conditions are relatively dry and high soil salinities are often found in the upper geolittoral – quite similar to those in the North Sea region. This is confirmed by Vestergaard (1998) who found that in the lower geolittoral, a shift occurred between *Puccinellia maritima* dominated communities to *Agrostis stolonifera* communities at 10-12 psu in South-eastern Denmark. He could not detect a similar shift in the upper geolittoral and presumes that this occurs in the inner Baltic at much lower sea water salinity levels. Jeschke (1987) mentioned that the climatic gradient already along the coast of Mecklenburg-Vorpommern (towards a more continental climate and increasing evaporation eastwards) counteracts the decreasing salinity.

The salt indicator values did not differ between the three western regions. As in many other parameters, the more fundamental change occurred only in Estonia. This may indicate that there is a certain salinity threshold, below which salinity does not exclude many species. Only above the threshold, are specific adaptations necessary to tolerate the salinity impact.

Nutrient gradient

The higher phosphate content of the soil in Denmark and (also slightly) Schleswig-Holstein compared to Estonia and Mecklenburg-Vorpommern is likely to be caused by higher phosphate loads in the Western Baltic mainly from diffuse sources such as agriculture and scattered dwellings (Knuuttila 2007). Total phosphorus loads in the year 2000 were 61 kg P/km² in the Danish part of the Kattegat (study region Northern Denmark), 30 kg P/km² in the German part of the Western Baltic (study region Schleswig-Holstein), but only 14 kg P/km² in the German part of the Baltic proper (study region Mecklenburg-Vorpommern) and 10 kg P/km² in the Estonian part of the Gulf of Riga (study region Estonia, HELCOM 2004).

Soil phosphate contents at the Danish sites on the island of Læsø were slightly lower (mean of 7.2 mg P_2O_5/100g) than at mainland sites (12.6 P_2O_5/100g, $p=0.055$), which may indicate that phosphate was not mainly imported by inundation of sea water, but by direct run-off from adjacent agricultural fields, which neighboured most of the mainland, but not the island sites.

In contrast to phosphate, nitrogen content did not steadily increase towards the Western Baltic, although nitrogen loads showed similar spatial patterns as phosphorus loads. Total waterborne nitrogen loads in the year 2000 decreased from 2,126 kg N/km² in Northern Denmark to 1,199 kg N/km² in Schleswig-Holstein, 487 kg N/km² in Mecklenburg-Vorpommern and 582 kg N/km² in Estonia (HELCOM 2004). Instead, the nitrogen content of the soil was strongly correlated to the organic matter content ($r^2=0.97$). Nitrogen content thus seemed to depend primarily on soil type, being higher in sites of the 'deep soil type'. This indicates that nitrogen is predominantly taken up by the salt grassland vegetation and – together with carbon – accumulated in the organic layer, especially when peat is formed.

Ellemann et al. (2001) mentioned eutrophication – directly by fertilisers to salt grasslands or adjacent areas, and indirectly through the inundating sea water and atmospheric deposition – as one of the factors threatening salt grasslands. Fertilisation affected at least 12-39% of salt grassland localities (Ellemann et al. 2001). According to Fyns Amt (1993), nutrient input favoured grass species such as *Elymus repens, Lolium perenne* and *Festuca rubra* at the cost of species of nutrient poor soils, and resulted in a marked decline of species numbers. In the Danish list of criteria for a favourable conservation status following the Habitats Directive, a 'natural nutrient level' is included as one of the parameters of structure and function of Atlantic Salt meadows (type 1330), which must not exceed 30-40 kg N/ha*year (Søgaard et al. 2005). Puurmann & Ratas (1995) assume that the expansion of reed beds in Estonia is associated with the eutrophication of the Baltic Sea. Whether the increased atmospheric and waterborne nitrogen input in the last decades has affected salt marsh vegetation along the North Sea coast and in particular the spread of *Elymus athericus* (even in intensively grazed sites, Gettner et al. 2000), is discussed controversially (Leendertse 1995, Hennings 1995, Bockelmann & Neuhaus 1999, van Wijnen & Bakker 1999, Rozema et al. 2000, Bockelmann 2002).

Plant growth in temperate salt marshes in Europe and North-America is mostly nitrogen limited (Kiehl et al. 1997, Rozema et al. 2000), but in a few cases phosphorus limitation was also demonstrated (e.g. Tyler 1967). That no steady increase in nitrogen content of the soil towards the west (correlated to higher nitrogen loads in the Baltic) was found, does not necessarily mean that these nitrogen loads do not affect the salt grasslands. It is also possible that the additional nitrogen was not stored in the soil, but taken up by the plants and therefore was not measured in the soil. This may be indicated by the increasing Ellenberg nitrogen value in the Western part of the Baltic Sea region compared to Estonia. However, this pattern may have also been caused by the increased frequency of the 'deep soil type' with higher nitrogen values, visible in the strong correlation between mean nitrogen value and organic layer.

Stress gradient

The analysis of CSR-strategy types revealed that the S-component increased towards higher salinities, while the competitor-component slightly (marginally non-significantly) decreased. The decrease of the C-component may be explained in two ways: on the one hand, it might be an indicator for a factual decrease of competition towards higher salinities. On the other hand, it might be caused by the enforced constraint of the C-, S- and R-components to always add up to one. Thus, the C-component automatically decreases if the S-component increases and the R-component does not change (see Loehle 1988 for problems caused by the constrained geometry of Grime's triangular model).

Upon closer inspection of the distribution of (the original) CSR-strategy types, S- and SR-strategists increased towards higher salinities, while CSR-strategists decreased. CSR-strategists had a significantly higher relative (and even higher absolute) species number only in Estonia, and were responsible for the increase of the C-component in Estonia. They dominate for example in unfertilised pastures in temperate regions characterised by mineral nutrient stress and moderate intensities of disturbances by defoliation by grazing animals (Grime 1979). Therefore, they represent different site conditions and a different relevance of competition compared to 'pure' C-strategists. Thus, it may be concluded that the investigated Baltic Sea ecological gradient is primarily a gradient of abiotic (salt) stress.

Salt grassland soil types

Some abiotic conditions (such as organic layer, nitrogen content, organic matter content and pH) varied between the regions, but were to a large extent correlated to the occurrence of the two salt grassland soil types. These two salt grassland soil types represent a different development (history) of salt grasslands that is associated with a number of abiotic parameters and consequently differences in the vegetation – not only in species richness.

The **'deep soil type'** dominated in Mecklenburg-Vorpommern and Schleswig-Holstein (in both regions 80% of the sites) and also occurred in Northern Denmark at the mainland coast (6 of 7 mainland sites). It represents coastal peatlands with a deep organic layer (in most cases at least 30 cm), a high organic matter content (> 30% in Mecklenburg-Vorpommern, >15% in all regions), high N-content, and comparatively low pH. The vegetation is – due to the relatively high nutrient content - characterised by a high mean Ellenberg nitrogen value, and by a low species richness (Grime 1973).

As described in chapter 2 (2.3), the formation of these coastal peatlands is enhanced in particular in regions of land subsidence, such as the Southern Baltic Sea coast (Schleswig-Holstein and Mecklenburg-Vorpommern). In shallow, sheltered coastal areas first brackish reed beds developed and started to form (reed) peat. Grazing and trampling by cattle led to the transformation of brackish reed beds to salt grasslands and further enhanced peat growth above the mean water level Jeschke (1987). Thus all older, 'ripe' salt grasslands in the eastern part of Mecklenburg-Vorpommern are located on peat soils (Jeschke 1983). After the start of agricultural use for grazing, salt grasslands were also formed directly without an initial reed bed phase. On the Graswarder peninsula in Schleswig-Holstein, a reed peat layer was found only under beach ridges older than 300 years, where presumably grazing was started (Perschke 1974, Schmeisky 1974).

The Danish sites of the 'deep soil type' were located at the mainland coast (which is slightly rising by 0.25 mm/year, Christiansen et al. 1991, Fenger et al. 2008) and often in sheltered inner parts of fjord mouths (Randers and Mariager fjord). Their organic layer was shallower than in Schleswig-Holstein and Mecklenburg-Vorpommern and the organic matter content mostly somewhat lower. Thus, most sites in Mecklenburg-Vorpommern and Schleswig-Holstein fulfil the definition of a peatland with an organic layer >30 cm and an organic matter content >30%, while a few – and all in Denmark – are intermediate and could be called 'developing coastal peatlands'.

The '**shallow soil type'** was represented by all Estonian sites and the majority of Danish sites, in particular of those on the island of Læsø, and by three sites each in Schleswig-Holstein and Mecklenburg-Vorpommern. Estonia as well as Northern Denmark are located in the part of the Baltic Sea, which is subjected to an isostatic land rise (see 2.3). This land rise reaches 2-3 mm/year in Estonia (Puurmann et al. 2002), 0.25 mm/year at the Kattegat mainland coast (Fenger et al. 2008) and 5 mm/year on the island of Læsø (Hansen 1995). Thus in these regions, salt grasslands are formed on former sea beds rising from the sea. An organic layer is formed only slowly after the first colonisation by plants, and these young, shallow, mineral soils are comparatively poor in organic matter and nutrients. In Estonia and Schleswig-Holstein, they have a rather high pH, and in Estonia the content of inorganic carbon (carbonate) is higher than in the other regions.

Since the relief of this 'shallow soil type' still represents the former sea bed, it is more varied resulting in a more variable microrelief of the salt grassland, a higher variation of soil chemical properties and more different microhabitats. The formation of beach ridges, together with the land-rise, takes part in the development of salt grasslands (Christiansen et al. 1991) and leads to a variable relief (Vestergaard 2003). This probably contributes to the higher species richness, as well as the lower nutrient availability.

While these similarities between Estonia and Northern Denmark were apparent at the first glance, it was more striking to find some species-rich sites with similar abiotic characteristics also in the land subsidence regions of Schleswig-Holstein and Mecklenburg-Vorpommern.

At the Southern Baltic coast, salt grasslands of the 'shallow soil type' were found on some of the beach ridge systems, where new land spits were formed by waterborne transport of sand and clay. These soils are also young and developing, but, in contrast to those in land rise regions, formed by erosion-sedimentation processes. On these sand, gravel and/or clay ridges, a shallow organic layer is likewise formed after colonisation by plants. Just like at the rising coasts, the microrelief is much more variable than in salt grasslands of the deep soil type. This leads to a mosaic of wet salt grassland (or even hydrophyte) vegetation in the depressions, where peat formation is enhanced by wet and oxygen-poor conditions (peat layers of up to 1 m depth at the bottom of the oldest beach ridges on Graswarder, Schmeisky 1974), and transitions to – non halophytic – dry grasslands (Schmeisky 1974, Erfurt & Dierschke 1992) or heathlands (Vestergaard 2003, Wilms 2008) on the highest sandy or gravely (former) beach ridges. At such locations, salt grasslands are part of a primary autogenic succession (Jeschke 1987). Grazing helps to maintain them in a rather early successional state for longer periods.

Such sites were found at the nature reserve Oehe-Schleimünde (see also Erfurt & Dierschke 1992), at the mouth of the coastal lagoon Sehlendorfer Binnensee, at the coast of the island Hiddensee and the Zingst peninsula and the lagoon system Landower Wedde on Western Rügen. Due to the mosaic patterns in these systems, also sites of the 'deep soil type' were found in some of these areas (Oehe-Schleimünde, Landower Wedde). The sand spit Graswarder represents a further good example of the 'beach ridge system type' although only patches of the 'deep soil type' in the depressions were sampled.

The more gradual transitions towards non-saline habitats such as heathlands (Vestergaard 2003), *Carex*-rich paludified meadows (Puurmann & Ratas 1998), dry calcareous grasslands (alvar grasslands, Puurmann et al. 2002, Kaljuste 2004b) or woodlands (Dijkema 1984) were a further difference to the salt grasslands of the 'deep soil type'. Dijkema (1984) emphasised these natural transitions to woodland, bog and heath communities as an 'exceptionally well-developed aspect of Baltic shore marshes', which have almost been lost in most European salt marshes. Also Doody (2008) mentioned that larger estuarine marshes especially in the southern North Sea were 'truncated' by land enclosure by dikes. Unfortunately, this is also true for most parts of the Southern land subsidence coast: in the Baltic, in most salt grassland sites in Schleswig-Holstein and Mecklenburg-Vorpommern, an 'upper salt marsh zone' – and any further transition to non-saline habitats – is nearly completely missing because it was lost when dikes were constructed. Such natural transitions exist at the southern Baltic coast only in the described beach-ridge systems with a highly varying microtopography.

A characteristic structural element of upper salt grasslands are anthills (mostly of the ant species *Lasius flavus,* Vestergaard 1998), which further enhances the diversity of microhabitats. These anthills are included as an indicator of high habitat quality of Atlantic Salt Meadows (Habitat type 1330) in the evaluation scheme for the Habitat Directive for Germany (BfN/Krause et al. 2007).

Still, they were hardly observed in the German study sites, but more frequently in Northern Denmark *and also Southern Sweden* (outside the study regions, pers. obs.).

On the island of Læsø, anthills form a characteristic part of the landscape and one of the most species-rich landscape elements, because they are colonised by halophytes and glycophytes, perennials and annuals (Wilms 2008). On these anthills, salt intolerant species may occur, such as *Calluna vulgaris, Nardus stricta* and *Empetrum nigrum* indicating the transition to heathland (Hansen 1995, Wilms 2008).

Vestergaard (1998) describes the colonisation of the upper part of grazed meadows by the ant species *Lasius flavus* as an indirect effect of grazing. However, anthills were also observed a long time after grazing abandonment on Oehe-Schleimünde in Schleswig-Holstein (Erfurt & Dierschke 1992), at the Landower Wedde in Meckleburg-Vorpommern (Dücker 1996) as well as in some Danish 'early' and 'late successional' sites of the shallow soil type on Læsø (pers. obs.).

According to the organic matter content and thickness of the organic layer (mostly 10-20 cm, up to more than 40 cm), the salt grasslands in south-eastern Denmark (Vestergaard 1998) can be assigned to the 'deep soil type' with partly very high organic matter content (more than 50%) especially in the middle geolittoral. In contrast, salt grasslands in the land rise area at the Swedish Baltic Sea coast (60-150 km south of Stockholm) had low organic matter content and no distinct humus layer (Tyler 1971b), which corresponds to the 'shallow soil type'. The organic layer in Finnish (Jutila 1997) and Estonian salt grasslands (Puurmann & Ratas 1998) was also rather thin. In comparison to this report's Estonian study sites, Sammul (2008) found a thicker organic layer of 10-13 cm (vs. 6-15 cm, mean 9.6 cm*),* a higher organic matter content (35-47% vs 7-27%, mean of 15.8%), a higher nitrogen content (1.3-1.5& vs. 0.37-1.22%, mean 0.7%) and a lower pH (5.6-6.1 vs. 5.2-6.8, mean of 6.3). Thus their study sites were 'peatier' and richer in nitrogen than here, but still corresponding to the 'shallow soil type'.

In the sedimentary tidal salt marshes of the North Sea area, organic matter content is rather low compared to the peaty soils of the 'deep soil type' (mean of 8.4% in Great Britain, Gray & Bunce 1972, and 10-13% in the upper soil layer in the middle part of Dutch marshes, Beeftink 1977).

The two Baltic salt grassland soil types differentiated here largely correspond to two of three types of shore salt marshes developing on autochthonous material distinguished by Dijkema (1984). The 'deep soil type' is identical with the 'peat type salt marsh', whereas the 'shallow soil type' largely corresponds to the 'land upheaval salt marsh, flat type'. Following Dijkema (1984), the land upheaval type is confined to the Northern Baltic Sea region, whereas he mentioned the peat type also for western Ireland. The third type, 'land upheaval salt marsh, skerry type' does not occur in any of the study regions, but along the Swedish and Finnish coastline (Dijkema 1984).

5.3 Plant geographic perspective

5.3.1 Comparison of the Baltic with the North Sea region

The similarity of Baltic and North Sea salt grasslands decreases towards the East. In general, in the Baltic seems to be a rather gradual transition with a very high similarity to North Sea salt marshes in the Kattegat region (pers. obs.) and to a large extent, also still in Schleswig-Holstein (Härdtle 1984).

However, with *Elymus athericus*, *Atriplex portulacoides* and *Spartina anglica*, the three species dominant in the terminal phase of succession in ungrazed conditions at the North Sea coast are (more or less) totally missing in the Baltic Sea salt grasslands. This is a fundamental difference in particular when regarding the course (and result) of succession after abandonment. That Raabe (1950) and Härdtle (1984) emphasise the high floristic affinity of the Schleswig-Holstein Baltic coast to the Atlantic west, may be explained by their rather phytosociological than vegetation ecological (and functional) perspective: both authors do not evaluate species according to their relevance in successional processes. It could also be due to the fact that at that time (1950s and 1980s) ungrazed salt grasslands – dominated by the mentioned species – were very rare, since almost all salt grasslands at the Wadden Sea coast were intensively grazed by sheep (Kempf et al. 1987).

Here, the geographic distribution limits of these three species and (possible) reasons why they are not present in the Baltic will shortly be described – including an estimate on future changes of their distribution ranges, where possible.

Spartina anglica was introduced to the Wadden Sea coast since 1927, and today often dominates the pioneer zone close to mean high water level. It was also introduced to a few places at the Kattegat coasts of Northern Denmark around 1950, where it established well, too (e.g. Randers and Mariager Fjord, Limfjord entrance, Nehring & Adsersen 2006, personal observation). It tolerates salinities of 5-40 psu (Nehring & Adsersen 2006). Its northern limit is at present at 57.5 °N (Metzing 2005) and seems to be caused by its sensitivity to frost (Adam 1990, Metzing 2005, Nehring & Adsersen 2006). Metzing (2005) mentioned that it is unclear whether the distribution area of *Spartina anglica* is saturated. He expects an extension of its distribution range further north, since it apparently benefits from global warming and as it has been becoming more abundant during the last decades (Loebl et al. 2006, Nehring & Hesse 2008). Since it is rather adapted to the intertidal zone, Metzing (2005) considers an extension of its range to the Baltic region as unlikely because the tidal effects are missing there. However, this does not seem to hold for the Danish Baltic, since *Spartina anglica* recorded on the island of Læsø in 1997 and further south on the island of Funen in 2005, where it seems to have established itself after long-distance dispersal either by water or by waterfowl (Nehring & Adsersen 2006). Vestergaard (1989) assumes that the distribution reflects the combined effect of high sea water salinity and high tidal amplitude in the Wadden Sea, and that a further spread to the inner waters may be prohibited by too high a frequency of frost and formation of an ice-cover in winter, which produces anaerobic conditions in the substrate (Ranwell 1972).

Atriplex portulacoides is characteristic for the North Sea lower salt marshes, where it becomes dominant without grazing. Its northern distribution limit is at the Southern Danish North Sea coast, probably because of its sensitivity to frost and/or low winter temperatures (Metzing 2005). Metzing (2005) mentioned some insecure sources of records from the Baltic coast from the 19th century, and Hultén (1950), Meusel et al. (1965) and Mossberg (1992) indicated one or two locations in the Danish Belt Sea (island Endelave, Northern Sjaelland). That *Atriplex portulacoides* does not occur in the Baltic further south (e.g. Schleswig-Holstein) may either be related to climate which is more continental than at the North Sea coast, or due to historical reasons. *Atriplex portulacoides* might have – so far – not invaded into the Baltic Sea Region, since it would have (had) to spread around the Danish mainland first north and then south again. However, with global warming, Metzing (2005) predicts a spread to the Baltic Sea region. Also Normand et al. (2007) found a high increase in the bioclimatic suitability of Denmark for *Atriplex portulacoides* under a climate change scenario. Dijkema (1984) already reported a northward extension of the distribution area of i.a. *Atriplex portulacoides* on the Danish west coast.

Atriplex portulacoides as a 'southern species' is one of the differential species by which Géhu & Rivas-Martinez (1984) separated three sectors in the 'North-Atlantic-Baltic sub zone': The southern sector *with Atriplex portulacoides* ranges from Southern Ireland to the Belgian, Dutch and Wadden Sea coast. The northern sector includes Northern Ireland, Scotland, southern Norway, Western Sweden, Denmark (starting north of the Danish Wadden Sea), Schleswig-Holstein and the Wismar Bight. The Baltic sector comprises the whole Baltic from a line east of the Wismar Bight to the southern tip of Sweden, and is characterised by the appearance of continental species (such as *Puccinellia distans*).

Elymus athericus is native to the salt marshes along the North Sea coast, but can also occur further south (Bockelmann et al. 2003). In the Baltic, a hybrid with *Elymus repens* seems to have been introduced with ballast water in one location on Sjælland and two in Northern Sweden (Hultén 1950), but there are no records of any further spread. For the Danish west coast, Dijkema (1984) mentioned a northward extension of the distribution area of *Elymus athericus* (with reference to sources from the 1950ies). Vestergaard (1989) attributes the nearly total absence from inner Danish waters to too low temperatures in winter or dispersal failure, but also mentioned a local spreading of the species from an anthropochorous occurrence at the Baltic.

5.3.2 Shift of ecological species groups

A gradual shift of socio-ecological species groups from the more saline west to the eastern part of the Baltic with low salinity was observed. Salt marsh species decreased, while flood meadow species increased (in particular in Mecklenburg-Vorpommern). Fen and grassland species only increased in Estonia. Ruderal species slightly increased in Schleswig-Holstein and Mecklenburg-Vorpommern and decreased in Estonia, while reed bed species increased in Estonia.

The shift of ecological species groups reflects on the one hand the salinity gradient because salt marsh species are replaced by flood meadow, fen or reed bed species. On the other hand it illustrates the impact of the salt grassland soil types – visible in the increase of grassland species (which comprise moist and dry grasslands as well as heathlands) in Estonia, and also slightly in Denmark. Here, the shallow soil type and the more natural transitions to non-saline habitats might have caused these changes in species groups.

Rebassoo (1975) described the well-developed and most widespread Estonian plant community of the geolittoral Glauco maritimae-Juncetum gerardii as being considerably species-richer than noted by other authors due to a high number of non-halophytes, which have here been classified as flood meadow (e.g. *Agrostis stolonifera, Potentilla anserina*), grassland (e.g. *Leontodon autumnalis, Lotus corniculatus*), fen (e.g. *Triglochin palustre, Carex nigra*) or reed bed species (e.g. *Phragmites australis, Eleocharis uniglumis, Bolboschoenus maritimus*).

The high cover of flood meadow species in grazed sites in Mecklenburg-Vorpommern results from the high cover of *Agrostis stolonifera*, which Jeschke (1987) described for the eastern parts of Mecklenburg-Vorpommern as characteristic in the lower geolittoral on peaty substrates – as counterpart to *Puccinellia maritima* further west (see also Dijkema 1990). In Estonia, *Eleocharis uniglumis* plays a greater role in the lower geolittoral (Dijkema 1990), visible in a (slight) increase of reed bed species also in grazed sites.

Particularly in grazed sites, more different species groups play a role in Estonia and the distribution between species groups becomes more even. Since in Estonia – in absolute numbers – less salt marsh species disappear than species from other groups appear the total species number increases. This holds both for the species richness on subplot- and plot scale and/as well as the size of the regional species pool, of which the total number of species recorded per region can serve as an indicator.

The diversity of socio-ecological species groups may also serve as an indicator for habitat diversity, which is higher in Estonia than in the other regions. Also Adam (1990) described an increase in species number with increased number of communities per site, and concluded that 'habitat diversity [rather than area] is the significant factor controlling species richness'. Vestergaard (1998) found a positive correlation between the number of species and the number of vegetation clusters (species groups) per area in Danish salt grasslands, which he interpreted as an expression of beta-diversity, since it largely reflects the turn-over rate in species composition along the elevational gradient.

5.3.3 Species' distribution patterns along the Baltic Sea ecological gradient

Not only socio-ecological species groups showed different distribution patterns along the Baltic Sea gradient, but also individual species. They can be grouped according to their distribution along the studied gradient. Also halophytes and coastal species differ in their distribution patterns.

Halophytes decreasing with decreasing salinity

A number of halophyte species decreased towards lower salinity levels, and was/were missing in study sites in Schleswig-Holstein and further east (*Cochlearia officinalis, Cochlearia danica, Atriplex pedunculata)*, in (*study sites of*) Mecklenburg-Vorpommern and Estonia (e.g. *Salicornia europaea, Suaeda maritima, Limonium vulgare, Plantago coronopus, Sagina maritima*) or only in Estonian sites (*Puccinellia maritima, Spergularia salina, Spergularia media*). *Artemisia maritima* and *Armeria maritima* strongly decreased in Mecklenburg-Vorpommern and were missing in Estonian study sites.

However, some of these species were just not detected in the study plots, because their abundance decreases towards their distribution limit. Only a few of these species reached their geographical distribution limits between the study regions (Hultén 1950, Tyler 1969a), such as *Cochlearia officinalis* and *Limonium vulgare* on Rügen island in Mecklenburg-Vorpommern, and *Spergularia media* and *Plantago coronopus* at the Polish coast (Tyler 1969a). *Suaeda maritima, Atriplex pedunculata, Puccinellia maritima* and *Artemisia maritima* reach their distribution limit in Estonia. The first two of them were also observed in the visited Estonian salt grassland sites, but outside the study plots.

Coastal species with peak at intermediate salinities

Some coastal species had their frequency peak at intermediate salinities, in Schleswig-Holstein and/or Mecklenburg-Vorpommern. *Oenanthe lachenalii* occurred in study sites of all three western regions. It reaches its frequency peak and its geographical distribution limit in Mecklenburg-Vorpommern (limit: east of Greifswald, Tyler 1969a, floraweb.de), its northern distribution limit passes through Denmark (Vestergaard 1989). *Juncus maritimus* occurred only in Schleswig-Holstein and Mecklenburg-Vorpommern and reaches its eastern limit in Mecklenburg-Vorpommern

(Usedom, Tyler 1969a, Härdtle 1984). *Cochlearia anglica* was found only in Schleswig-Holstein and reached its distribution limit in Mecklenburg-Vorpommern (near Stralsund, Härdtle 1984).

Coastal species with peak at low salinities (in Estonia)

There was also a number of coastal species increasing in frequency towards Estonia: *Eleocharis uniglumis* and *Schoenoplectus tabernaemontani* both occur in salt grasslands of relatively low salinities at the whole Baltic Sea coast (Hultén 1950, Tyler 1969a, Vestergaard 1998), even if the latter was not found in Danish and Schleswig-Holstein study sites. *Festuca arundinacea* has its northern distribution limit in the Bothnian Sea (Hultén 1950, Tyler 1969a). *Blysmus rufus* was only found in Estonian study sites, and has its northern distribution limit at the Bothnian Sea (Hultén 1950). It is very rare and threatened with extinction at the German Baltic coast (Berg et al. 1996, Mierwald & Romahn 2006) occurring only at low salinity sites as e.g. the inner Schlei fjord (Härdtle 1984, Kieckbusch 1998).

Halophytes with peaks in Denmark and Estonia - typical for shallow soil type

There was also a group of halophytes that occurred only or with higher frequency in Estonia and Denmark, thus at both ends of the salinity gradient, such as *Centaurium littorale, C. pulchellum, Odontites litoralis*, *Leontodon autumnalis* and *Carex distans*. The first three are small, short-lived species indicative for disturbances (Jutila 1997). They occur primarily at exposed shores in more open canopies (Tyler 1969a), which are characteristic for the 'shallow soil type' that dominates in Denmark as well as in Estonia. Härdtle (1984) described *Centaurium pulchellum* and *C. littorale* in the upper geolittoral in the elevation of maximum water levels, partly in contact with beach ridges on sandy, well-drained soils. *Leontodon autumnalis* is found in the middle and upper part of salt grasslands often dominated by *Festuca rubra* (Ellenberg 1996) at the western Baltic (Gillner 1960, Vestergaard 1998) as well as at the eastern Baltic (Jutila 2001). *Carex distans* is typical for grazed salt grasslands on sandy, rather dry substrates (Jeschke 1987) as found with the 'shallow soil type', and has its northern limit at the Åland islands (Tyler 1969a). It was not found in Mecklenburg-Vorpommern study sites, probably because these did not comprise grazed sites of the shallow type, which plays only a minor role in the eastern part of Mecklenburg-Vorpommern (Jeschke 1987).

Northern Species

The only coastal species found with a northern/arctic distribution was *Carex glareosa*, which is at its southern distribution limit in Estonia (Rebassoo 1975, Tyler 1969a, Dijkema 1990).

Species indicating calcareous soils

Many of the species only occurring in Estonia (or in Estonia and Denmark) indicate a high pH value (Ellenberg R ≥ 7). This is in accordance with the measurements of pH and inorganic carbon content. In this group, Festuco-Brometea species indicate dry conditions (*Medicago lupulina, Filipendula vulgaris, Galium verum*) and the Scheuchzerio-Caricetea (*Sesleria caerulea, Primula farinosa* and *Parnassia palustris)*, Molinietalia (*Inula salicina*, *Galium boreale*, *Lathyrus palustris* and *Dactylorhiza majalis)* and Phragmitetea species (*Carex disticha, Sium latifolium)* indicate moist conditions. Rebassoo (1975) mentioned that *Trifolium fragiferum* and *Carex nigra* are connected with calcareous soils in Estonia. *Trifolium fragiferum* is slightly more frequent in Estonia than in the other regions, and *Carex nigra* occurs only in Estonian sites.

This group of species demonstrates the gradual transition of Estonian salt grasslands to calcareous ‘alvar’ grasslands. Out of 81 ‘characteristic species of Estonian alvar grasslands’ listed by Pärtel et al. (1999), 24 occurred also in the studied Estonian salt grasslands (30%). These were primarily species typical of the concave, moist alvar type (‘Molinietum alvarense’, with 13 out of 15 most typical species also in the studied salt grasslands) and also of the most typical alvar grasslands in Estonia ‘ryhk-alvars’ (‘Avenetum alvarense’, with 14 of 43 most typical species, Pärtel et al. 1999).

5.3.4 Distribution boundaries

It was demonstrated that species composition differed between the four regions along the Baltic Sea ecological gradient, and that many species showed distinct distribution patterns along this gradient. However, it is unclear whether the observed distribution boundaries along the Baltic Sea ecological gradient are caused by salinity, climate and/or competition.

It has been stated that in environments with strong physical gradients, the boundary towards the more extreme end of the gradient is mainly determined by abiotic factors and the physiological tolerance of a species (e.g. salt tolerance), whereas the boundary towards less extreme conditions (e.g. less salt) is determined by competition (for salt marshes see i.a. Bertness & Ellison 1987, Bertness 1991, further studies also from other ecosystems see Bockelmann & Neuhaus 1999). This applies to the (vertical) zonation of plant communities, but also to horizontal gradients such as the salinity gradient in estuaries (Crain et al. 2004).

However, the example of *Elymus athericus* being competitively excluded from the more saline and thus more stressful lower salt marsh by *Atriplex portulacoides* (Bockelmann & Neuhaus 1999) is in contradiction to this general hypothesis. Emery et al. (2001) demonstrated that addition of nutrients completely reversed the competitive hierarchy in a New England salt marsh.

The question whether a distribution limit is determined by physiological tolerance – be it to climatic constraints or to salt stress – or by competitive exclusion can finally only be answered by carrying out experiments on autecological tolerance as well as on competitive ability under different abiotic stress levels (e.g. transplant-experiments in the field, see Crain et al. 2004, Engels & Jensen in prep.).

Nevertheless, at least preliminary conclusions can be drawn from the distribution pattern of species along the studied gradient in combination with expertise from the literature. In particular, the findings of this study can be compared with those of a similar study at the Schlei fjord within Schleswig-Holstein (Lübsen 2007). Along the Schlei fjord, a rather similar salinity gradient ranging from 15-18 psu to 2-4 psu can be found in a smaller and thus more homogenous region with respect to soil and climatic conditions. Thus, it is assumed that the Schlei gradient is a more or less ‘pure’ salinity gradient. If distribution patterns along the salinity ‘zones’ of the Schlei are similar to the studied Baltic Sea gradient, then salt and/or competition should be relevant, but not climatic conditions.

Artemisia maritima decreased in the inner Schlei (at 2-6 psu) and was intermediate in the middle Schlei (with 6-12 psu, Lübsen 2007). In this study, it decreased in Mecklenburg-Vorpommern and Estonia (at 5-9 psu). Thus, the border to lower salinities seems to be in both cases determined primarily by competition of less salt tolerant species. Since the species reaches its northern limit south of the Oslo fjord (Hultén 1950) and in Scotland, climatic constraints are likely to play an additional role for the Baltic northern limit in Estonia.

Also *Puccinellia maritima* decreased in the inner Schlei (at 2-6 psu, Lübsen 2007) and in Mecklenburg-Vorpommern (this study), whereas it was absent from the Estonian study sites (at 5-7 psu). Statements on the (north-) eastern distribution limit in the Baltic somewhat deviate: Härdtle (1984) mentioned that the Puccinellietum maritimae approaches its eastern distribution limit on Fehmarn (see also: Schmeisky 1974), since it does not form extensive stands any more there (following Raabe 1950), even when the species has been mentioned from areas further east (in Mecklenburg-Vorpommern). In contrast, such stands were still observed e.g. on Western Rügen island (Ummanz, pers. obs.). Fukarek (1969?) claims that the eastern distribution limit of *Puccinellia maritima* was at the island of Bock at the eastern tip of the Zingst pensinsula (in Mecklenburg-Vorpommern), while Passarge (1964, after Härdtle 1984) suspected it around the Vistula mouth (at the polish coast). Rebassoo (1975) described the species and the community for Estonia as well, even when rare, as a species-poor facies of the West-European association. In agreement with her, Tyler (1969a) located the north-eastern border around Öland and on the Estonian island Saaremaa. *Puccinellia maritima* ranges up the whole Norwegian coast (Hultén 1950) and to Southern Iceland (Adam 1990). Thus, climatic constraints seem weaker than for *Artemisia maritima*. They may, however, still be limiting, since Dijkema (1984) emphasised that the maritime climate and in particular the influence of the gulf stream makes conditions much milder along the Norwegian coast, causing many Scandinavian salt marsh species to extend far north. Thus, it may still be the boreal-continental climate that limits the range of *Puccinellia maritima* in Estonia.

In contrast to the distribution patterns discussed so far, *Eleocharis uniglumis* increased in the inner Schlei (2-6 psu) and in Estonia (5-7 psu). It typically occurs in salt grasslands of relatively low salinities at the whole Baltic Sea coast (Hultén 1950, Tyler 1969a, Vestergaard 1998). Thus, its limit towards higher salinity seems to be caused by its low salinity tolerance. However, in contrast to many glycophytes in upper salt grasslands which are often widespread inland, *Eleocharis uniglumis* is still restricted to coastal, permanently brackish habitats (as well as *Blysmus rufus* in Northern Europe, and *Carex divisa* and *Alopecurus bulbosus* further south, Adam 1990). Adam (1990) wonders whether there are certain physiological features which limit these species to this narrow range of habitats.

5.4 Impact of management

5.4.1 Changes of vegetation structure

Substantial changes of vegetation structure were observed in the course of succession: vegetation height as well as thickness of litter layer increased in early and even more in late successional sites. Vegetation cover was generally very high, but still increased in late successional sites.

These changes probably underlie the mechanisms that lead to a change in species composition (visible in the ordination diagrams, the shift of life history, socio-ecological groups and strategy types), on the one hand, affecting regenerative strategies, such as germination and establishment, clonal regeneration and persistence in the seed bank (see part 2), on the other hand affecting the adult plant representing different established strategies (Grime 1988, see below). Strongly reduced light availability in dense grass swards (Schrautzer & Jensen 2006) or reed beds (Kotowski & van Diggelen 2004, Ekstam 2007) enhances light competition and may also inhibit germination and establishment (Tilman 1993, Goldberg & Werner 1983, Spackova et al. 1998, Jensen & Gutekunst 2003). Especially annual and biennial species are negatively affected by this process and decreased in early in early or latest in late successional sites (see 4.5.3), such as *Spergularia salina* and *S. media, Salicornia europaea, Suaeda maritima, Odentites litoralis, Centaurium littorale* and *C. pulchellum.* That annual species benefit from gap formation due to grazing has also been reported by Bakker (1989) and Bullock et al. (1994). In contrast, Jutila (1997) did not confirm this impact of grazing for all her study transects at the Finnish coast. She found large differences between transects, which she attributed to the degree of exposure of the coastal sites. She concluded that disturbances by the fluctuating water table and erosive forces of waves, ice and wind are more important for the vegetation than disturbances by cattle. The sites closest to the open sea and most severely affected by these disturbances were richest in species and also annuals. It has also been suggested that the land uplift at the Finnish coast offers competition free sites for plants (Ericson 1980, Jutila 2001).

Specific changes of vegetation structure and soil conditions in the course of succession may also lead to a further acceleration of succession: Zimmek (1972) demonstrated that soils of ungrazed salt grasslands had lower temperature fluctuations and were better aerated, which led to a higher availability of nitrogen, resulting in a higher biomass production. Although biomass was not directly measured in this study, the measured vegetation structure parameters (vegetation height, thickness of litter layer) can be used as indicators for total biomass production of the different salt grassland successional stages.

5.4.2 Length of the successional trajectory

With increasing reed cover (and thus increasing biomass), species richness (on small scale) declined in late successional sites (see 4.4.2). This fact points at the probable long-term development of many abandoned Baltic salt grasslands, that in the further course of succession, when reed becomes denser and more uniform, species richness will decrease. The investigated ‘late successional’ sites thus do not yet mark the terminal phase of succession, but rather an intermediate phase. Tyler (1969b) described that geolittoral reed beds in Sweden were often so thinly spaced that the typical vegetation of the primary zonation could still develop, whereas in dense stands, colonisation of shore meadow plants was prevented – resulting in low species numbers. Species richness as well as the number of rare fen plant species in (freshwater/terrestrial) reed beds has been shown to be inversely related to the degree of reed dominance (Wheeler & Giller 1982, Wheeler & Shaw 1991). Vestergaard (1998) described a reed bed type with dense ground cover of *Agrostis stolonifera* as intermediate between the grazed *Puccinellia maritima* meadow and a dense reed bed with sparse ground cover. He considered the latter type as subclimax vegetation of the lower geolittoral in South-eastern Denmark. Species numbers declined from the *Puccinellia maritima* meadow to the intermediate reed bed by only 10%, but by further ca. 44% from the intermediate to the dense reed bed.

That small-scale species richness of late successional sites decreased in this study only in Schleswig-Holstein, probably attributes to the fact that those successional sites were abandoned for a significantly longer time period (mean of 28 years in late successional sites, in contrast to 13-22 in the other three regions), and that these sites had already developed further towards the species-poor terminal phase of brackish reed beds (as the second type of Vestergaard 1998).

Sammul et al. (2008) found that species numbers in abandoned Estonian salt grasslands were significantly lower than in continuously managed salt grasslands. Their abandoned sites were reed dominated and abandoned since already 30-50 years (in contrast to this study’s Estonian sites abandoned since 10-17 years). Thus, this supports the assumption that species numbers will further decrease in the course of succession. Vestergaard (1998) also found that time since abandonment was significantly negatively correlated to the number of species in salt grasslands in South-eastern Denmark.

5.4.3 Change of strategy types

In the course of succession, the competitive(C-)strategy-component increased, while the ruderal (R-)strategy component decreased (see 4.5.3). This is in accordance with empirical results on grassland (Moog et al. 2005) and old-field succession (Dölle et al. 2008) and also succession of human made habitats (Prach & Pyšek 1999). It has been also shown previously that R-strategists increased with increasing grazing intensity, whereas C-strategists decreased at the same time (Bullock et al. 2001, Pakeman 2004).

The stress-tolerator (S-)component also decreased in early and late successional sites. Again, this may be caused by a factual decrease of abiotic stress, or by the constraint that C-, S- and R-components add up to one for methodological reasons, thus inevitably perform inverse trends (see 5.2).

A factual decrease of stress in the course of succession may for example be caused by the fact that grazing may increase salinity of the soil (Kauppi 1967, Siira 1970, Schmeisky 1974, Esselink et al. 2002). No differences in soil salinity between management classes were found in this study, whereas several authors stated that soil salinity was increased by grazing. Schmeisky (1974) showed that grazing increased evaporation (due to reduced canopy) and that soil compaction by trampling decreased drainage and hereby favoured halophytes. Higher salinity values of grazed sites have also been measured by Esselink et al. (2002) for the Dollard estuary and by Siira (1970) and Kauppi (1967) for the Finnish Baltic coast, but not by Bakker (1989) for salt marshes in the Netherlands. That the salt indicator values were higher for grazed and early successional sites than for late successional sites, may either indicate that salinity was indeed increased by grazing in this study's sites (although this was not visible in the measured values representing just a snapshot) or may suggest that grazing indirectly favours halophytes. These species are often small-growing and are favoured by a higher light availability of grazed sites (Bakker 1985, Bakker & de Vries 1992, Scherfose 1993). They also often have a short life cycle and depend on gaps in the vegetation cover for germination and establishment, and are thus favoured by grazing and trampling of cattle. In addition, some halophytes are light-demanding because active salt excretion (with glands or hairs) is energetically costly (e.g. *Glaux maritima,* Jerling 1999).

Pure S-strategists are characterised by low growth rates, which are a strong disadvantage in the course of succession. This is why a shift from S-to CS-strategists, which are more competitive but at the same time tolerate a certain level of abiotic stress, was observed. However, it has to be kept in mind that in particular species in the presented dataset representing the secondary stress-tolerant strategy types (SR- and CS-) are not all classified as stress tolerant due to their tolerance to salt stress but also to inundation (and consequently anoxia) stress (such as *Phragmites australis, Schoenoplectus tabernaemontani*) or mineral nutrient stress (such as *Molinia caerulea, Hierochloe odorata*, or *Linum catharticum*). The 'pure' S-strategists, in contrast, are all more or less salt-tolerant.

Furthermore, strategy type groups showed a shift in the course of succession from SR- and CSR- to CR-strategists. SR-strategists were – all except for *Puccinellia maritima* – small-growing, annual or biennial species colonizing vegetation gaps and adapted to either salt stress (such as *Centaurium* *pulchellum, Cochlearia offinicalis, C. danica*), mineral nutrient or periodical desiccation stress (such as *Linum catharticum, Radiola linoides*). Most of them declined because these open, disturbed and stressful habitats disappeared after abandonment, primarily since the vegetation cover and litter layer increased.

Thus it is concluded that the competition component increases in the observed course of succession and that the – rather low – component of ruderal strategies decreases when grazing stops and the associated disturbances of plant biomass and soil disappear. The decrease in stress tolerance seems to be rather a 'by-product' than a true decrease of abiotic stress intensity.

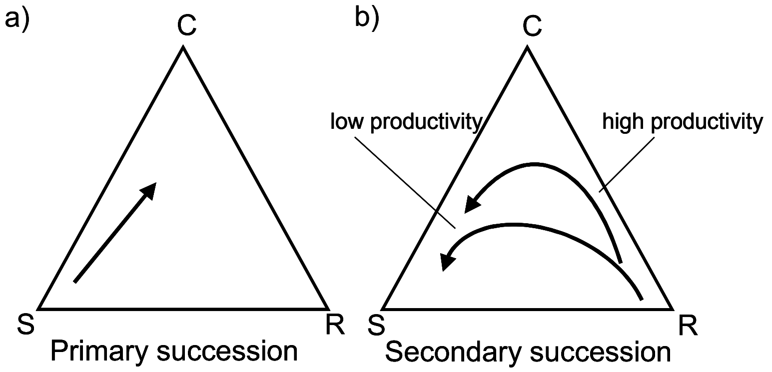


Fig. 5-2: Triangular diagram of primary and secondary progressive succession, after Grime (1988). The three dimensions represent the three strategies competition (C), stress (S) and ruderal (R). The arrows indicate the course of succession.

The general model of secondary succession by Grime (1979) predicts an arch-formed movement from an R-dominated early phase to a C-dominated intermediate phase and finally to an S-dominated terminal phase, with a higher, rounder arch (a higher C-component) in productive, and a lower arch in less productive systems (fig. 5-2b). Autogenic processes such as nutrient accumulation in the course of succession, which was observed in Estonian salt grasslands by Sammul et al. (2008), may further modify these curves (Grime 1979). In contrast, the studied successional stages showed a movement from S towards C (with a slight decrease in the R-component, see fig. 4-12). This pattern may still be in accordance with Grime's (1979) assumption, if it can be suspected that the studied 'late successional stage' still represents an intermediate, but not yet the terminal phase (discussed below), and that the high S-component somewhat masks the changes in the R-component. It is clear that the starting point of secondary succession of grazed salt grasslands is not strongly dominated by R-strategists, such as fallow arable land (Grime 1974). The positions of the grazed sites are close to those found for sheep pastures, but somewhat more strongly dominated by the S-component, and early and late successional sites are close to those theoretically predicted for 'abandoned pastures and wastelands' in Grime (1974). Why the movement of this study's sites resembles closely the pattern proposed for primary succession by Grime (1988, fig. 5.2a), remains, however, unclear.

Ecke & Rydin (2000) applied Grime's CSR-strategy types to transects through the zonation at the emerging sea-shore at the northern Gulf of Bothnia, which they interpreted as a series of primary succession. They could not detect any significant changes in C-, S- or R-component and concluded that other structuring forces than those that the CSR-system accounts for, are more important in the studied system. However, their presumed time series represented also a strong environmental gradient, whose influence seemed to override successional changes, which was also observed by Zobel & Kont (1992) in a transect through a land-rise area at the Estonian coast.

Dierßen (2006) showed that in the regional flora of the county of Schleswig-Holstein, S-, SR-, CS- and CSR-strategists are much more threatened than C-, CR- and R-strategists due to their poorer adaptation to the present form of land use in the region. Salt marshes, presumably at the North Sea coast, representing extreme site conditions, were dominated by S-strategists (with 56 ± 22% cover, Dierßen 2006), a value close to that determined in this study for grazed Baltic Sea salt grasslands in Schleswig-Holstein (50% cover) and in Denmark (56% cover).

5.4.4 Change of individual species

The species, for which significant changes in frequency and/or cover during succession in one or all regions were found, are listed in table 5-1. A comparison with estimates of their reaction to grazing from several literature sources from the Baltic and the North Sea is also given. In agreement with this study's results, the 15 species favoured by grazing were largely classified to the successional categories A (12 out of 15) or B (2 out of 15) by Ekstam & Forshed (1992), indicating that they decrease rather quickly after abandonment. 40% of them are annuals. The majority of these species belongs to the stress-tolerators (8), while each of 3 are SR- and CSR-strategists, respectively.

Six species showing a peak in early successional sites are perennial. They are mostly classified to successional category B (3), C and D (each 1 species) by Ekstam & Forshed (1992). They belong mainly to the competitive strategy (3), to CS- (2) or S-strategists (1). The six species which significantly increased in late successional sites are also mainly perennial (except for one annual species, *Sonchus asper*), and are classified to the successional category D (2), C (1) or A (1). They represent either CS- (2), CSR- (2) or CR-strategists (1).

For most species, the majority of assessments of grazing impact by other authors showed good accordance with the results of this study. The most obvious deviation was found for *Eleocharis uniglumis*, which was assessed as being favoured by grazing by Jutila (1999), Scherfose (1993) and Härdtle (1984, only related to moderate grazing). In contrast, it was found here that the species significantly increased in frequency and cover in Estonian late successional sites (and slightly in early successional sites, too). Rebassoo (1975) describes that the Eleocharetum uniglumis community has increased in Estonia in recent decades while the influence of grazing decreased. Dahlbeck (1945) also found that grazing hindered the development of the association in the Øresund region. Tyler (1969b) mentioned *E. uniglumis* as being rather indifferent to grazing. According to Scherfose (1993), *Eleocharis uniglumis* is only favoured by low-density grazing, while grazing in the investigated salt grasslands sometimes could be described as high density, which may explain different assessments by the mentioned authors.

Table 5-1: Changes of frequency and/or cover of plant species during succession in the presented data set (species grouped after their maximum in grazed, early and late successional sites) and their reaction to grazing in the literature. Härdtle (1984), Jutila (1999): Baltic Sea coast; Jensen (1985): reviewed literature from the North Sea (number of positive/negative/indifferent indications given); Bakker et al. (2003a): Wadden Sea; Scherfose (1993): North and Baltic Sea coasts (included were only indications related to cattle grazing). **+**: favoured by grazing, **-**: inhibited by grazing/favoured by abandonment, **0**: indifferent. **int:** intensive grazing, **mod**: moderate grazing, **upp**: upper salt marsh, **low**: lower salt marsh, **mid**: middle salt marsh. Suc cat: successional category according to Ekstam & Forshed (1992): **A**: Species which already during an early successional phase decrease in quantity. **B**: Species which during an intermediate phase in the succession decrease in quantity**. C**: Species which during a late phase in the succession decrease in quantity (and increase in the early phase). **D**: Species which increase in quantity during the early, intermediate and late phase of the succession when grassland management has ceased. Life cycle: **a:** annual, **b:** biennial, **p:** perennial. CSR: CSR-strategy types after Grime et al. (1979), categories derived from Frank & Klotz (1990).

	Härdtle (1984)		Jutila (1999)	Jensen (1985)	Bakker et al. (2003a)	Scherfose (1993)*		succ. cat.	life cycle	CSR
	int.	mod.				int.	mod.			
Maximum in grazed										
Spergularia salina		+			+	+	+/ 0 low	A	a	S
Puccinellia maritima	+	+		12+	+	+	+	A	p	SR
Juncus gerardii	+		+		+	+	+	A	p	SR
Trifolium fragiferum	+					+	0	A	p	CSR
Agrostis stolonifera	+		+		+	+	+	B	p	CSR
Centaurium littorale						+	?	A	a	S
Spergularia media	0	0		5+	+	0	+ upp	A	p	S
Triglochin maritimum	0	0		4+, 1 0	+	- (low)	0	B	p	S
Plantago maritima	0	0	+	4+, 1-, 2 0	+	0	+ upp	A	p	S
Glaux maritima	0	0	+	2+, 2 0	+	+	+, 0 upp	A	p	S
Odontites litoralis			+			+ upp, ? mid	+ upp, ? mid	A	a	_
Leontodon autumnalis			+		+	+	0	A	p	CSR
Salicornia europaea		+		5+, 1-	+	+	+ upp	A	a	S
Suaeda maritima	0	0		3+, 1-, 1 0	+	+	+ mid/upp	_	a	S
Centaurium pulchellum		+				+	+	A	a	SR
Maximum in early succ.										
Festuca rubra agg.	-	-	+	11-, 1+, 1 0, 1(+?)	no diff	-	0	B	p	C
Artemisia maritima		+		6-, 1- only int.	-	-	-	B	p	CS
Festuca arundinacea			-			0	0	D	p	C
Elymus repens	-	-	+			-	0	C	p	C
Carex distans	-	-				+	0	_	p	CS
Limonium vulgare		+		15-, 3 0	+	-	0	B	p	S
Maximum in late succ.										
Phragmites australis	-	-	-		+	-	-	D	p	CS
Sonchus asper								_	a	CR
Oenanthe lachenalii						- upp, ? mid	0	_	p	_
Bolboschoenus maritimus	-	-				-	-	D	p	CS
Galium palustre			-					C	p	CSR
Eleocharis uniglumis		+	+			+	+	A	p	CSR

5.4.5 Factors steering the speed and direction of succession

Various factors (such as elevation and salinity, Bakker et al. 1997) determine which late successional species becomes dominant and how quickly these vegetation changes occur. For brackish salt grasslands such as at the Baltic Sea coast, the most important late successional plant species that may become dominant is *Phragmites australis.* Many authors reported its more or less rapid encroachment after abandonment (Kauppi 1967, Jeschke 1987, Raabe 1981, Härdtle 1984, Pehrsson 1988, Dijkema 1990, Puurmann et al. 2002, Rannap et al. 2004). Other species that may increase after abandonment and also persist up to several decades are e.g. *Festuca rubra, Elymus repens, Artemisia maritima* (e.g. Schmeisky 1974, 1977, pers. obs.) and *Festuca arundinacea* (Luhamaa et al. 2001, pers. obs.), and for upper salt grasslands e.g. in Estonia also shrub species such as *Juniperus communis* (Luhamaa et al. 2001).

In the following, it will be discussed which factors may determine whether and how quickly *Phragmites australis* becomes dominant and thus which factors are responsible for the speed and direction of vegetation succession. After that, more attention will be made to the differences between the four study regions.

Salinity

Salinity is one potentially important factor determining the speed and direction of succession, because it may determine which late successional plant species can occur according to their differing salt tolerance. For *Phragmites australis*, different salt tolerance limits are given in the literature. While Jeschke (1987) and Raabe (1981) mentioned that *Phragmites australis* is precluded from becoming dominant at salinities above 6‰, Lissner & Schierup (1997) quoted different studies of *Phragmites*' salt tolerance limits ranging from 5 to 25‰ in different regions, and even up to 60‰ for individual clones. For the Danish coasts, Lissner & Schierup (1997) determined a salt tolerance limit of about 15‰, above which die-back in the lower fringe was observed. Also for the Dollard, Esselink et al. (2000) found stands that tolerated salinity levels of 15-20‰, and suggested that *Phragmites australis* is the climax vegetation in this area, as well as predicted for most of the Baltic coastal areas (Schmeisky 1977, Härdtle 1984). Taylor (1939) experimentally determined a salinity tolerance limit of 12.5‰, and Ranwell et al. (1964) a field limit of 13‰ (in Ranwell 1972).

Setting a specific limit of salt tolerance is complicated by the fact that salinity of flooding water in most cases deviates from salinity in the entire rooting depth ranging down to 1.5 m, which is often (strongly) reduced by groundwater flow from the landward side (Lissner & Schierup 1997). Where salinity was above 15‰ in the entire rooting system, such as at a site near Helberskov at the outer Kattegat coast, close to two of this study's sites, die-back at the water front and aphid infestation were observed (Lissner & Schierup 1997).

Even if salinity is not lethal, intermediate levels of salinity still affect productivity, vegetation height and density of *Phragmites* negatively (Hellings & Gallagher 1992, Lissner & Schierup 1997). Lissner & Schierup (1997) demonstrated that growth rates and leaf production of *Phragmites* decreased above a salinity of 5‰. Esselink et al. (2000) reported lower replacement rates of *Spartina anglica* by *Phragmites australis* at higher salinities (15-20‰) and concludes that succession to brackish reed bed is stopped or delayed at higher salinities. Lower productivity is also found in the geolittoral – the elevation zone of salt grasslands in the Baltic – than in the hydrolittoral or at the mean water line (Krisch 1989). If *Phragmites australis* stands are lower and less dense, more subordinate species may still co-occur (Tyler 1969b, Wheeler & Giller 1982, Wheeler & Shaw 1991, Vestergaard 1998). Further, younger stages of *Phragmites* are more sensitive to high salinity levels (Lissner & Schierup 1997), and while seeds still germinated at 10‰, they could not establish (Ranwell et al. 1964). Thus, new colonisation is rather unlikely in more saline areas, whereas vegetative spread from higher elevations or freshwater-influenced parts of the salt grassland may still be possible. Also vegetative spread may be slowed down by high salinity levels, because e.g. a drought year with increased salinity level due to higher evaporation may cause a die-back at the seaward side (Lissner & Schierup 1997).

It is concluded that the higher the salinity, the higher the chances are that other species than *Phragmites australis* persist with comparatively high cover, and the slower succession towards brackish reed beds proceeds. Esselink et al. (2000) also suspect that under brackish conditions, secondary pioneer vegetation is sooner or later overgrown by *Phragmites australis*, while it may be more stable under more saline conditions.

Abiotic disturbances

Krisch (1989, 1992) suggests that (for the Baltic coast in eastern Mecklenburg-Vorpommern) exposition and wave action rather than salinity, are limiting for the coastal distribution of brackish reed beds. In addition, other mechanic disturbances such as ice scouring might be important (Krisch 1989, Dijkema 1990, Puurmann et al 2002). In Estonia, ice-scouring plays an important role in keeping the shore-line free from reed and thus climate change with less frequent ice winters is seen as an additional threat to salt grassland maintenance in the Northern Baltic region (Roosaluste 2002).

Nutrient availability, salt grassland soil type

Since productivity of *Phragmites australis* also depends on the percentage of organic matter in the substrate (Krisch 1978), sites of the shallow soil type may become dominated by *Phragmites* more slowly and less densely. This may contribute to their higher species richness also in the *Phragmites* dominated ‘late successional’ stage. In general, the speed of succession is higher in fertile sites than under unfertile conditions (Prach 1993). Olff et al. (1997) showed at the North Sea coast that higher nitrogen availability favoured species of late successional stages (such as *Elymus athericus*), whereas halophytes of early successional stages declined. This confirms that nutrient availability may steer the speed of succession also in salt marshes (Van Wijnen & Bakker 1999).

Presence of *Phragmites australis*

One important factor determining the speed of succession is the presence of ‘late successional’ species in or very close to the site (Ekstam & Forshed 1992, Vestergaard 1998). The ‘late successional’ species *Phragmites australis* grows in many grazed sites with low vegetation cover and cattle prevents a spread that can occur quickly after grazing has ceased (Vestergaard 1998, Esselink et al. 2000, pers. obs.). At abandoned sites, it was often observed that *Phragmites* spread from ditches or suppressions into higher elevations (see also Härdtle 1984). *Phragmites australis* establishes only rarely from seeds because of its specific requirements for germination and early establishment (light in combination with exposed moist, open mud or soil and calm, low water table for several days, Rodewald-Rudescu 1974, Weisner & Ekstam 1993, Alvarez et al. 2005). *Phragmites* seeds are only rarely found in the seed bank (see part 2) and were classified as transient by Thompson et al. (1997), but as short-term persistent by Ludewig (2009).

Grime (1973) stated that species density in herbaceous vegetation will rapidly decline after grazing has ceased, if species with high potential relative growth rates are present. In contrast, reduction of species density will proceed at a relatively slow rate, where only species with low relative growth rates are present. The 'invasibility' is also dependent on the present 'early successional' species, which can either accelerate (succession promoters as defined by Connell & Slatyer 1977) or slow down successional processes (succession inhibitors sensu Connell & Slatyer 1977, such as tall sedges or *Phragmites australis*). This is known from other ecosystems such as abandoned fen grasslands where establishment of shrub and tree species is delayed by a dense sward of grasses and/or sedges and by dense litter layers. Falinska (1991, 1995) demonstrated that during abandoned fen grassland succession in Poland *Filipendula ulmaria*, dominated patches were invaded by willows, whereas the appearance of woodland species was retarded by at least 10 or 15 years in patches dominated by (tall) sedges (*Carex acutiformis, C. cespitosa*). In the case of salt grasslands, where the establishment of shrub and tree species is prevented by salinity levels, *Phragmites australis* is in most cases the dominant species of the terminal stage of succession, and thus cannot be considered as a succession inhibitor.

Prach & Pyšek (1999) mentioned *Phragmites australis* as an example of a 'super-species'– a term used by Huston & Smith (1987) for species that possess a combination of traits which usually would follow a trade-off, such as traits typical for early successional species (production of large numbers of seeds that are easily dispersed) and traits typical for late successional species (high competitive ability, ability to spread vegetatively). These species have both the ability to colonise new space and to achieve dominance and persist in late successional stages, especially in productive environments.

Geese and other herbivores

Another factor that may prevent a quick change in vegetation composition and structure, thus keeping succession in the 'early stage', are other ('natural') herbivores such as geese, hares, rabbits, moose or deer. In chapter 4.2, it was shown that late successional sites were never used by such herbivores, whereas many early successional sites were 'naturally grazed' (except for in Mecklenburg-Vorpommern), even when the intensity of habitat use was significantly lower than at sites grazed by livestock animals.

The question whether geese and other small herbivores can control or retard succession, has been addressed by various authors. Bazely & Jefferies (1986) and Hik et al. (1992) showed that grazing of lesser snow geese (*Anser caerulescens caerulescens* L.) retarded succession in an Arctic salt marsh system. Van der Wal et al. (2000a, b) demonstrated that hares (*Lepus europaeus*) can prevent the spread of a late-successional species (*Atriplex portulacoides*) in a salt marsh in The Netherlands for more than 25 years. Although late successional, tall-growing species are often not preferred by herbivores due to their low palatability (high fibre content), herbivores can have a long-lasting impact on vegetation succession by preventing the establishment of these species at young stages, as Kuijper et al. (2004) demonstrated for *Elymus athericus* in Dutch salt marshes. For brackish salt grasslands at the Western Swedish coast (Kattegat), Pehrsson (1988) showed that intensive goose grazing may prolong the early stage of succession dominated by *Puccinellia maritima*. On Langli in the Danish Wadden Sea, the combined impact of a high density of hares and watervoles (*Arvicola terrestris*) seems to be strong enough to halt vegetation succession (Bos et al. 2005a).

The effects of herbivores on vegetation succession strongly depends on the herbivore species present. Also within goose species, different foraging strategies have to be distinguished: While brent and barnacle geese (*Branta bernicla* and *Branta leucopsis*) are primarily grazers, *Anser* species such as greylag geese (*Anser anser*) or snow geese (*Anser chaerulescens)* forage not only by grazing aboveground plant biomass, but also by grubbing to feed on tubers, roots or rhizomes (e.g. Baltic greylags in winter, Andersson et al. 2001; at moulting sites in summer, Fox et al. 1998; snow geese in spring, Jefferies 1988). This destructive foraging strategy may have a much more severe impact on vegetation composition and succession than ‘only’ grazing (Bazely & Jefferies 1986, Hik et al. 1992, Esselink et al. 2000, Esselink 2000, Jefferies & Rockwell 2002).

No significant differences in (the intensity of) habitat use by geese, rabbits and other ‘natural’ herbivores between the regions were found. Nevertheless, the habitat use by these herbivores may be of different relevance in different regions, because their presence was only recorded once per site during the field work season between July and September. Goose droppings at this time represent primarily the autumn migration of geese, as well as local breeding or moulting sites.

However, apart from the goose species and foraging strategy, the total number of geese and their duration of staging will be of crucial importance for their impact on the vegetation in a specific area. Western Estonian salt grasslands (e.g. in Matsalu Bay) are used as breeding and moulting sites e.g. for greylag geese (Mägi 2003). First of all, they are the most important staging area for geese in Estonia in spring and, to a slightly lower extent, in autumn (Lotman 2001, Mägi & Kaisel 2001, Leito 2008). Between March and May, up to 60,000 geese (up to 45,000 barnacle geese, plus several thousand of greater white-fronted, bean and lesser white-fronted geese, Leito 2008) stage/roost in Matsalu Bay, preferring coastal grasslands as feeding grounds (Mägi & Kaisel 2001). In the whole of Western Estonia, a total of 180,000-200,000 barnacle geese are roosting in spring (Kalamees et al. 2001). These high numbers could not be considered in the presented ‘intensity of habitat use by geese’ for methodological reasons. Haapsalu Bay, where some more of the study sites are located, is also an important staging site in spring and autumn (Leito 2008). However, Leito & Truu (2008) attributed the observed recent decrease and change in staging area locations of barnacle geese in Estonia since 2000 to the degradation of many coastal grasslands in the West Estonian archipelago (except for Matsalu Bay, Leito 2008) and to the increased predation by white-tailed eagles. Eichhorn et al. (2009) hypothesised that a new migratory strategy has evolved: a part of the barnacle geese skip the spring stop-over in the Baltic (e.g. Estonia) responding to increased competition for food at these spring staging sites, which seem to have reached their goose grazing capacity.

The Northern Danish study region at the Kattegat coast also lies along a north-south migration route. Migrating geese in autumn graze on salt grasslands that have been kept short by cattle (Christiansen et al. 1991). Rønnerne at the southern coast of Læsø is a very important stop-over site for dark-bellied brent geese, but there seem to be no goose species breeding on Læsø/Rønnerne (Rasmussen 1996). Also for Mecklenburg-Vorpommern, Jeschke (1983) mentioned staging geese as ‚tertiary grazers’ (e.g. in the meadows of Koos) which contribute to the reduction of biomass as long as salt grasslands are not invaded by reed. In all regions, habitat use by geese differs locally and may have a higher impact at breeding or moulting sites (e.g. in Schleswig-Holstein: Sehlendorfer Binnensee, Christensen et al. 2000, Oehe-Schleimünde, Erfurt & Dierschke 1992, Graswarder, NABU Schleswig-Holstein 2009, Neustädter Binnenwasser, Koop unpubl. data).

Geese prefer sites grazed by livestock animals because of the low canopy height and the high cover of palatable species (Bakker et al. 1993, Olff et al. 1997). Early successional sites are preferred over late successional sites, since the vegetation canopy is still comparatively low there. Of the plant species preferred by geese at the Baltic Sea coast (barnacle geese on Öland, Sweden: *Festuca rubra, Juncus gerardii, Poa* spec., *Triglochin maritimum, Plantago maritima, Agrostis stolonifera,* Van der Graaf et al. 2007; moulting greylag geese on Saltholm, Denmark: primarily *Puccinellia maritima*, also *Bolboschoenus maritimus, Festuca rubra, Plantago maritima, Elymus repens* flowers, Fox et al. 1998), some had a similar or even higher cover in early successional sites than in grazed sites (*Triglochin maritimum, Plantago maritima, Festuca rubra, Bolboschoenus maritimus*). *Elymus repens* had a higher cover in early and late successional sites, and some species were intermediate between grazed and late successional sites (*Agrostis stolonifera, Puccinellia maritima*). *Juncus gerardii* already decreased in cover in early successional sites (see chapter 4.6).

However, early successional sites that are not grazed by any herbivores in spring will probably have a vegetation structure in autumn that is no longer favoured by geese, since the high sward with a high fibre and low nitrogen content has a low palatability. This is why goose grazing at early successional sites may be stronger in spring, when vegetation development is just starting, than in autumn, when geese preferentially select areas with short canopies (previously grazed by livestock; compare Stock & Hofeditz 2000). Thus, goose grazing during spring migration may also potentially have stronger effects on the plant species composition and vegetation succession than goose grazing during autumn migration.

A relationship between short canopy height and goose grazing was detected also for other regions, such as the Russian breeding site of Barnacle geese (Van der Graaf et al. 2004) and spring staging sites in the Wadden Sea (Van de Koppel et al. 1996, Vickery et al. 1997, Van der Wal et al. 1998, Van der Graaf et al. 2002, Bos et al. 2005a). Also other parameters than vegetation composition and structure may be relevant for the habitat utilisation by geese, such as predators, the dimension of salt grasslands and neighbouring structures. Small patches in the vicinity of tall vegetation such as reed beds or forests (as was the case for several of the early successional sites) may be less suitable for landing of geese than large, open coastal areas. This is a possible reason why early successional sites in Mecklenburg-Vorpommern, all comprising mosaics of reed dominated and low vegetation, were never used by geese. Madsen et al. (1990) mentioned that the narrow Danish North Sea mainland marshes were less suitable for brent geese than the wide Schleswig-Holstein North Sea mainland marshes.

In general, a relationship between successional stages and habitat use by geese does not tell anything about causal relationships. Either the geese prefer low canopy height or the low canopy height is a result of the grazing pressure by geese. To disentangle these two processes, factorial experiments would be needed, but it is not possible to determine cause and effect with this descriptive approach (see also Van der Graaf et al. 2007). There is experimental evidence for both causal relationships: It was shown that geese prefer relatively short swards (of up to 8 cm, Bos et al. 2004, Van der Graaf et al. 2002, 2006), but also that geese can create and maintain short swards (Bos et al. 2004, 2005b, van der Graaf et al. 2005).

That habitat use declined already in early successional sites may point in the direction that vegetation succession rather than goose grazing is the steering factor that may affect geese to choose alternative sites for foraging. Also van der Wal et al. (2000a) concluded that (brent) geese are largely excluded as vegetation succession progresses. Only locally, for example at sites with high numbers of breeding or moulting geese or possibly at the most intensively used spring-staging sites, a high intensity of habitat use by geese may halt or retard vegetation succession.

Apart from grazing or browsing of other herbivores such as rabbits, hares, moose and deer, also wild boars may locally create patches of disturbed soil, which are recolonised by annuals and other early successional plant species, creating small patches of cyclic successions (see part 2, personal observation, Dücker 1996).

5.4.6 Differences in speed and direction of succession between regions

In general, indications on speed and direction of succession can only be derived indirectly from the presented data set and personal observations. For a systematic, thorough analysis, alternative research approaches would be necessary.

The approach of 'space-for-time' substitution assumes that successional stages close to each other are different, consecutive stages of the same successional series. However, even if environmental conditions are very similar, this approach cannot directly tell how quickly one stage develops to the next stage, since this can deviate a lot, depending on many factors. Long-term observations can give much more reliable information on the speed of succession, but take a long time and are often not feasible or practicable. Furthermore, different 'successional stages' were selected following a hypothesised successional pathway, assuming that salt grasslands after abandonment still display a low vegetation structure for a certain period and then develop to brackish reed beds. However, this may not necessarily be true for all sites in all regions, since also other 'terminal' stages of succession may be possible, and the studied 'early successional stage' may not change into brackish reed bed in all cases. This cannot be proven by the selected method, but by some facts of the presented study and by personal observations in the field, at least some indications on the speed and on alternative directions of succession can be indirectly derived.

Regions may thus differ in the possible alternative vegetation types of the 'terminal successional stage', in transition probabilities of these alternative 'terminal vegetation types' and in the speed of succession.

Estonia

In Estonia, *Phragmites australis* brackish reed beds seem to be the predominating 'terminal stage' of succession for the lower and middle geolittoral. For higher elevations (upper geolittoral and primarily epilittoral), more alternative dominant species of 'terminal stages' seem to be possible, such as *Juniperus* shrubs, and also – at least for intermediate phases – *Festuca arundinacea* or *Elymus repens.* 'Tall grass and scrub' communities, dominated by *Festuca arundinacea* and *Elymus repens*, and woody species were also identified as indicators for abandonment in this region by Burnside et al. (2007).

Study sites were selected in the lower to middle geolittoral which were obviously regularly flooded and salt influenced (by using *Plantago maritima, Triglochin maritimum, Glaux maritima*, *Aster tripolium* etc. as indicator species) to make sure that sites with a potentially different development in the course of succession were not included. Higher elevations may only sometimes have been included as small patches within the study plots due to the highly variable microtopography (visible in a few young *Juniperus* plants in the plots).

Since at practically all studied ‘early successional’ sites, reed invasion was observed in some parts of a larger site, it is concluded that the succession towards brackish reed beds seems to be quick in Estonia. How quickly reed will dominate the whole site, is largely determined by the speed of vegetative spread of reed (by rhizomes and aerial shoots), since reed was already present in most grazed sites in shallow, wet parts and/or at the shoreline. ‘Late successional’ sites were reed dominated after 10-17 years, early successional sites had the same age. Thus, within this time period, a part, but not the whole area of a larger salt grassland site was converted to brackish reed beds. Although *Phragmites australis* stands can expand many meters per year (Huhta 2007), it may take more than 10 or 20 years to colonise a site of 300 metres width or more. Burnside et al. (2007) stated that coastal wet grassland sites were generally dominated by *Phragmites australis*, tall grassland and scrub within 25 years.

Successional speed is further modified by local differences in frequency and intensity of disturbances by wave action and ice scouring, and possibly goose grazing. Reed beds remained of low density and species-rich because of very shallow soils with a comparatively low nutrient stock (and probably the comparatively short time since abandonment). Nutrient stock may, however, increase in the course of succession by the high biomass and litter of reed and other plant species (Sammul et al. 2008).

Mecklenburg-Vorpommern

In Mecklenburg-Vorpommern, *Phragmites australis* brackish reed beds strongly dominated in abandoned salt grasslands. Succession towards brackish reed beds seems to be particularly rapid in this region, since salinity is low (up to 9 psu) and nutrient stocks are higher than in Estonia. In general, it was difficult to find abandoned sites which were not reed dominated yet. An exception is the area around the Landower Wedde (in the west of the island Rügen), which has been abandoned for 30-35 years, and still consists of a mosaic of salt grasslands (dominated e.g. by *Artemisia maritima, Aster tripolium, Juncus maritimus*) and brackish reed beds (and drier vegetation types in higher elevations). Dücker (1996) discussed that a combination of ice scouring, erosion, wild boar grubbing and grazing of deer was responsible for the still relatively open character of parts of the area, together with its large size (total of 61 ha) where reed invasion to the whole area may take a long time. Soil conditions also strongly varied between relatively deep coastal peatlands and more shallow gleyic soils (Dücker 1996 and own soil sampling), where lower nutrient stocks may decrease successional speed. Other authors also indicate very quick transitions from salt grasslands to brackish reed beds for the low-salinity region of Mecklenburg-Vorpommern. Fukarek (1969) observed that the Juncetum gerardii transformed to a dense reed bed within a maximum of 5 years on the Darß peninsula, only in drier salt grassland types the transition took longer. For the described Landower Wedde, Wendland (1978, after Dücker 1996) reported a transition to reed bed already three years after abandonment (in Dücker 1996). This rapid development seems to support the hypothesis of Sammul et al. (2008) that a high nutrient stock accelerates succession towards dense reed beds.

Schleswig-Holstein

In contrast to Schmeisky's (1977) assumption that nearly all salt grasslands at the Schleswig-Holstein Baltic coast would disappear at the cost of extensive reed beds if grazing ceased, the studied 'early successional' stage of salt grassland seems to be rather stable, since these sites have not been grazed for 15-50 years, without being invaded by *Phragmites australis*. Thus, the *Phragmites australis* dominated brackish reed bed and the 'early stage' with *Festuca rubra, Artemisia maritima, Juncus gerardii, Agrostis stolonifera* or *Plantago maritima* seem to be alternative successional pathways at least for time periods up to 50 years and more. In the outer, polyhaline part of the Schlei fjord, *Phragmites australis* was only dominant in small, apparently freshwater influenced patches, whereas *Phragmites australis* reed beds were more extensive at the inner, less saline parts – probably due to a combination of high salinity and mechanical stress in the outer part (Kieckbusch 1998).

Since *Phragmites australis* also reached dominance rather quickly in some of the Schleswig-Holstein localities, the speed and direction of succession seems to depend not only (or primarily) on salinity, but also on other, more local factors. Graswarder and Oehe-Schleimünde, where large areas of the 'early successional' stage persisted for at least 50 and 30 years respectively, are both quite variable beach ridge systems rather exposed to active coastal dynamics, which may contribute to keeping the shores open. On Graswarder, *Phragmites australis* exists in the ungrazed part in small areas around small open water bodies, as already described by Schmeisky (1974, 1977) 30 years earlier. Since then, the picture has apparently not changed much, *Phragmites australis* does not quickly invade the whole ungrazed part, possibly due to 'barriers' of higher, dry and relatively nutrient poor soils at the beach ridges. At Oehe-Schleimünde, *Phragmites australis* has spread over 7 ha 13 years after abandonment (Erfurt & Dierscke 1992). For an area of 122 ha, of which the large majority lies <1 m above sea level, this does not seem a serious danger to the remaining salt grasslands. The more exposed outer spits were completely free of reed in 1987. Locally, herbivory by geese and other animals might also play a role in restricting or slowing down reed invasion in Schleswig-Holstein.

Northern Denmark

At the Northern Danish Kattegat mainland coast and on the island of Læsø, the large majority of abandoned salt grasslands was not invaded by reed. In contrast, it was rather difficult to find the necessary number of replicates of the predefined 'late successional' *Phragmites australis* dominated stage. This 'stage' seems to be rather restricted to 'specific situations' where environmental factors alleviate the high salinity stress. These might be freshwater influence in the root zone (as demonstrated by Lissner & Schierup (1997) for *Phragmites australis* stands in the same region), and/or by low exposure and disturbance at very sheltered locations at the inner Fjord entrance (e.g. at Randers Fjord), where salinity may also have been slightly lower. Possibly *Phragmites australis* growth was also enhanced by high nutrient levels through agricultural run-off at the mainland sites, which was also mentioned as an additional factor favouring the spread of *Phragmites australis* after the reduction of grazing by Lundberg (1996). At most of the coast line, abandoned sites were dominated by *Festuca rubra* and *Artemisia maritim*a, which seem to represent the main successional pathway and are likely to persist in the majority of sites also in a long-term perspective.

Christiansen et al. (1991) described that salt grasslands at the Kattegat coast and Mariager Fjord develop to brackish reed beds after abandonment, but these were primarily dominated by *Bol-*

boschoenus maritimus or *Schoenoplectus tabernaemontani*. Ungrazed stretches of the outer coast line (e.g. at Helberskov, where two of this study's sites were located as well) were described as being dominated by *Festuca rubra, Artemisia maritima, Limonium vulgare, Juncus gerardii, Elymus repens, Agrostis stolonifera/capillaris* and *Potentilla anserina,* whereas *Phragmites australis* occurred only under freshwater influence (Christiansen et al. 1991).

On Læsø, Buttenschøn (1997) did not detect any reed expansion in a cattle exclosures 5 years after the start of the experiment, and this picture did not change until 2005 (18 years after the exclosures were established). Wilms (2008) hardly observed *Phragmites australis* in ungrazed, fenced-off areas at the outer shore of Rønnerne, where primarily *Artemisia maritima* dominated, but only at the more sheltered inner part (in depressions in the less salt influenced heathlands). On Rønnerne, *Bolboschoenus maritimus* and *Schoenoplectus tabernaemontani* were largely restricted to more or less freshwater influenced depressions in the upper salt grasslands (Wilms 2008). Hansen (1995) mentioned the occurrence of *Phragmites australis* only in ungrazed paludified former lagoons in the southwest that are not salt influenced any more. In this study on Læsø, *Phragmites australis* dominated salt grassland stages were found only at the sheltered fjord Floden at higher elevations in transition to heathland, which were probably less salt influenced. These were considered as 'late successional' sites, they had shallow soils and a low organic matter content (between 4.5 and 17.2) and a comparatively low cover of *Phragmites australis* (and one of them had the highest species number of all Danish sites).

The situation at the neighbouring Swedish and Norwegian coasts is similar: The reports of a quick spread of *Phragmites* in ungrazed salt grasslands at the Swedish west coast (Pehrsson 1988) and at the Norwegian Skagerrak coast (Lundberg 1996) refer all to sites that were freshwater influenced (located by river or stream mouths). According to Gillner (1960), *Phragmites australis* is restricted to freshwater influenced sites at the Swedish west coast, the Kattegat coast opposite to the Northern Danish study region. Jerling (1999) described for the Swedish west coast that salt grasslands may be kept open by tides and salt spray even when not grazed or mown, whereas at the low salinity Swedish east coast, *Phragmites australis* may almost totally dominate after a few years.

5.5 Diversity

5.5.1 Diversity along environmental gradients

All different diversity measurements indicated that diversity was higher in Estonia than in the other three regions. This is attributed to a combination of the lower salinity, which enables a higher number of species of low or no salt tolerance to occur in salt grasslands, the comparatively low nutrient availability which decreases competition (or excludes strong competitors), the higher spatial heterogeneity (microrelief etc.) and more natural gradients to non-saline habitats. Except for salinity, these points coincide with features of the 'shallow soil type' which in all regions showed a higher diversity than the 'deep soil type'.

Thus, two environmental stress gradients of salinity and of mineral nutrient deficiency interact with an additional disturbance gradient in determining species richness (Grime 1973, Connell 1978).

Salinity

A negative relationship between soil salinity and species richness was also demonstrated for Baltic salt grasslands in Denmark by Vestergaard (2002a) and in Estonia by Märtson (1996). Krause et al (2007/2008) described that salt grasslands in the western part coast were more species rich than the oligohaline salt grasslands in the eastern parts or the inner fjords (such as the Schlei) because of the natural salinity gradient along the German Baltic coast. In contrast, this study showed no significant differences in species richness between Schleswig-Holstein and Mecklenburg-Vorpommern, either in total species number or in richness at different spatial scales. Species richness of grazed sites was slightly higher in Schleswig-Holstein, that of early successional sites was similar in both regions and species richness of late successional sites was slightly lower in Schleswig-Holstein. Lübsen (2007) even observed a significant increase in species richness towards the inner Schlei, where species number on 625 m² was about double of that at the outer Schlei.

The assumption of Krause et al. (2007/2008) may, however, refer only to halophytes or specific coastal species in accordance with general descriptions of the ‘floristic impoverishment’ of salt grassland communities (in general or of specific plant communities) with decreasing salinity (e.g. Raabe 1950, Rebassoo 1975, Härdtle 1984). This was also observed in the study sites of the presented study as a decline of (the absolute number of) salt marsh species.

Salt grassland soil types

As a consequence of the described abiotic differences between the two soil types, also vegetation differed: the higher nutrient availability in the deep soil type was reflected in a higher Ellenberg nitrogen value, which explains the lower mean nitrogen value in Estonia where only the shallow soil type was found. The vegetation canopy was also higher in the deep soil type (data not shown). The higher mean salt value in sites of the deep soil type probably results from a lower number of subordinate non-halophyte species, which were more frequent in the shallow soil type due to the higher spatial variation, and due to the lower nutrient availability.

Species richness was higher in the shallow soil type, caused by the mentioned two factors: the lower nutrient availability and lower competition allowing more species to coexist (Grime 1973), and the higher variability in micro-patterns including the more gradual transitions to non-saline habitats.

Jeschke (1987) described different vegetation types in the salt grassland zonation depending on the substrate – along the salinity gradient of the coast of Mecklenburg-Vorpommern. His division of sand versus peat corresponds well to the separation of the two soil types presented here. In his succession schemes, differences between substrates occur only under grazing, while succession after abandonment leads to the same vegetation types on sand and peat. In contrast, even more pronounced differences between soil types in species richness of late successional sites were found – probably because the investigated ‘late successional’ stages still represent a transitional stage between grazed salt grassland and dense brackish reed bed. The speed of succession may also differ between the types (see below).

In accordance with the presented results, species number in south-eastern Danish salt grasslands was negatively correlated to the thickness of the organic horizon (Vestergaard 1998). In contrast, Märtson (1996, see also Puurmann et al. 2002) found a strong positive relationship between thickness of the organic horizon and species richness in Estonian salt grasslands. Jutila (1997) found a weak, but significant positive linear regression between the depth of organic layer and species richness at the Finish seashore. She suggested that the relationship seemed to be of a nonlinear, hump-shaped type, indicating that the highest richness has to be expected at an intermediate level of soil organic layer. Such a hump-shaped relationship may explain the differences between Vestergaard's (1998) observations in the Danish salt grasslands with deeper soil and Märtson's (1996) in Estonian salt grasslands with shallow soil. The results presented here may support this assumption, since depth of organic layer was not included in the Estonian multiple regression model (comprising only sites of the 'shallow soil type'), but had a strong explanatory power in the Danish model and the late successional model, which both comprised a large range of depths of the organic layer of both soil types (see 4.4.6, table 4-13, multiple regression).

A positive relationship between a more varied microtopography and species richness was also confirmed by Vestergaard (1998): Hillocks at lower elevations and anthills at higher elevations increased the number of species in his study. Also salt pans and erosion cliffs increased habitat heterogeneity and hence strongly increased the spatial variation in species composition and species richness within the locality (Vestergaard 2002a). He also ascribed the higher species richness of grazed salt grasslands to a more varied microtopography and therefore higher habitat diversity, created by trampling and grazing of domestic animals (Jensen et al. 1990, Vestergaard 2002a). A decline of species richness after the cessation of grazing is then also due to the decline in habitat diversity, caused by e.g. a less marked microrelief and the 'death' and subsequent flattening of anthills (Vestergaard 1999). Puurmann & Ratas (1998) stress that Estonian salt grasslands are intrinsically species poor due to their extreme abiotic conditions, but as a whole support considerable botanical diversity because of the diversity of ecological conditions.

Diversity and spatial scale – regional differences

The **total species number per region**, an indicator of the size of the regional species pool of salt grasslands, was much higher in Estonia than in the other three regions. The loss of a few halophyte species (towards low salinities) was by far overcompensated by an increase of non-halophytes. In general, it can be expected that the size of the regional species pool of salt grasslands decreases with increasing salinity due to more extreme conditions that exclude species with no or low salt tolerance. In contrast, total species number slightly increased again in Northern Denmark compared to Schleswig-Holstein and Mecklenburg-Vorpommern. This can be attributed to the second ecological gradient: the lower nutrient availability of the 'shallow soil type' together with the more varied microtopography and the more gradual transitions to non-saline habitats increase total species number in Denmark, and also contributed to the high total species number in Estonia. It is also possible that the species pool in Estonia was particularly large, because of the calcareous soil, which in general is connected to higher species richness than acidic soils (Ewald 2003). This might be one reason for the higher richness in Estonian salt grasslands compared to those in Southern Finland on acidic soils (Jutila 1997).

The regional species pool of vascular plants in Baltic hydro- and geolittoral salt grasslands of south-eastern Denmark contained 80 halophytic species or subspecies (Vestergaard 2002a). The number of halophytic species declined gradually towards northern Denmark to about 51 species (Vestergaard 2002a). The relatively large pool in south-eastern Denmark was partly due to the presence of an element of continental species as well as of south-European species. This case confirms the species-pool concept which emphasises that also large-scale, evolutionary and historical processes are of importance for species richness patterns, not only the present-day ecological conditions (Zobel 1997, Godfray & Lawton 2001).

The **slope of the species-area-curve** was higher in Estonia because of higher environmental heterogeneity and microrelief within the 625 m²-plots. The intercept, related to species number on 1 m² was also higher in Estonia and in sites of the shallow soil type. At the Schlei fjord in Schleswig-Holstein, the intercept was also found to be higher at low and intermediate salinity levels (Lübsen 2007*).*

Evenness was higher in Estonia than in the other three regions. Presumably, there were in total more species with a more even distribution, and less single species were dominant. This may indicate that evenness is not independent of species richness, as discussed by Gosselin (2006).

5.5.2 Diversity and management – different diversity measures

The **total species number per management class** showed different patterns in the four regions: In Estonia, it decreased by 24% in early successional sites, and then slightly increased again, resulting in an overall decrease of 8%. In Schleswig-Holstein, total species number increased by 8% in early successional sites compared to grazed sites, and then slightly decreased in late successional sites. The decrease in late successional sites in Schleswig-Holstein is in line with the decrease of species richness observed only there (see below).

In Mecklenburg-Vorpommern and Denmark, total species number increased from grazed to late successional sites (by 81% and 31%, respectively). This increase illustrates that the loss of a few 'early successional species' from late successional sites is overcompensated by newly appearing 'late successional' species. At least in Mecklenburg-Vorpommern, the strong increase is probably partly due to the 'shallow soil type', which was not represented in grazed sites and which offers more variable site conditions for different species (such as *Odontites litoralis, Inula britannica, Carex viridula* var. *viridula, Mentha aquatica, Plantago winteri, Lathyrus pratensis*). In total, these numbers indicate also that – except in Schleswig-Holstein – hardly any species are totally lost from late successional sites (yet).

Species richness decreased in the course of succession only in Schleswig-Holstein in 1 m²- and 25 m²-subplots. Successional sites there were abandoned for a significantly longer time period than in the other three regions, and these sites already developed further towards the species-poor terminal phase of brackish reed beds (see 4.4.1). However, species richness on 625 m² was not affected by management. After abandonment, a more coarse-grained mosaic of dominance patches developed. Consequently, species numbers decreased on small scales, but changed less on larger scales, or even increased compared to grazed sites (e.g. Chaneton & Facelli 1991). These differences between small and large scales were also observed in abandoned fen grasslands (Falinska 1991, Rosenthal 1992, Schreiber 1997), and confirmed for Baltic Sea salt grasslands in Sweden (Dupré & Diekmann 2001) and for Wadden Sea salt marshes in Schleswig-Holstein (Kiehl 1997). In contrast, Bakker et al. (2003a) found consistently higher species numbers in intensively grazed sites on all studied scales (from 0.01 to 2500 m²) in Dutch Wadden Sea salt marshes. The differences between the findings of Kiehl (1997) and Bakker et al. (2003a) may be related to time since abandonment, which was only five years in Schleswig-Holstein, and at least 30 years in The Netherlands. According to Bakker et al. (2003b), the dominance of *Elymus athericus* (and a subsequent decline in the number of plant communities and species) was found only in salt marshes that were abandoned for at least 10 years. However, Kiehl (1997) also compared the young abandonment stages with a long-term abandoned salt marsh (Süderhafen, abandoned for more than 20 years), which showed somewhat lower species numbers on small scales (1 and 4 m²), but no significant differences in species numbers on larger scale (20 m²) compared to intensively grazed sites. Furthermore, the livestock species may also play a role (Scherfose 1993), since the grazed study sites in Schleswig-Holstein were intensively grazed by sheep, whereas the Dutch sites were cattle grazed (partly in combination with sheep and/or horses, Bakker et al. 2003a). Vestergaard (2002a) found a similar relationship as this study did on much larger scales (1-100 ha): species richness of grazed and ungrazed salt grasslands at the Danish island Funen were similar on 1 ha, but on larger scales (10 and 100 ha) grazed sites had a much higher species number. In contrast, Jutila (1997) found a more coarse-grained vegetation pattern in grazed salt grassland sites compared to ungrazed sites in Southern Finland, with lower species numbers on 1 m² scale, but similar numbers for whole sites (hectares).

Apart from Schleswig-Holstein, in the other three regions, no decline of species richness was observed at any of the studied scales. However, as indicated by the negative correlation between reed cover and species number (on 1 m²), it can be expected that species richness will decrease in the course of succession, if reed beds become denser.

Species richness was not only higher in sites of the shallow than the deep soil type, but species richness of the two soil types also developed differently in the course of succession: In late successional sites, species richness decreased in the deep soil type, whereas it slightly increased in the shallow soil type (see 4.4.5). Also evenness only decreased in late successional sites of the deep soil type, but remained at the same level in the shallow soil type. This supports the assumption that succession is quicker in the deep soil type with a higher nutrient availability, and that the higher spatial heterogeneity of the shallow soil type supports high species richness and evenness also in late successional stages.

The **slope of the species-area-curve**, indicating the accumulation of species with increasing scale, was steeper in late successional sites than in grazed sites because of the more coarse-grained vegetation pattern in late successional sites. This is in good accordance with the results of Dupré & Diekmann (2001) for Baltic salt grasslands in Sweden, and of Kiehl (1997) for Wadden Sea salt marshes in Schleswig-Holstein. Also Lübsen (2007) found a steeper species-area-curve in abandoned (corresponding to this study's 'early successional') sites than in grazed salt grasslands at the Schlei fjord in Schleswig-Holstein. Contrasting results were achieved for North Sea salt marshes in The Netherlands (Bakker et al. 2003 a, b, see above).

Evenness was higher in grazed and early successional sites which illustrates the stronger dominance structure in late successional sites. This effect was not significant on 1 m²-scale, because on this small scale, only few species may be dominant in all management classes.

In summary, it becomes clear that spatial scale and patterns have to be considered when interpreting the impact of management on species richness patterns, and in particular before drawing conclusions for an 'optimal' management of salt grasslands.

Most other authors have investigated successional processes only at one spatial scale, and mostly on small plot sizes between 1 m² (e.g. Christiansen 1937, Jutila 1997, Puurmann et al. 2002), 4 m² (e.g. Kiehl et al. 1996, Bos et al. 2002) and 25 m² (e.g. Vestergaard 1994 related to mowing). Most of these authors reported a decline of species numbers after abandonment (salt marshes in general:

Adam 1990, North Sea salt marshes: Bakker et al. 1993, 2003a, b, Berg et al. 1997, Baltic Sea salt grasslands: Puurmann & Ratas 1998, Vestergaard 1999, Dupré & Diekmann 2001 – only on small scales, Puurmann et al. 2002, Sammul 2008). At the Schleswig-Holstein Wadden Sea coast, species numbers only decreased slightly (but insignificantly) in the high marsh, but increased in all other marsh zones, within 9 years of abandonment (Schröder et al. 2002). The overall increase in species richness is explained by large-scale processes after the changes in grazing management: in the intensively grazed monotonous landscape before the establishment of the National Park, the species pool was restricted (Olff & Ritchie 1998, Chaneton & Facelli 1991) because only grazing tolerant species were selected. After parts of the salt marshes were abandoned or grazing pressure was reduced, grazing sensitive species (such as *Atriplex portulacoides, Aster tripolium, Artemisia maritima, Elymus athericus*) appeared also in the (continuously) intensively grazed salt marshes, because these species increased in abandoned areas and enough seeds were provided to establish in gaps of grazed salt marshes (Schröder et al. 2002, Gettner 2003). This may also illustrate that permanent plot studies on small-scale ex- or enclosures may not mirror the full picture of processes occurring at larger scales, including such neighbourhood effects.

In accordance with the intermediate disturbance hypothesis (Connell 1978), lower species numbers were also found in long-term intensively grazed sites (in general: Doody 2001, 2008, lower salt marsh at the North Sea coast: Bakker 1989, Kiehl 1997, Baltic Sea coast: Dupré & Diekmann 2001). Bakker et al. (2003a) conclude that a maximal diversity of plant communities, structure classes and species on small and large scales can be maintained with the help of intermediate stocking rates (‘intermediate disturbance level’).

In contrast to most authors cited above, Jutila (1997, 1999, 2001) found less species in grazed than in abandoned salt grasslands in Southwest Finland, but also mentioned that grazing pressure between transects differed and was partly very low (0.3 animals/ha) or that grazing was re-introduced only a few years before (after 10-20 years of abandonment, Jutila 1999). Furthermore, exposure and thus disturbance frequency differed a lot and had a strong impact on species richness (Jutila 1997). Jutila (2001) argued that water level fluctuation stress and salinity may make these salt grasslands more sensitive to grazing than other ecosystems.

From a nature conservation point of view, not only the number of species is relevant, but also which species increase or decrease in response to grazing or abandonment. The impact of management on ‘characteristic’ species (defined for the Habitats Directive) and rare and endangered species (categorised in the Red List) as target species will be discussed in 10.2 (below).

Part 2: Impact of grazing, abandonment and restoration on vegetation and seed banks of salt grasslands in Estonia

Introduction

Due to the recent changes in land use, the cessation of traditional use is a particularly pressing problem for nature conservation of salt grasslands in Estonia. In the 1950s, salt grasslands were overexploited in many places, whilst some others were abandoned. After Estonia regained its independence in 1991, the introduction of a market economy reduced agricultural production dramatically (Ehrlich 1996). The start of re-privatisation further enhanced abandonment of low productive semi-natural grasslands such as salt grasslands. Hence, the maintenance of salt grasslands became seriously threatened in the early 1990s (Leibak 1996).

Since 2001, national subsidies were paid by the ministry of environment for maintaining salt grasslands in protected areas (Roosaluste 2002). With Estonia's accession to the European Union in 2004, EU-funds became available to support agricultural production and implement agri-environmental policies. In recent years, several restoration projects in Estonia have aimed and still aim to counteract the loss and deterioration of salt grasslands by reintroducing grazing regimes (Rannap et al. 2004, Lotman et al. 2005, LIFE-project Silma 2004, LIFE-project Rannametsa 2004, LIFE Baltcoast 2006).

In the following part 2, the changes of plant species composition, abundances and richness in Estonian salt grasslands were investigated

- during progressive succession from grazed salt grasslands towards brackish reed beds after abandonment as well as
- during retrogressive succession from reed invaded abandoned sites towards salt grasslands after re-introduction of grazing

using the approach of a 'space-for-time substitution' (see part 1, introduction).

Persistence in the seed bank is considered as an important 'reserve' for the restoration of grassland communities, since seeds persist in the soil as a 'memory' of former vegetation (Bakker et al. 1996b). It affects seed availability qualitatively as well as quantitatively and can act as a bottleneck for restoration success (Strykstra et al. 1998). Seed banks of Baltic salt grasslands are generally quite poorly studied (Adam 1990, Jerling 1999). Jerling (1983) and Grandin (2001) studied the seed bank in Swedish salt grasslands, whereas Jutila (1998a, 2003) and Folkowski & Seiberling (2002) focussed on sites in Southern Finland and Germany, respectively. So far, there are apparently no known seed bank studies from Estonian salt grasslands at all.

Studies on the impact of grazing on species composition and richness of the seed bank gained contrasting results: While in some studies species numbers were higher at grazed sites (Donelan & Thompson 1980, Gibson and Brown 1991), other studies revealed the opposite (McDonald et al. 1996, Bakker et al. 1996b, Jutila 1998a). Jutila (1998a) discussed that species richness of the seed bank under grazing impact may follow the hump-shaped optimum curve as postulated by the Intermediate Disturbance Hypothesis (Connell 1978). The functional role and potential contribution of the seed bank for the re-establishment of target species – and hence restoration success – is still discussed controversially. Bakker et al. (2005) concluded that the seed bank was not the dominant source for newly establishing species after top soil removal in wet dune slacks, but rather dispersal from nearby populations and successional processes. McDonald et al. (1996) stated that managers attempting to restore flood-meadows cannot rely on the seed bank as a source of the original vegetation. In contrast, Kalamees & Zobel (2002) found that the seed bank had an important functional role for the recolonisation of small gaps in a perennial calcareous grassland community in western Estonia. Jensen (2004) argues that persistence and hence the potential role of seed banks in restoration has often been underestimated for methodological reasons.

The described changes in agricultural use and management of salt grasslands during the last decades make Estonia an excellent case study for progressive and retrogressive successional processes. At the same time, nature conservation managers urgently need scientifically-sound knowledge on how to continue their efforts in restoring Estonian salt grasslands.

Thus, the following research questions shall be answered:

- How does vegetation change after abandonment and restorative grazing?
- Which species form a (transient/persistent) seed bank in Estonian salt grasslands?
- How is the seed bank influenced by abandonment?
- May the seed bank provide a potential for the re-establishment of characteristic salt grassland species after re-introduction of grazing?

6 Methods

In the study region Estonia (see chapter 2), continuously grazed salt grasslands were compared with early and late successional stages of abandoned salt grasslands (see chapter 3, 5 replicates per management class, except for 'grazed' with 7 replicates). 'Late successional stage' was determined by the invasion of *Phragmites australis* with a cover of > 25%. In addition, five 'restored' sites were investigated: formerly 'late successional' sites where grazing has been reintroduced 2-4 years ago. A table with information on all study sites can be found in chapter 2 (table 2-2). For the vegetation analysis, the same methods as for part 1 were applied. They are presented in chapter 3.

6.1 Soil seed bank

The seed bank was sampled following the procedure developed by Ter Heerdt et al. (1996). Five grazed and six ungrazed sites (four 'early successional' and two 'late successional' sites) of the sites which had already been selected for the vegetation analysis were sampled in November 2004. On each of the five 25 m²-subplots per site (see fig. 3-1), five soil cores were taken (4.5 cm diameter to a depth of 10 cm), which resulted in a sample volume of approx. 800 ml and a sampled area of approx. 80 cm² per subplot.

The five soil cores per subplot were divided in two horizons (0-5 cm, 5-10 cm) and the soil of each horizon and subplot was pooled. The pooled soil samples were washed over a sieve (mesh size 0.2 mm) to reduce the amount of soil and to remove vegetative parts as roots and rhizomes. The remaining material was spread on trays on sterile soil (peat-sand mixture) in a layer of 2-3 mm. The samples were exposed to outdoor temperatures, covered with glass against contamination by wind-borne seeds and watered regularly. Emerging seedlings were identified following Csapody (1968) and Muller (1978), counted and removed as soon as possible from spring 2005 to spring 2007. Unidentified specimens were planted in pots and cultivated until identification was possible.

All woody species (mainly *Salix* spec., also *Betula* spec. and some others) were excluded from the analysis, since some specimen were also found in the control trays, and thus they had probably been imported by wind dispersal. Some species were excluded from analysis, because they were found in controls and/or the direct surroundings of the glasshouse (such as *Epilobium adnatum, Stellaria media, Urtica dioica, Cerastium* spec., *Cardamine hirsuta, Conyza canadensis, Senecio vulgaris, Arabidopsis thaliana*).

For some species, germination or vegetative reproduction in autumn and/or the second year was excluded because ripening of seeds or vegetative reproduction from vegetative parts left in the sample could not be prevented in spring or in the first year (such as *Sonchus oleraceus, Sagina procumbens, Cardamine pratensis*). Inclusion of these seedlings would have led to an overestimation of these species' seed densities.

6.2 Data analysis

To allow for a comparison of vegetation and seed bank, data was transformed to 'relative species number' (species number of group A/total species number) and 'relative abundance' (vegetation: cover of species (group) A/cover sum of all species, seed bank: seedlings of species (group) A/sum of all seedlings) in each relevé/sample. For the analysis, the same species traits were used as described in chapter 3 (part 1).

6.2.1 Classification of the seed bank and longevity of seeds

The species occurring in the seed bank were classified by comparing the presence of the species in the aboveground vegetation and the number of seeds in the two soil horizons (0-5 cm, 5-10 cm), according to the classification key by Thompson et al. (1997). Seed banks are classified as transient, when a species is present in the vegetation and absent from the seed bank or present only in the upper seed bank horizon. Seeds are assigned as short-term persistent when they are more abundant in the upper than the lower horizon, and as long-term persistent when there are at least as many seeds in the lower horizon as in the upper horizon. For this classification, seeds were only counted as present with at least three seeds per horizon (as recommended by Thompson et al. 1997).

The seed bank type of each species was classified for each site separately (data from the five subplots pooled) and subsequently, the longevity index was calculated according to Bekker et al. (1998a) as follows:

$$LI = \frac{SP + LP}{T + SP + LP}$$

LI is the Longevity index, SP, LP and T represent the numbers of sites in which a species was classified as short-term (SP) or long-term persistent (LP) or transient (T). This index ranges from 0 (strictly transient) to 1 (strictly persistent). The index calculated by my own classifications is addressed as ‘internal LI’, while the index derived from the Thompson database (Thompson et al. 1997) is addressed as ‘Bekker LI’. Both data sources were combined by adding all internal classifications (for each site with at least 3 seeds per horizon) to the records of the database of Thompson et al. (1997). Then, the longevity index (LI_Bekker+intern) was calculated from the combined data set. In general, a longevity index was only calculated for species with at least 5 categorized records or with 3-4 unanimously categorized records (see Bekker et al. 1998b).

6.2.2 Diversity and similarity indices

Evenness (Hobohm 2000) was calculated for the vegetation of 1- and 25-m²-subplots and for the seed bank samples of each 25-m²-subplot (both seed bank horizons separately).

The degree of **spatial heterogeneity** of the species composition of vegetation and seed bank was tested separately as subplot similarity between all (ten) possible pairs of subplots per site. For each pair of subplots of one site, Sørensen-Similarity-Index was calculated (for vegetation and seed bank horizons separately, for vegetation: for 1 and 25 m²-subplots separately). Then the average of all subplot-pairs of one site was calculated and used for statistical analysis. Finally, the Similarity-Index was transformed to heterogeneity (=1- Sørensen-Similarity-Index). Thus the heterogeneity index ranged from 1 (high heterogeneity = completely different) to 0 (lowest similarity = identical).

To estimate the **similarity** of the species composition between **aboveground vegetation and seed bank**, two indices were calculated:

- Sørensen-Index (Sørensen 1948, Hobohm 2000),

- Bray-Curtis-Similarity-Index, which is based on relative abundances (Bray & Curtis 1957). It was transformed from Bray-Curtis-Distance to Bray-Curtis-Similarity (BC-Similarity = 1 – BC-Distance), so that both indices ranged from 1 (high similarity = identical) to 0 (lowest similarity = completely different).

Similarity was first calculated for each 25 m²-subplot (vegetation and pooled seed bank sample), then the average similarity of all subplots at one site was calculated.

6.3 Statistical Analysis

Statistical analyses were carried out separately for two data sets. The impact of abandonment and restoration on the vegetation of Estonian salt grasslands was analysed based on the 'complete vegetation data set' comprising data of all four management classes (grazed, early successional, late successional and restored sites, with 5-7 replicates each). The changes of the seed bank and the corresponding vegetation in the course of progressive succession was analysed based on the 'matched seed bank-vegetation data set' which comprises only data of five grazed, four early and two late successional sites (where both seed bank and vegetation were sampled on the same 25-m²-subplots).

Because in most cases 'sites' were significantly different (in a nested ANOVA design with site as a random factor nested in management), but differences between sites were not of primary interest, the mean of the five 1- or 25-m²-subplots was calculated and used in subsequent statistical tests. Individual subplots were only used for multiple regression analyses and for calculating species-area-curves and subplot similarities.

Statistics were performed with the software package Statistica 8.1 (StatSoft 2007), except for the detrended correspondence analyses (DCAs) which were performed with PC-Ord version 4 (MjM software design 2002). Similarity indices and evenness were calculated with MVSP (Kovach Computing Systems 2003).

Although data transformations or non-parametric tests were applied in many cases, the untransformed mean (and not the median) was generally displayed in tables and figures to allow for an easier comparison of the results. In figures and tables, the following abbreviations were used for the management classes: grazed = G, early successional = ES or early succ., late successional = LS or late succ., restored = R, and for the sample source: vegetation = V, upper seed bank horizon (0-5 cm) = upp, lower seed bank horizon (5-10 cm) = low.

Analysis of the complete vegetation data set

In the analysis of the complete vegetation data set, the impact of management on the following variables was tested with one-factorial ANOVAs: elevation, elevation range, soil parameters (all measured parameters except for C/N-ratio), the mean Ellenberg nitrogen value, the degree of 'natural' grazing and vegetation structure parameters (vegetation height, thickness of the litter layer, vegetation cover). The impact of management on cover/frequency of selected individual plant species and on relative species number/relative cover of several species groups (annual and biennial species, socio-ecological species groups, species characteristic for BBCM) was also analysed with one-factorial ANOVAs, as well as the impact of management on the intercept and slope of the species-area-curves.

The impact of management and spatial scale on species number, evenness and spatial heterogeneity was tested with two-factorial (within-subjects-)ANOVAs with scale as a within-(subjects-)factor and management as between-(subjects-)factor.

If necessary, data was log-, root- or arcsin-transformed to meet ANOVA assumptions. If ANOVA assumptions were still not fulfilled after data transformation, Kruskal-Wallis-tests were carried out. This was the case for analysing the impact of management on the C/N-ratio of the soil and mean Ellenberg values for moisture and salinity. The impact of management on cover/frequency of selected plant species and on relative species number/relative cover of several species groups (annual and biennial species, socio-ecological species groups, species characteristic for BBCM) was also analysed using Kruskal-Wallis-Tests.

The impact of management on cover (1 m²) and frequency (25 m²) was analysed for all 38 species with a mean frequency of at least 10%, but results are only shown for species significantly affected by management. Whether the impact of management on cover and/or frequency of a specific plant species or on relative species number and/or relative cover of a specific species group was analysed by a one-factorial ANOVA or a Kruskal-Wallis-Test is noted in the respective results tables, where all F- and H-values are listed (for ANOVA/Kruskal-Wallis-Tests, respectively). Differences between the four management classes or between the two/three spatial scales were tested with Post-Hoc-Tests (Tukeys HSD, HSD for unequal n, or multiple comparisons in case of a Kruskal-Wallis-Test).

Similarities and differences in vegetation composition between management classes were visualized by a detrended correspondence analysis (DCA). In this analysis, all sites with %-cover data of all 117 taxa present in the 625 m²-plots were used. Rare species were down weighted. The ordination plot was overlaid and the first two axes correlated with environmental variables such as vegetation structure parameters (vegetation height, thickness of litter layer, vegetation cover), elevation and elevation range, soil parameters (thickness of the organic layer, pH, salinity, soil content of C, N, P_2O_5, K_2O, Mg, organic matter, inorganic C and C/N-ratio), mean Ellenberg values for moisture, salinity and nitrogen, degree of 'natural grazing' and time since abandonment. Only environmental variables with correlations of $r^2>0.10$ were shown. Management categories were included as dummy variables and were displayed as centroids (symbols, irrespective of the r^2-values). In spite of rather short gradients, a DCA was preferred to a principal component analysis (PCA) because in the PCA, some plots strongly dominated the overall pattern (due to a high cover of one or a few uncommon species) and differences between the other plots were not recognisable any more.

Linear regression was used to analyse the relationship between cover of *Phragmites australis* and species richness of late successional 1-m²-subplots. Only subplots with at least 20% cover of *Phragmites australis* were included, since a lower cover of *Phragmites australis* was not assessed as characteristic for the 'late successional' stage. The relationship between measured soil salinity and unweighted mean salt indicator value was also analysed with regression analyses (linear and power function).

Linear regression analyses were also used to investigate the relationship between parameters of vegetation structure (vegetation height, thickness of litter layer, vegetation cover, cover of *Phragmites australis*), degree of 'natural grazing', time since abandonment and species number (on 1 m²), as well as between abiotic conditions (elevation, elevation range, thickness of the organic layer, pH, salinity, soil content of C, N, P_2O_5, K_2O, Mg, organic matter, inorganic C and C/N-ratio) and species number (on 1 m²).

In addition, the impact of ten parameters of site conditions and vegetation structure on species richness of 1-m²-subplots was investigated with a multiple linear regression model. From the parameters listed above (included in the single linear regressions), variables with an internal correlation of >0.5 were excluded, thus 10 variables remained in the model for stepwise forward selection (soil salinity, elevation, elevation range, thickness of the litter layer, vegetation cover, pH, C/N-ratio, organic matter content, depth of the organic layer, P_2O_5 content). By stepwise forward selection of variables, the former six variables were included into the multiple regression model.

Analysis of the matched seed bank-vegetation data set

In the analysis of the matched seed bank-vegetation data set, the impact of management on seed density of selected individual species and on mean longevity of socio-ecological species groups and of species characteristic for BBCM (versus non-BBCM species) was tested with one-factorial ANOVAs.

The impact of management and of the seed bank horizon on total seed density, the number of species in the seed bank and seed density of *Galium palustre* was tested with two-factorial (within-subjects-)ANOVAs with seed bank horizon as a within-(subjects-)factor and management as between-(subjects-)factor.

The impact of management and of the sample source (vegetation, upper and lower seed bank horizon) on species number per sample, evenness, seed bank-vegetation-similarity and spatial heterogeneity was tested with two-factorial (within-subjects-)ANOVAs with vegetation/seed bank horizon as a within-(subjects-)factor and management as between-(subjects-)factor. The same analysis was applied for the impact of management and sample source on relative abundance of selected individual species and relative species number/relative abundance of several species groups (annual and biennial species, socio-ecological species groups, species characteristic for BBCM). The ANOVA of relative abundance of *Centaurium littorale* in vegetation and seed bank was carried out excluding data of the lower seed bank horizon, since only very few seeds were found there and ANOVA assumptions could otherwise not be fulfilled.

If necessary, data was log-, root- or arcsin-transformed to meet ANOVA assumptions. If ANOVA assumptions were still not fulfilled after data transformation, Kruskal-Wallis-tests were carried out. This was the case for analysing the impact of management on seed density of selected individual species. The impact of the sample source (vegetation/seed bank horizon) on relative abundance of selected individual species in the vegetation and seed bank was analysed with Friedman-Tests. If visual inspection of the results revealed that differences between vegetation and seed bank horizons occurred only in one management class, the Friedman-Test was carried out for this management class separately (which was noted in the results-table).

Relative abundances in seed bank horizons and vegetation were compared for all 18 species which were present in the vegetation and found in the seed bank with more than 50 seeds (in all seed bank samples together). Whether the impact of sample source (vegetation/seed bank horizon) on the relative abundance of a specific plant species was analysed by a two-factorial ANOVA (including also management as between-factor) or a Friedman-Test is noted in the respective results tables, where all F- and χ^2-values are listed (for ANOVA/Friedman-Tests, respectively). For all individual plant species for which ANOVA assumptions were met, 2-factorial ANOVAs (instead of one-factorial ANOVAs) were carried out to be able to also analyse the interaction between management and sample source (vegetation/seed bank horizon).

Differences between the three management classes and between the three sample sources (vegetation and seed bank horizons) were tested with Post-Hoc-Tests (Tukeys HSD, HSD for unequal n, or multiple comparisons in case of a Kruskal-Wallis-Test). A species was described as ‘overrepresented’ (or ‘underrepresented’) in the vegetation if the cover of this species relative to the vegetation cover of all species in the relevés was higher (or lower, respectively) than the share of its seeds relative to all seeds in the respective seed bank samples.

Similarities and differences in species composition between management classes and between vegetation and seed bank horizons were visualized by a detrended correspondence analysis (DCA). In this analysis, presence-absence-data of all taxa present in the pooled samples/relevés (pooled per seed bank horizon/vegetation data of the five 25-m²-subplots pooled) were used. Rare species were down weighted. The ordination plot was overlaid and the first two axes correlated with environmental variables such as vegetation structure parameters (vegetation height, thickness of litter layer, vegetation cover), elevation and elevation range, soil parameters (thickness of the organic layer, pH, salinity, soil content of C, N, P_2O_5, K_2O, Mg, organic matter, inorganic C and C/N-ratio), degree of ‘natural grazing’ and time since abandonment. Only environmental variables with correlations of $r^2>0.10$ were shown. Management categories and seed bank horizon/vegetation were included as dummy variables and were displayed as centroids (symbols, irrespective of the r^2-values). In spite of rather short gradients, a DCA was preferred to a principal component analysis (PCA) because in the PCA, some plots strongly dominated the overall pattern (due to a high cover of one or a few uncommon species) and differences between the other plots were not recognizable any more.

7 Results

7.1 Site conditions

The study sites were located at elevations between 5 and 44 cm (mean: 26.5 cm) above sea level (asl, mean of 45 measuring points per site), the 1 m²-plots were at elevations between -5 to 56 cm above sea level (asl). This corresponds to an average of 12.4 (at 44 cm asl) up to 130 (at 5 cm asl) days of flooding per year (fig. 7-1, calculated for the water level station of Heltermaa). Thus the sites were primarily located in the lower (0-20 cm asl) and middle geolittoral zones (20-40 cm asl), with some extending into the upper geolittoral zone (40-80 cm asl). The elevation range varied between 9 and 55 cm with a mean of 27.9 cm.

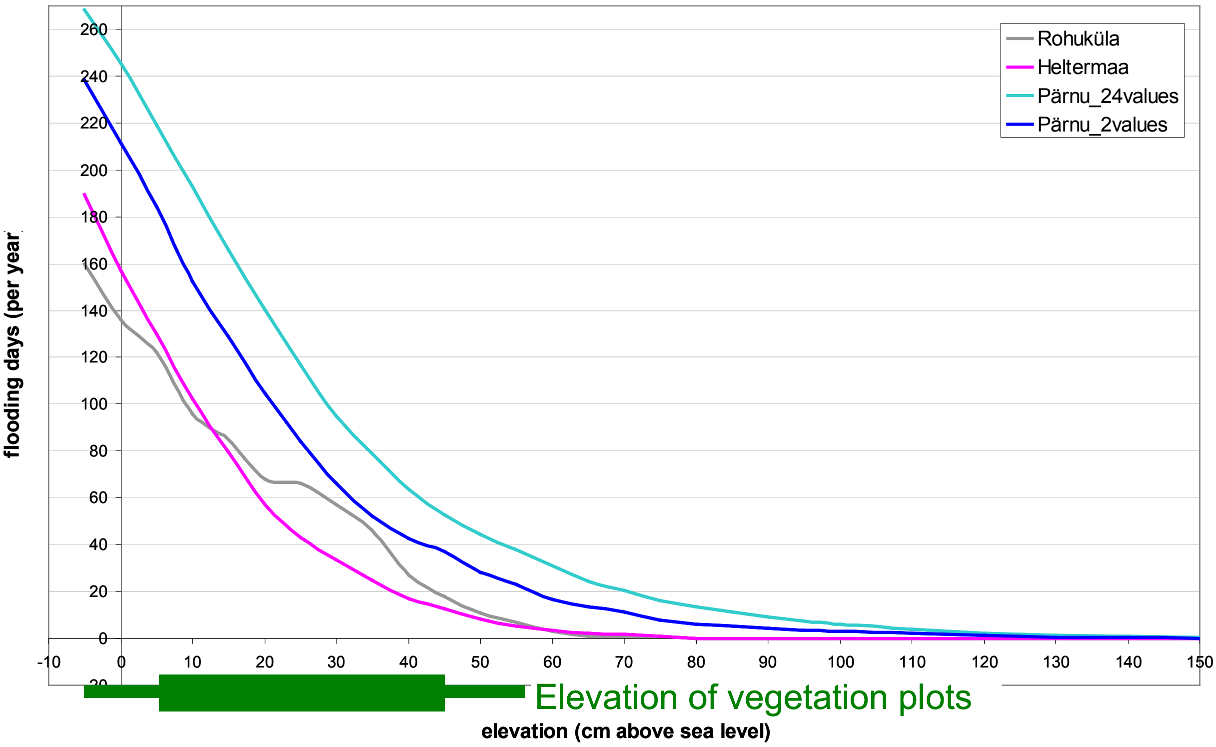


Fig. 7-1: Mean number of flooding days per year in Pärnu (1998-2005), Heltermaa (1998-2005, but 1997 and 2000 excluded due to many days of missing data) and Rohuküla (2006), at different levels of elevation (cm above sea level). For Pärnu, the curve calculated according to the full data set (=24 values per day) is given as well as the curve for 2 values per day (6 and 18 o'clock). For the curves of Rohuküla and Heltermaa, only 2 values per day were available (see discussion). Maximum flooding height: Pärnu (9.1.2005): 275 cm, Heltermaa: 82 cm (11.1.2005). The elevation of the vegetation plots is marked (big bar: range of means of 625 m²-plots, narrow bar: range of means of 1 m²-subplots).

The soils of the study sites were characterised by a thin organic layer (mean per site: 3.2-15.1 cm) with an organic matter content of 7.3-27.4% (mean 15.7%). The nitrogen content varied between 0.37% and 1.22% (mean of 0.71), the C/N-ratio between 11 and 16 (mean: 12.9). The content of inorganic carbon ranged between 0% and 3.59% (mean 0.59%). The pH varied between 5.2 and 6.8 (mean of 6.3).

Soils were rich in magnesium (62-638 mg/100 g, mean 215 mg/100 g) and mostly rich in potassium (9-70 mg/100 g, mean: 39 mg/100g). The phosphate content was low (2-10 mg/100 g, mean: 5.7 mg/100 g). Soil salinity (related to soil dry matter) ranged between 2.91 and 19.96 psu (mean: 10.25 psu).

The sites of the four management classes differed only in one abiotic parameter: the content of phosphate (P_2O_5) was significantly higher in grazed than in late successional sites, whereas early successional and restored sites showed intermediate phosphate contents (see table 7-1).

Table 7-1: Abiotic parameters and Ellenberg indicator values of all sites (625 m^2, mean of n=5 in each management class except for grazed with n=7). Results of one-factorial ANOVAs (F, p)/Kruskal-Wallis-ANOVAs (H, p). a,b,c: significant differences according to Post-Hoc-tests (Tukey for unequal N/multiple comparisons) are indicated by different letters. Natural grazing: degree of habitat use by geese, rabbits, hares, deer or moose on a scale from 0 (no) to 2 (strong). Vegetation indicators (unweighted mean values) according to Ellenberg et al. (1992), except for salt indicator value: combined from Ellenberg et al. (1992) and Scherfose (1990), ranging from 0 (intolerant to salt) to 6: extremely high salt tolerance.

					effect of management			transf.	Post-Hoc-Test			
	grazed	early succ.	late succ.	restored	F	H	p		G	ES	LS	R
Abiotic conditions												
Elevation (cm a. sl.)	24.87	30.57	21.32	34.21	1.30		0.31					
Elevation range (cm)	34.29	29.40	27.20	19.00	2.58		0.09	log				
Organic layer (cm)	9.71	10.50	8.58	6.93	1.53		0.24					
PH	6.43	6.24	6.00	6.42	1.22		0.33					
P_2O_5 (mg/100g)	6.71	6.20	3.60	6.40	3.97		*	log	a	ab	b	ab
K_2O (mg/100g)	41.00	38.00	32.00	49.00	0.67		0.58	sqrt				
Mg (mg/100g)	276.00	165.80	216.20	209.40	1.15		0.36	log				
Salinity (psu)*	9.71	10.90	8.09	13.38	1.77		0.19	log				
Organic matter (%)	15.44	16.92	15.04	16.88	0.18		0.91					
Total N (%)	0.67	0.79	0.66	0.80	0.54		0.66					
C/N	13.57	12.60	13.20	12.00		4.40	0.22					
C inorganic (%)	0.84	0.24	0.81	0.47	0.42		0.74	log				
Total C (%)	8.96	9.81	8.72	9.79	0.18		0.91					
Vegetation indicators												
Mean moisture value	7.01	7.06	7.29	7.11		1.63	0.65					
Mean salt value	2.17	2.24	2.06	2.40		0.67	0.88					
Mean nitrogen	4.29	4.56	4.70	4.69	0.76		0.53					

* The given soil salinity values are related to soil dry matter, salinity values related to soil solution are much lower (approx. 30% of these) and significantly correlated to salinity values related to soil dry matter (see 5.1)

The mean Ellenberg values indicated moist, α- to β-mesohaline (low to medium chloride content of 0.3-0.7% Cl^-), moderately acid to neutral site conditions, moderately rich in nitrogen with a suboceanic to intermediate (weakly suboceanic to weakly subcontinental) flora.

Measured soil salinity was correlated to the unweighted mean salt indicator value ($r^2=0.44$ for the linear function $y= 0.996x + 1.2525$, and $r^2=0.53$ for the power function $y= 2.2543x^{0.3985}$, calculated with the 625 m^2-relevés).

7.2 Vegetation analysis

7.2.1 Species diversity

Overall, 117 taxa were found in all sites (see annex 5). Management had no significant impact on species number on any of the studied scales (F=0.05, p=0.98). Species number strongly increased with increasing plot size (F=218.4, p<0.001, 2-factorial ANOVA with scale as within-factor). Species number (on 1 m^2) in 'late' successional sites with at least 20% reed cover significantly decreased with increasing cover of *Phragmites australis* (from 12 species at 20% to 8 species at 88% cover, r= -0.50, $r^2=0.25$, p<0.01, fig. 7-2).

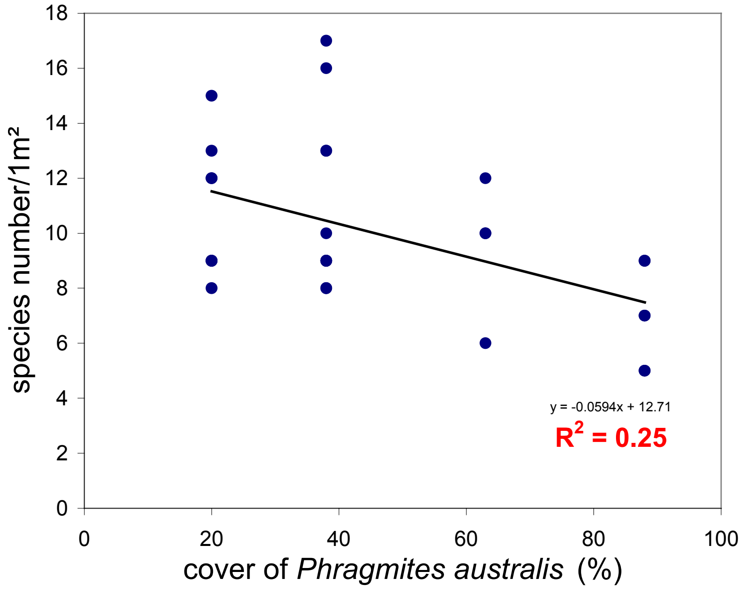


Fig. 7-2: Relationship between reed cover (%) and species number on 1-m²-plots in late successional sites (all 1 m²-plots with at least 20% reed cover, n=29).

Evenness showed a trend to decrease from grazed (0.84) and restored (0.83) to early (0.80) and late successional sites (0.75). Differences in evenness between management classes were marginally insignificant (F=2.73, p=0.074). The increase of evenness with increasing scale from 0.77 at 1 m² to 0.81 at 25 m² and 0.86 at 625 m² was highly significant (F=45.17, p<0.001, 2-factorial ANOVA with scale as within-factor).

The (log-log) species-area-curves showed no significant differences in intercept (F=0.11, p=0.96) or slope (F=0.96, p=0.43) between management classes.

7.2.2 Vegetation structure

The vegetation was highest in 'late' successional sites (mean ± SD: 119.0 ± 24.9 cm). Vegetation of 'early' successional (34.3 ± 2.2 cm) and restored sites (31.6 ± 5.8 cm) were still significantly higher than grazed sites (18 ± 11.2 cm, ANOVA, data log-transformed: F=34.2, p<0.001). The litter layer was thicker in 'early' (mean ± SD: 5.1 ± 1.6 cm) and 'late' successional sites (6.0 ± 2.3 cm) than in grazed (0.53 ± 0.33 cm) and restored sites (0.43 ± 0.25 cm, ANOVA, data log-transformed: F=46.6, p<0.001). Vegetation cover (mean of 1 m²-subplots) was significantly higher in late successional sites than in restored sites. Grazed and early successional sites were intermediate (see table 7-2).

Natural grazing was significantly higher in grazed than in early and late successional sites, and intermediate in restored sites (table 7-2). Late successional sites were not grazed by small herbivores at all.

Table 7-2: Vegetation structure parameters of all sites (625 m², mean of n=5 in each management class except for grazed with n=7). Results of one-factorial ANOVAs (F, p)/Kruskal-Wallis-ANOVAs (H, p). a,b,c: significant differences according to Post-Hoc-tests (Tukey for unequal N/multiple comparisons) are indicated by different letters. 'Natural grazing': degree of habitat use by geese, rabbits, hares, deer or moose on a scale from 0 (no) to 2 (strong, see general methods).

Vegetation structure		early	late				transf.	Post-Hoc-Test			
parameter	grazed	succ.	succ.	restored	F	p		G	ES	LS	R
Vegetation cover (%)	95.46	95.28	97.76	83.76	3.28	*	arcsin	ab	ab	a	b
Vegetation height (cm)	18.01	34.27	119.03	31.58	34.20	**	log	a	b	c	b
Thickness of litter layer (cm)	0.79	5.10	5.95	0.40	46.60	***	log	a	b	b	a
Degree of natural grazing	1.71	0.40	0.00	1.20	6.61	**		a	b	b	ab

7.2.3 Impact of management on species' cover and frequency

Six species showed significant differences in cover (per 1 m²) between the four management classes. *Eleocharis uniglumis, Elymus repens, Phragmites australis* and *Galium palustre* had significantly higher cover in late successional sites, while *Festuca rubra* had a higher cover in early successional sites than in restored sites (table 7-3). *Plantago maritima* showed a trend to higher cover in grazed than in late successional sites.

Table 7-3: Significant differences in cover (1 m²) of individual species in the aboveground vegetation: Results of 1-factorial ANOVA (F, p) or Kruskal-Wallis-ANOVAs (H, p). *: p<0.05, **:p<0.01, ***: p<0.001. A, b: significant differences according to Post-Hoc-Tests (HSD for unequal N/multiple comparisons test). N=5 for each management class, except for grazed n=7.

	Test			Post-Hoc-Test				Effect
	F	H	p	G	ES	LS	R	
Plantago maritima *		9.50	*	a	a	a	a	(G>LS, PHTest ns)
Festuca rubra *		7.37	*	ab	a	ab	b	ES>R
Eleocharis uniglumis *		8.89	*	a	ab	b	ab	LS>G
Elymus repens		10.38	*	a	ab	b	ab	LS>G
Phragmites australis		19.18	***	a	a	b	ab	LS>G/ES
Galium palustre	7.26		**	a	a	b	a	LS>G/ES/R

*: characteristic species of habitat type Boreal Baltic Coastal meadows (BBCM)

For 12 species, significant differences in frequency between the four management classes were found (table 7-4). The frequency of seven species decreased during secondary progressive succession: *Odontites litoralis, Centaurium littorale* and *Centaurium pulchellum* decreased in frequency already in early successional sites, while the frequency of *Plantago maritima, Leontodon autumnalis, Festuca rubra* and *Glaux maritima* decreased only in late successional sites. All of these species became more frequent again after the introduction of restorative grazing.

The frequency of five species increased during secondary progressive succession: *Elymus repens, Eleocharis uniglumis* and *Bolboschoenus maritimus* became more frequent already in early successional sites, *Galium palustre* increased continuously, while *Phragmites australis* became more frequent only in late successional sites. The frequency of *Galium palustre, Eleocharis uniglumis* and *Bolboschoenus maritimus* decreased again after restoration, whereas *Phragmites australis* and *Elymus repens* still remained quite frequent.

Table 7-4: Mean frequency (% of five 25 m^2-subplots) of individual species in the aboveground vegetation (mean given in last 4 columns): Results of 1-factorial ANOVA (F, p) or Kruskal-Wallis-ANOVAs (H, p). *: $p<0.05$, **:$p<0.01$, ***: $p<0.001$. A, b: significant differences according to Post-Hoc-Tests (HSD for unequal N/multiple comparisons test). Trend: direction of differences between management classes if Post-Hoc-test was insignificant. +/-: Increase (+) or decrease (-) during progressive secondary succession (progr. succ.; G→ES→LS) or retrogressive secondary succession (retro. succ., LS→R). G: grazed, ES: early successional, LS: late successional, R: restored.

				Post-Hoc-test						progr.	retro.	Mean frequency			
Species	F	H	p	G	ES	LS	R	transf.	trend	succ.	succ.	G	ES	LS	R
Plantago maritima *	8.52		***	a	a	b	ab			-	+	94.3	100.0	40.0	76.0
Leontodon autumnalis	3.81		*	ab	a	b	ab			-	+	82.9	88.0	32.0	56.0
Odontites litoralis *		9.40	*	a	ab	b	ab			-	+	74.3	68.0	8.0	60.0
Centaurium littorale *		9.66	*	a	ab	b	ab			-	+	48.6	12.0	4.0	36.0
Festuca rubra *		9.60	*						(G/ES>LS/R)	-	+	100.0	96.0	60.0	68.0
Glaux maritima		12.22	**						(ES>LS)	-	+	85.7	100.0	72.0	96.0
Centaurium pulchellum *	2.82		(*0.069)					log	(G/R>ES/LS)	-	+	37.1	4.0	8.0	32.0
Phragmites australis		16.95	***	a	ab	c	bc			+	(-)	17.1	24.0	100.0	92.0
Elymus repens		11.27	*	a	b	b	ab			+	(-)	5.7	64.0	64.0	52.0
Galium palustre		10.37	*	a	ab	b	ab			+	-	37.1	64.0	100.0	52.0
Eleocharis uniglumis *	3.30		*						(ES/LS>G/R)	+	-	42.9	92.0	80.0	44.0
*Bolboschoenus maritimus**		6.89	(*0.08)						(ES/LS>G)	+	-	0.0	20.0	36.0	8.0

*: characteristic species of habitat type Boreal Baltic Coastal meadows (BBCM)

7.2.4 Species groups

The relative cover of annuals and biennials was significantly higher in grazed (8.6%) than in late successional sites (2.4%), while early successional sites (4.8%) and restored sites (7.1%) had intermediate values (ANOVA F=4.74, p<0.05). The relative species number of annual and biennial species was not significantly different (Kruskal-Wallis-ANOVA: H=5.11, p=0.16).

The relative species number of reed bed species was higher in late successional than in grazed sites, with early successional and restored sites showing intermediate values (table 7-5, fig. 7-3a).

Relative cover of reed bed species was significantly higher in late successional sites than in restored sites. Relative cover of reed bed species in restored sites was still higher than in grazed sites, while early successional sites were intermediate between restored and grazed sites. Salt marsh species showed the opposite pattern: their cover was significantly higher in grazed and early successional sites than in late successional sites, while restored sites were intermediate between early and late successional sites (table 7-5, fig. 7-3b).

Relative cover of the 16 'characteristic plant species' of BBCM was significantly lower in 'late' successional sites (mean ± SD: 30 ± 13%) than in grazed (61 ± 23 %) and 'early' successional sites (62 ± 15%), while restored sites were intermediate with 54 ± 19% cover (ANOVA: F=4.9, p<0.05, data log-transformed). The relative species number of 'characteristic species' of BBCM was not significantly different (H=2.77, p=0.43), but also decreased slightly from grazed (48%) to early (45%) and late successional sites (38%) and increased again in restored sites (44%).

Table 7-5: Impact of management on relative species number and relative cover of socio-ecological species groups (mean given in last 4 columns): Results of 1-factorial ANOVAs (F, p) or Kruskal-Wallis-ANOVAs (H, p). *: p<0.05, **:p<0.01, ***: p<0.001. A, b, c: significant differences according to Post-Hoc-Tests (HSD for unequal N). G: grazed, ES: early successional, LS: late successional, R: restored.

				Post-Hoc-test					Mean			
	F	H	p	G	ES	LS	R	transf.	G	ES	LS	R
Relative species number (%)												
Reed bed	6.93		**	a	ab	b	ab	log	6.9	14.5	29.6	14.1
Fen	0.9		0.46					log	8.0	1.6	5.0	8.7
Salt marsh	1.59		0.23						41.7	37.0	25.6	38.5
Ruderal	0.95		0.44						4.1	7.1	7.8	8.2
Flood meadow	1.03		0.4						12.8	13.8	14.3	10.7
Grassland	0.74		0.54						16.8	16.8	13.1	10.7
Forest		7.55	0.06						2.1	0.0	0.0	0.3
Indifferent									7.7	9.1	4.6	8.9
Relative cover (%)												
Reed bed	30.4		***	a	ab	c	b	sqrt	5.5	9.1	57.9	17.7
Fen		2.72	0.44						5.5	1.1	2.1	10.0
Salt marsh	6.23		**	a	a	b	ab		58.7	55.1	18.5	38.2
Ruderal	1.25		0.32					log	2.6	5.4	5.7	4.9
Flood meadow		4.14	0.25						8.6	14.2	7.4	15.1
Grassland	0.74		0.54						12.6	9.8	6.6	8.2
Forest		7.96	0.05						1.4	0.0	0.0	0.1
Indifferent									5.1	5.3	1.8	6.0

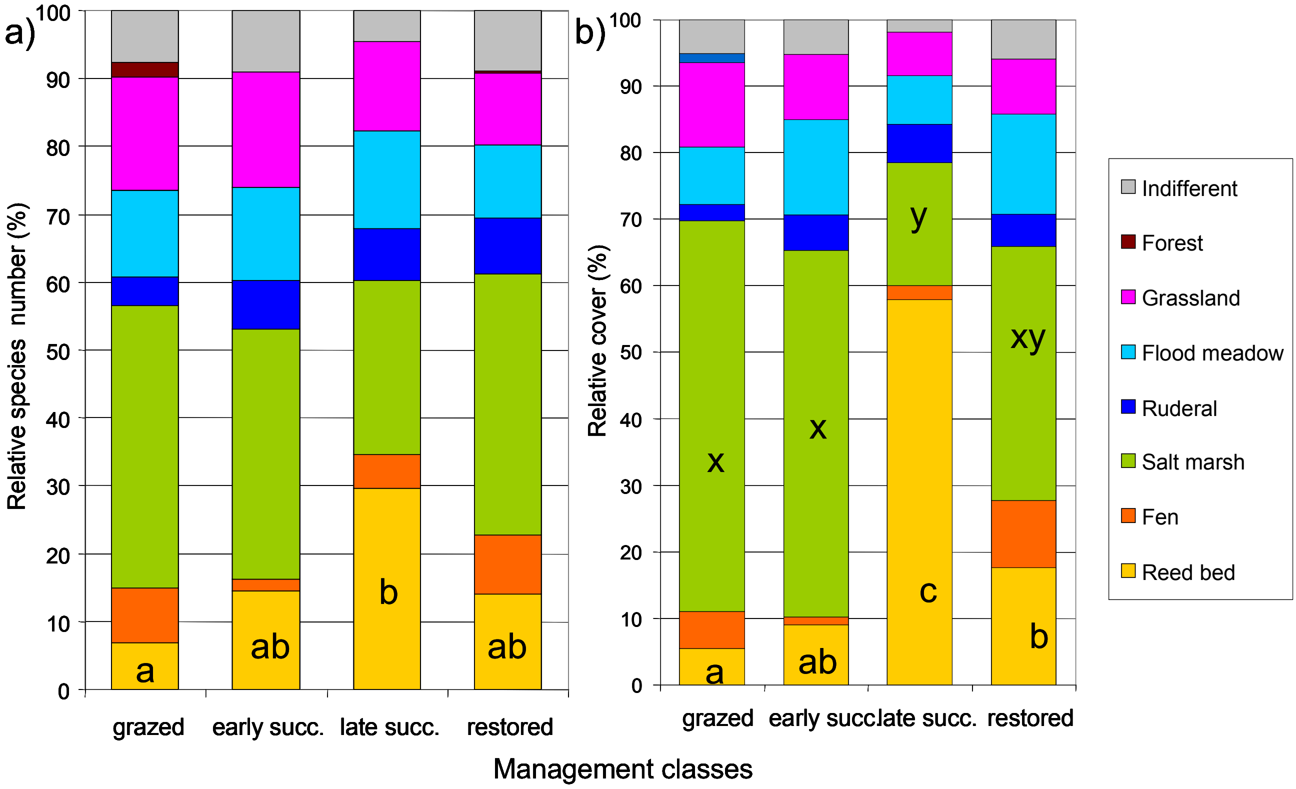


Fig. 7-3: a) Relative species number (%) and b) relative cover (%) of socio-ecological species groups in the four management classes. a, b, c/x,y: significant differences according to Post-Hoc-Tests (HSD for unequal N).

7.2.5 Spatial heterogeneity

Spatial heterogeneity was significantly higher in late successional sites (0.37) than in grazed sites (0.25), while early successional sites and restored sites had intermediate values (0.33 and 0.32, respectively, F=3.68, $p<0.05$). Heterogeneity between 25 m²-subplots was significantly lower than between 1 m²-subplots (F=10.0, $p<0.01$, interaction management*scale: F=0.44, p=0.73, 2-factorial ANOVA with scale as within-factor).

7.2.6 Species composition and relation to abiotic conditions

The detrended correspondence analysis (DCA, fig. 7-4) showed that late successional sites were separated from the others, while early successional and restored sites were found in-between grazed and late successional sites. The first axis of the DCA was strongly correlated with the management classes late successional (right) and grazed (left), with related vegetation parameters (vegetation height, thickness of litter layer) and with 'natural' grazing (by geese, hares, rabbits, deer or moose), but also with pH and phosphate content. The second axis was related to salinity – shown by the (negative) correlation with the mean salt indicator value and with soil salinity –, to the mean Ellenberg values for nitrogen and moisture and to the elevation range.

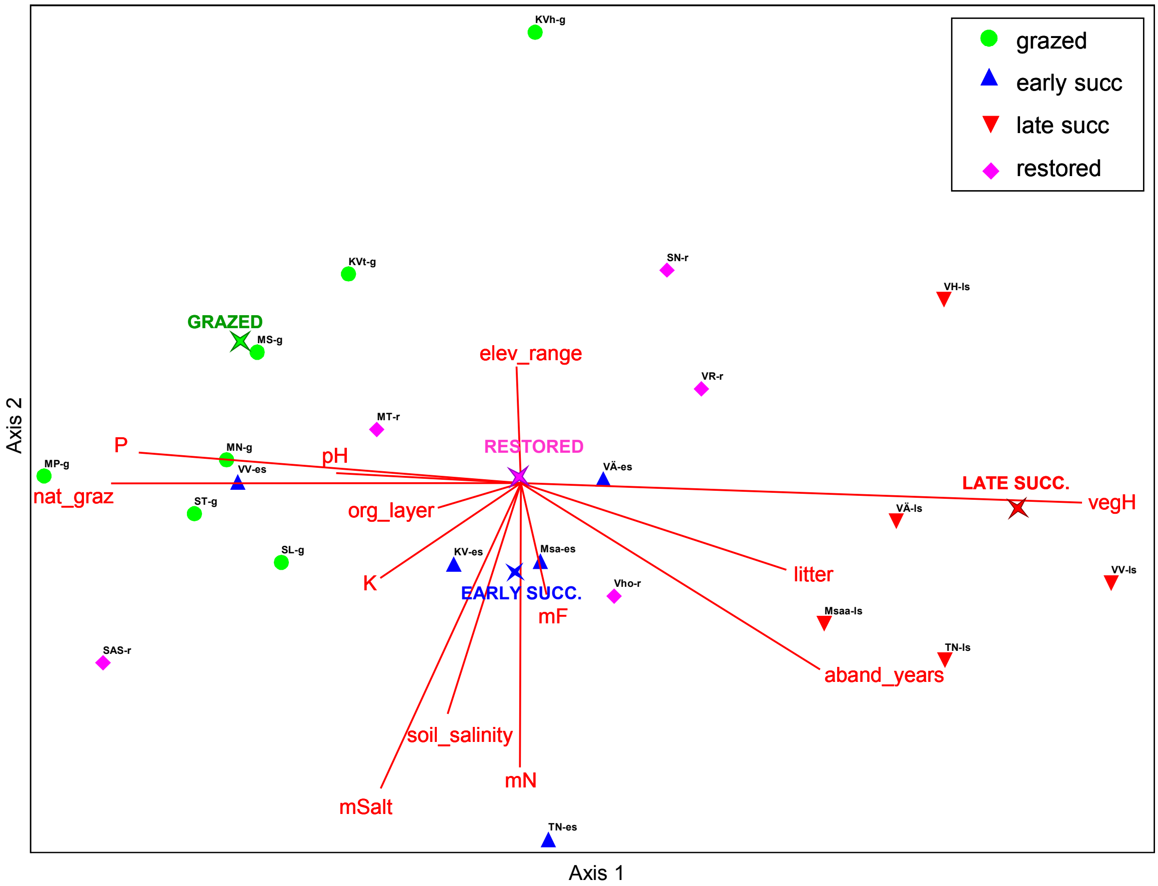


Fig. 7-4: Detrended correspondence analysis (DCA) with the cover (%) of all taxa occurring in the vegetation of the 625 m²-plots (rare species downweighted). Correlations with environmental variables are shown if $r^2>0.10$. All management categories (dummy variables) are displayed as centroids (symbols, irrespective of the r²-values). First and second axis eigenvalues: 0.29/0.12, first and second axis length of gradient: 2.16/1.64. VegH: vegetation height (cm), Litter: thickness of the litter layer (cm), aband_years: time since abandonment in years (0 for grazed sites), mF: mean Ellenberg moisture value, mN: mean Ellenberg nitrogen value, Soil salinity: salinity in the upper soil layer (psu), mSalt: mean salt indicator value (combined after Ellenberg et al. 1992 and Scherfose 1990), K: potassium content of the soil (mg K_2O/100g), Org_layer: depth of the organic layer (cm), nat_grazing: degree of 'natural' grazing by geese, rabbits, hares, deer or moose, P: Phosphate content of the soil (mg P_2O_5/100g), pH: pH-value of the upper soil layer, elev_range: elevation range (cm).

7.2.7 Impact of vegetation structure and site conditions on species richness

Single regressions of vegetation structure and site conditions with species number (on 1 m²) revealed several significant relationships (table 7-6). Species richness increased with increasing vegetation cover, with increasing elevation and elevation range. Species richness declined with increasing salinity and potassium in the soil.

Table 7-6: Results of univariate regression analysis: Impact on vegetation structure and abiotic parameters on species number (1 m²), n=110. *: $p<0.05$, **:$p<0.01$, ***: $p<0.001$. Variables: time since abandonment in years (0 for grazed sites), vegetation cover: total vegetation cover (%), Vegetation height: canopy height (cm), Litter: thickness of the litter layer (cm), cover *Phrag_aus*: cover of *Phragmites australis* (%), natural grazing: degree of habitat use by geese, rabbits, hares, deer or moose on a scale from 0 (no) to 2 (strong, see general methods), elevation range: elevation range of each subplot (cm), elevation: mean elevation above sea level (cm), Organic layer: depth of the organic layer (cm), pH: pH-value of the upper soil layer, P: Phosphate content of the soil (mg P_2O_5/100g), K: potassium content of the soil (mg K_2O/100g), Mg: Magnesium content of the soil (mg/100g), Soil salinity: salinity in the upper soil layer (psu), Organic matter: organic matter content of the upper soil layer, Total nitrogen content of the soil (%),C/N-ratio of the upper soil layer, Cinorganic: inorganic carbon content of the soil (%).

	r	r²	p
Management/vegetation structure			
Time since abandonment (years)	-0.12	0.02	0.20
Vegetation cover (%)	0.22	0.05	*
Vegetation height (cm)	-0.09	0.01	0.33
Thickness of litter layer (cm)	-0.03	0.00	0.75
Cover of *Phragmites australis* (%)	-0.16	0.03	0.10
Natural grazing	-0.09	0.01	0.33
Abiotic conditions			
Elevation range (cm)	0.36	0.13	***
Elevation (cm)	0.24	0.06	*
Organic layer (cm)	0.04	0.00	0.66
pH	0.15	0.02	0.12
P (mg P2O5/100g)	0.05	0.00	0.64
K (mg K2O/100g),	-0.27	0.07	**
Mg (mg/100g),	0.03	0.00	0.76
Soil salinity (psu)	-0.37	0.14	***
Organic matter (%)	0.05	0.00	0.59
Total nitrogen (%)	0.02	0.00	0.86
C/N-ratio	0.16	0.02	0.11
Cinorganic (%)	0.06	0.00	0.55

A multiple regression model revealed that 47% of the variation in species number (on 1 m²) could be explained by six variables (table 7-7). The environmental variables soil salinity, elevation and elevation range together explained 39% of the variation, the inclusion of vegetation structure (thickness of litter layer and vegetation cover) accounted for an additional 7.6% and the pH-value explained a further 2% of the variation in species number.

Table 7-7: Results of multiple regression analysis: Impact on vegetation structure and abiotic parameters on species number (1 m²), n=110. *: p<0.05, **:p<0.01, ***: p<0.001. Variables with a(n internal) correlation of >0.5 were excluded from the analysis, thus 10 variables were included into stepwise forward selection of variables (not selected for the model: C/N-ratio of the upper soil layer, organic matter content of the upper soil layer (%), depth of the organic layer (cm), phosphate content (mg P_2O_5/100g)). Variables: Soil salinity: salinity in the upper soil layer (psu), elevation: mean elevation above sea level (cm), elevation range: elevation range of each subplot (cm), Litter: thickness of the litter layer (cm), cover: total vegetation cover (%), pH: pH-value of the upper soil layer.

							ANOVA-results	
	B	SE of B	t	p	corr. cumulative r²	% var. exp.	F for incl./excl.	p
Constant	-3.88	5.37	-0.72	0.47				
Soil salinity (psu)	-5.75	0.93	-6.15	***	0.13	12.9	17.17	***
Elevation (cm)	0.15	0.02	6.59	***	0.28	14.7	22.87	***
Elevation range (cm)	0.26	0.06	4.50	***	0.39	11.4	20.94	***
Litter (cm)	-0.32	0.10	-3.30	**	0.43	4.1	7.70	**
Cover (%)	0.07	0.02	3.07	**	0.46	3.5	7.02	**
pH	1.44	0.71	2.03	*	0.47	2.0	4.14	*

7.3 Seed bank analysis

21,068 individuals of 78 taxa were identified in the seed bank samples, 17 of these taxa were represented by only one individual. 85 taxa occurred in the aboveground vegetation of the 25 m²-plots of the matched data set (vegetation and seed bank sampling, see Table in annex).

40 species occurred both in seed bank and aboveground vegetation (of all 25 m²-plots), 3 of them were represented in the seed bank by only one individual. 20% of the species common to seed bank and aboveground vegetation were annuals and biennials. *Juncus gerardii, Juncus articulatus, Eleocharis uniglumis, Glaux maritima, Agrostis stolonifera, Centaurium littorale, Carex flacca* and *Centaurium pulchellum* were the most numerous species in the seed bank.

38 taxa occurred in the seed bank, but not in the aboveground vegetation, 6 of which were determined only to genus level. 14 species were represented by only one individual. 38% of these were annuals and biennials. *Juncus bufonius* agg., *Poa annua, Poa pratensis, Carex* spec., *Rorippa palustris* and *Linaria vulgaris* were the most common taxa in this group.

45 species occurred in the aboveground vegetation, but not in the seed bank samples, three of them determined only to genus level. 9% were annuals and biennials. Most frequent were *Angelica palustris, Blysmus rufus, Vicia cracca, Centaurea jacea, Frangula alnus* (seedlings), *Sonchus arvensis, Valeriana officinalis, Juniperus communis* and *Equisetum pratense.*

Management did not affect seed density (F=1.32, p=0.32) nor number of species in the seed bank (F=1.28, p=0.33) significantly. More seeds of more species were found in the upper than in the lower horizon (mean seed density in upper horizon: 35,085 seeds m^{-2}; in lower horizon: 15,468 seeds m^{-2}; ANOVA with log-transformed data: F=25.8, p<0.001; mean species number in upper horizon: 12/sample; in lower horizon: 7.4/sample; F=109.7, p<0.001). For seed density, the interaction management*seed bank horizon was marginally insignificant (F=4.26, p=0.055) indicating that seed density was higher in the upper horizon of grazed, but not of early and late successional sites. Seed density decreased in the upper horizon in early and late successional sites, while there was a (slight) peak in the lower horizon of early successional sites (fig. 7-5a).

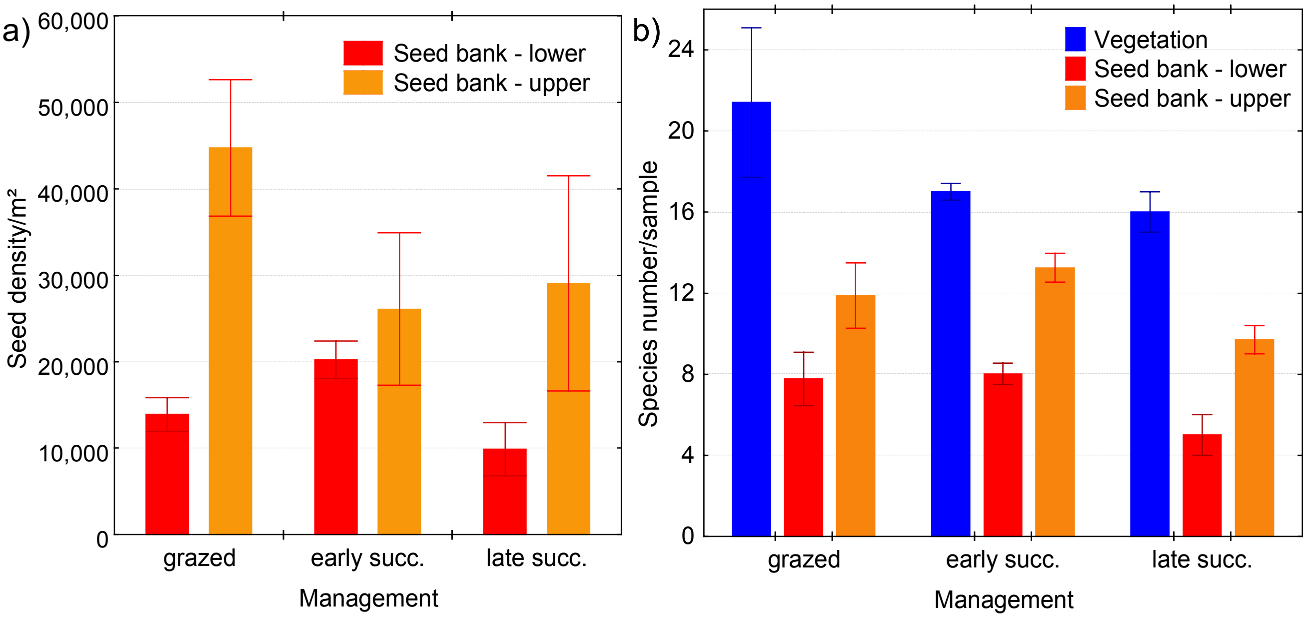


Fig. 7-5: Impact of management on a) seed density (per m²) in the upper and lower horizon (Mean ± SE), b) species number/sample (Mean ± SE) in the aboveground vegetation (25 m²) and in the upper and lower seed bank horizon (79.5 cm²). a) Results of 2-factorial ANOVA with seed bank horizon as within factor, data log-transformed: Management: F=1.32, p=0.32, seed bank horizon: F=25.8, p<0.001, interaction management*seed bank horizon: F=2.12, p=0.18). b) Results of 2-factorial ANOVA with vegetation/seed bank horizon as within factor: Management: F=0.79, p=0.48, vegetation/seed bank horizon: F=65.74, p<0.001, interaction management*vegetation/seed bank horizon: F=0.14, p=0.96).

Species number in the vegetation (mean of 18.5/25 m²) was significantly higher than in the upper seed bank horizon (12/sample), which was still significantly higher than that of the lower seed bank horizon (7.4/sample, fig. 7-5b, 2-factorial ANOVA with vegetation/seed bank horizon as within-factor: F=65.74, p<0.001, factor management: F=0.79, p=0.48, interaction management* vegetation/seed bank horizon: F=0.14, p=0.96).

Evenness of the vegetation (mean of 0.73) was higher than evenness of both of the seed bank horizons (0.49 for both horizons, F=17.63, p<0.001). A significant interaction between the factors management*vegetation/seed bank horizon (F=4.63, p<0.05) indicated that differences between seed bank horizons and vegetation disappeared in late successional sites. As a main factor, management had no significant effect on evenness (F=0.39, p=0.69).

7.3.1 Species composition

A detrended correspondence analysis (DCA) separated seed bank samples from vegetation relevés along the first axis (with nearly no overlap). Seed bank samples of the upper horizon were found closer to the vegetation samples than seed bank samples of the lower horizon (fig. 7-6).

Along the second axis, late successional vegetation sites were found in the upper part, while grazed vegetation relevés were found in the lowest parts. Grazed and early successional vegetation relevés strongly overlap. The seed bank samples are found in a similar order, but with a stronger overlap of all management groups. Most samples were closer together than the vegetation relevés.

The second axis was correlated to a number of environmental variables. It was negatively correlated to elevation range, elevation and phosphate content, and positively to vegetation height and time since abandonment, both associated with late successional sites.

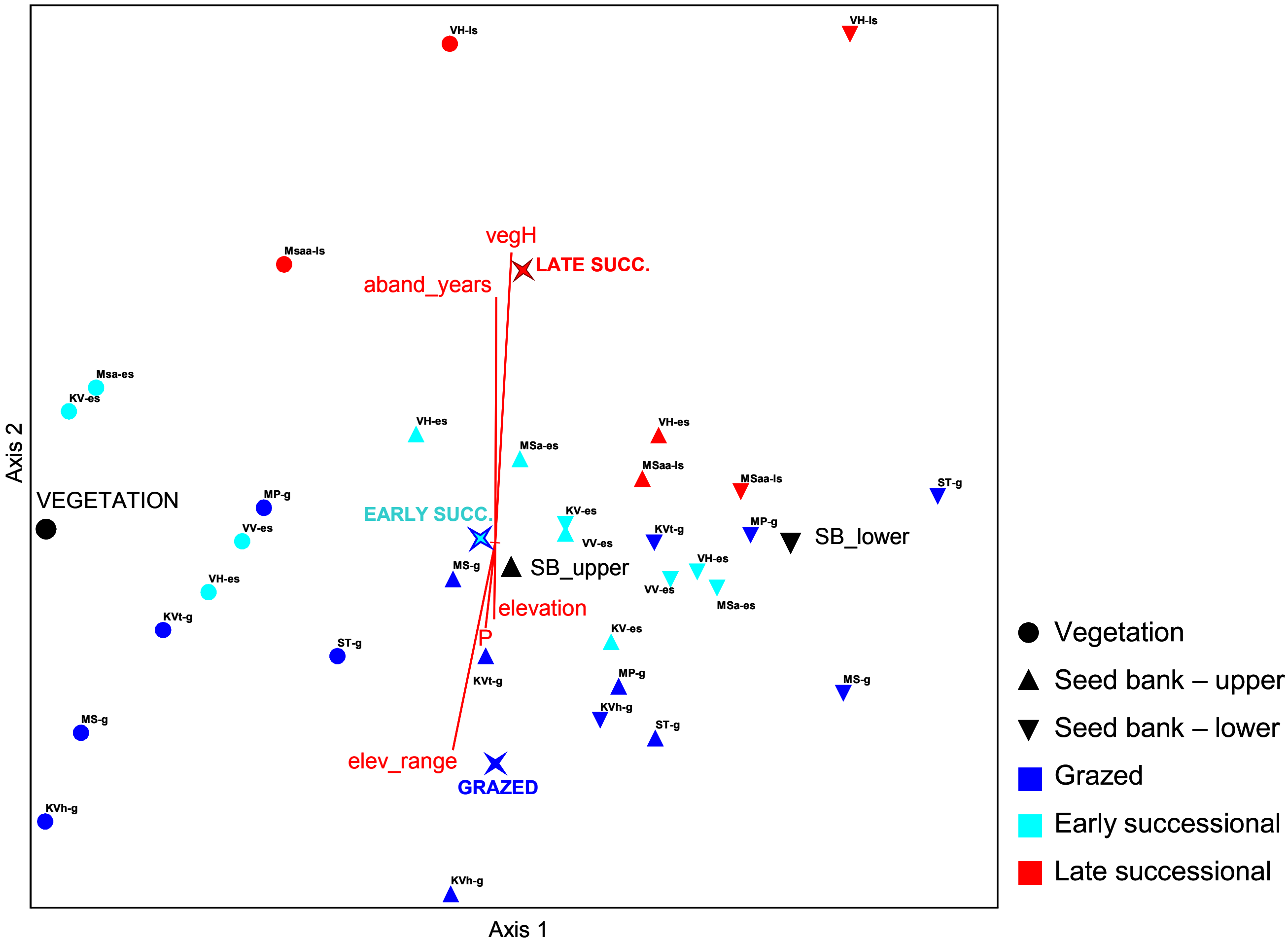


Fig. 7-6: Detrended correspondence analysis (DCA) with presence-absence-data of all 123 taxa occurring in the vegetation and/or seed bank (data pooled for each site). Correlations with environmental variables are shown if $r^2>0.10$. Categorical variables are displayed as centroids (symbols, irrespective of the r^2-values). First and second axis eigenvalues: 0.28/0.14, first and second axis length of gradient: 2.32/1.98. aband_years: time since abandonment in years (0 for grazed sites), vegH: vegetation height (cm), elevation: mean elevation of 625 m²-plot (cm above sea level), P: phosphate content of the soil, elev_range: elevation range of each 625 m²-plot (cm).

7.3.2 Impact of management on species' seed density and relative abundance in seed bank and aboveground vegetation

According to seed density in the seed bank, four species were significantly affected by management (table 7-8): *Galium palustre* was significantly more abundant in seed banks of late successional sites, and *Glaux maritima* was more abundant in seed banks of early successional sites than in those of grazed sites. *Centaurium littorale* was marginally more abundant in seed banks of grazed and early successional sites than those of late successional sites, while *Eleocharis uniglumis* was marginally more abundant in seed banks of late than of early successional sites (both: KWA p<0.1).

Table 7-8: Impact of management on seed density of individual species in the seed bank: Results of 2-factorial ANOVA (factor management, F, p, depth as within-factor, not shown) or Kruskal-Wallis-ANOVAs (H, p). *: p<0.05, **:p<0.01, ***: p<0.001. a, b: significant differences according to Post-Hoc-Tests (HSD for unequal N/multiple comparisons test). 'Effect' indicates in which management class seed densities are greater (>) than in another according to Post-Hoc-tests, results in brackets indicate insignificant trends. G: grazed, ES: early successional, LS: late successional sites.

				Post-Hoc-Test				Mean seed density (seeds/m²)			No of seeds (total)
	F	H	p	G	ES	LS	Effect	G	ES	LS	
Galium palustre	12.19		**	a	a	b	LS>G/ES	106	86	1551	108
Glaux maritima		6.6	*	a	b	ab	ES>G	1408	5057	3207	1197
Centaurium littorale		5.2	(*) 0.075				(G/ES>LS)	915	893	21	318
Eleocharis uniglumis		5.1	(*) 0.078				(LS>ES)	4130	2191	10019	1630

According to their relative abundance in seed bank and aboveground vegetation, *Leontodon autumnalis, Festuca rubra, Potentilla anserina, Triglochin maritimum, Carex nigra* and *Carex distans* were overrepresented in the aboveground vegetation compared to the upper and lower seed bank horizon (table 7-9). *Galium palustre, Plantago maritima* and *Agrostis stolonifera* were more abundant in the vegetation and upper horizon than in the lower horizon. *Eleocharis uniglumis* was underrepresented in the lower horizon, but only in early successional sites.

Table 7-9: Comparison of relative abundances between seed bank horizons and vegetation (for all species present in the vegetation and with more than 50 seeds in all seed bank samples). F, p: Results of 2-factorial ANOVA (management, vegetation-seed bank horizon as in between factor). X, p: Results of Friedman-test. *: p<0.05, **:p<0.01, ***: p<0.001. a, b: significant differences according to Post-Hoc-Tests (HSD for unequal N/Tukeys HSD). Results for management are only given if a (2-factorial) ANOVA was carried out. Data were transformed to relative abundances (vegetation: cover of a species relative to the cover sum of all species in a relevé, seed bank: number of seeds of a species relative to all seeds in the respective seed bank sample). 'Effect' indicates in which management class relative abundances are greater (>) than in another according to Post-Hoc-tests, results in brackets indicate insignificant trends (for p or Post-Hoc-test marginally insignificant). Interaction: Interaction management*vegetation/seed bank horizon. For *Centaurium littorale,* data of the lower seed bank horizon was excluded from the ANOVA, since only very few seeds were found there and ANOVA-assumptions could otherwise not be fulfilled. G: grazed, ES: early successional, LS: late successional sites. V: vegetation, upp: upper seed bank horizon (0-5 cm), low: lower seed bank horizon (5-10 cm), SB: both horizons.

	management			V-SB horizon				Interaction			seed
	F	p	Effect	F	χ^2	p	Effect	F	p	transf	(total)
Leontodon autumnalis					14.1	***	V>upp>low				63
Festuca rubra	5.0	*	G/ES>LS only in V	30.5		***	V>SB	3.6	*	log	70
Potentilla anserina					18.6	***	V>SB				111
Triglochin maritimum					15.9	***	V>SB				111
Carex nigra					6.2	*	V>low				158
Carex distans					6.9	*	V>low				146
Galium palustre	9.9	**	LS>G/ES	7.3		**	V/upp>low	0.4	ns	loglog	108
Plantago maritima					14.0	***	V/upp>low				162
Centaurium littorale	4.9	*	G>LS	2.4		*	upper>V only in ES	4.6	*	log	318
Juncus gerardii	0.4	ns		32.4		***	SB>V (but not in G)	3.3	*	log	11854
Schoenoplectus tabernaemontani					7.4	* (ES)	only ES: (upp>low/V)				168
Eleocharis uniglumis					8.0	* (ES)	only ES: V/upp>low				1630
Agrostis stolonifera	0.7	ns		3.4		(0.057)	(V/upp>low)	0.7	ns	log	594
Juncus articulatus	0.7	ns		3.4		(0.059)	(upper>V)	0.2	ns	log	3116
Glaux maritima	5.7	*	ES>G	0.2		ns		1.3	ns	log	1197
Carex flacca					1.6	ns					270
Centaurium pulchellum					3.8	ns					215
Trifolium fragiferum					3.5	ns					79

Juncus gerardii was strongly overrepresented in the seed bank; *Juncus articulatus* was more abundant in the upper horizon than in the vegetation. *Schoenoplectus tabernaemontani* was more abundant in the upper horizon than in the vegetation and the lower horizon, but only in early successional sites. *Centaurium littorale* was more abundant in the upper horizon than in the vegetation, but only in early successional sites (table 7-9).

7.3.3 Species groups

The relative species number of **annual and biennial species** did not differ between management classes (F=0.22, p=0.81). The lower seed bank horizon had a significantly higher relative number of annual and biennial species (19.6%) than the aboveground vegetation (11.7%, F=5.40, $p<0.05$, interaction management*vegetation/seed bank horizon: F=0.65, p=0.64, 2-factorial ANOVA with vegetation/seed bank horizon as within factor). The relative abundance of annual and biennial species was also not affected by management (F=1.33, p=0.32). In contrast to the relative species number, the relative abundance was slightly (but not significantly) higher in the vegetation (7.2%) than in the upper seed bank horizon (4%), while it was intermediate in the lower horizon (6%, F=2.78, p=0.09, interaction management*vegetation/seed bank horizon: F=0.39, p=0.81, 2-factorial ANOVA with vegetation/seed bank horizon as within factor).

Management affected the relative number of reed bed species, which had a higher share in late successional than in grazed and early successional sites, and for grassland species, which in contrast had a higher share in grazed than in late successional sites (fig. 7-7, table 7-10). With respect to relative species number, grassland species were overrepresented in the vegetation compared to the seed bank and flood meadow species were overrepresented in the vegetation and upper horizon. In contrast, reed bed species were overrepresented in the lower horizon compared to the vegetation, and ruderal species were overrepresented in the lower horizon compared to the upper horizon and the aboveground vegetation.

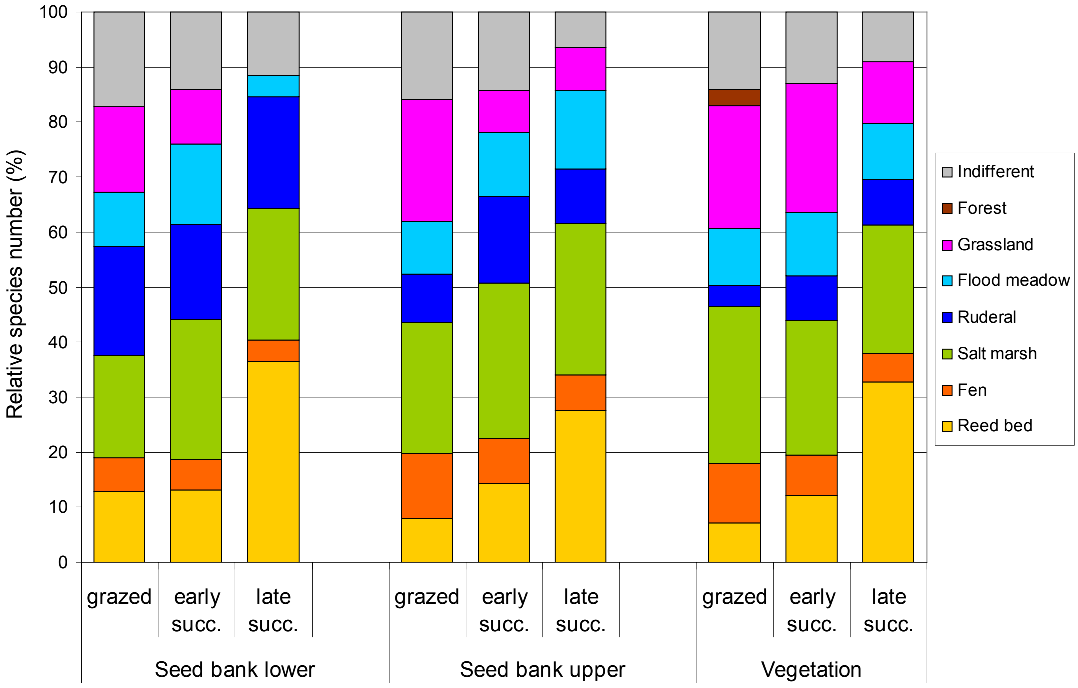


Fig. 7-7: Impact of management on relative number of species (%) of different socio-ecological species groups in the seed bank horizons and aboveground vegetation (species groups: see general methods). Results of statistical tests: see table 7-10.

Relative abundance of reed bed species was significantly higher in late successional sites than in grazed sites. Grassland species had a (marginally) higher relative abundance in grazed than in late successional sites (fig. 7-8, table 7-10). Flood meadow and grassland species were overrepresented in the aboveground vegetation in comparison to the seed bank, while salt marsh species were overrepresented in the seed bank (with respect to relative abundance).

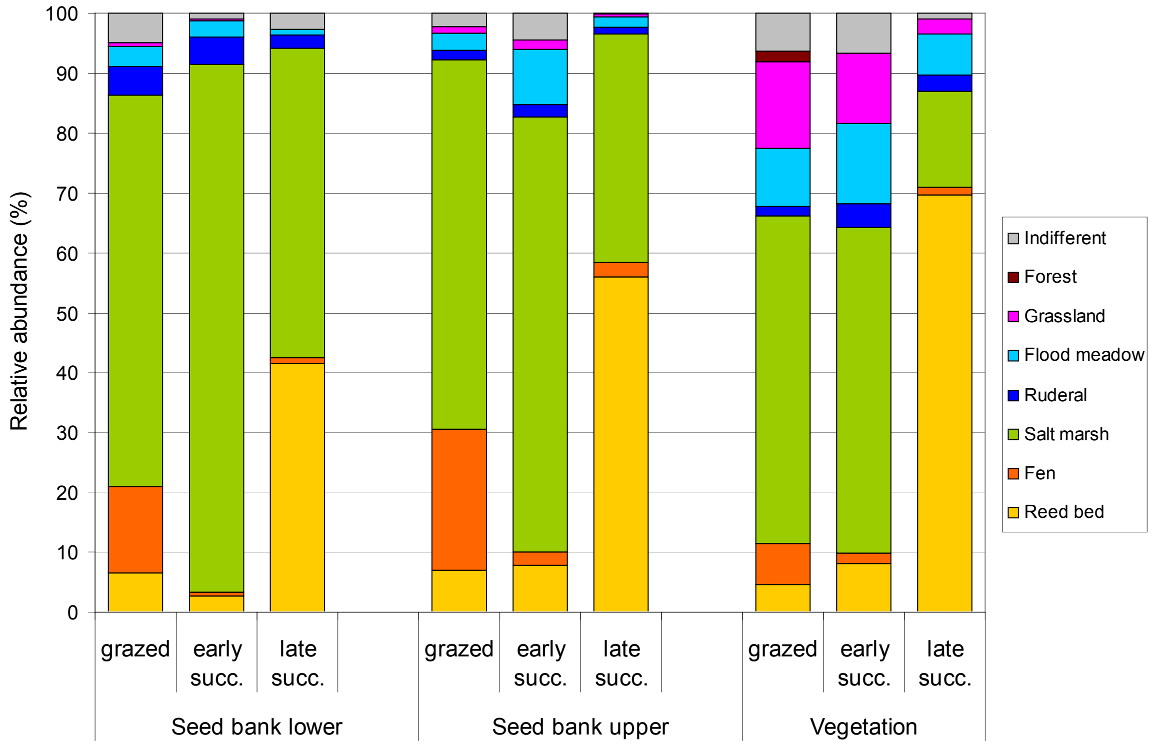


Fig. 7-8: Impact of management on relative abundance (percentage of cover/seeds) of different socio-ecological species groups in the seed bank horizons and aboveground vegetation (species groups: see general methods). Results of statistical tests: see Table 10.

Table 7-10: Relative species number and relative abundance (relative cover or relative number of seedlings) of socio-ecological species groups in the aboveground vegetation and seed bank: Results of 2-factorial ANOVAs (F, p) with vegetation/seed bank horizon as within-factor. *: p<0.05, **:p<0.01, ***: p<0.001. a, b: significant differences according to Post-Hoc-Tests (HSD for unequal N). 'Effect' indicates in which management class or seed bank horizon relative abundances are greater (>) than in another, according to Post-Hoc-tests. Results in brackets indicate insignificant trends. Interaction: Interaction management*vegetation/seed bank horizon. transf: data-transformation carried out to meet ANOVA assumptions. G: grazed, ES: early successional, LS: late successional sites. low: lower seed bank horizon (5-10 cm), upp: upper seed bank horizon (0-5 cm), V: vegetation.

Relative species number (%)	management		Post-Hoc-Test				V/SB-horizon		Post-Hoc-Test				interaction		transf.
	F	p	G	ES	LS	Effect	F	p	low	upp	V	Effect	F	p	
Reed bed	26.14	***	a	a	b	LS>ES/G	4.86	*	a	ab	b	low>V	1.80	0.18	
Fen	0.82	0.48					1.85	0.19					0.67	0.62	
Salt marsh	0.59	0.58					0.08	0.92					0.94	0.47	
Ruderal	0.03	0.97					10.71	**	a	b	b	low>upp/V	1.67	0.21	
Flood meadow	3.22	0.09					8.21	**	a	b	b	upp/V>low	2.73	0.07	log
Grassland	11.46	**	a	ab	b	G>LS	15.24	***	a	a	b	V>low/upp	1.93	0.15	log
Relative abundance (%)															
Reed bed	6.86	*	a	ab	b	LS>G	3.00	0.08					2.11	0.13	log
Fen	0.78	0.49					1.81	0.20					0.05	1.00	log
Salt marsh	1.16	0.36					19.13	***	a	a	b	low/upp>V	1.52	0.24	arcsin
Ruderal	1.75	0.23					1.46	0.26					0.38	0.82	log
Flood meadow	3.17	0.10					11.65	***	a	a	b	V>low/upp	0.64	0.64	log
Grassland	5.11	*				(G>LS; PhT p=0.07)	38.95	***	a	a	b	V>upp/low	1.08	0.40	log

The relative abundance of '**characteristic plant species' of BBCM** was significantly higher in the seed bank (upper: 73%, lower: 76%) than in the vegetation (50%). While management did not significantly affect relative abundance of BBCM, a significant interaction between management and vegetation/seed bank horizon revealed that the difference between seed bank and vegetation occurred only at 'early' and 'late' successional sites, but not at grazed sites (fig. 7-9, vegetation/seed bank horizon: F=37.7, p<0.001, management: F=0.17, p=0.85, interaction management*vegetation/seed bank horizon: F=5.4, p<0.01, 2-factorial ANOVA with vegetation/seed bank horizon as within-factor).

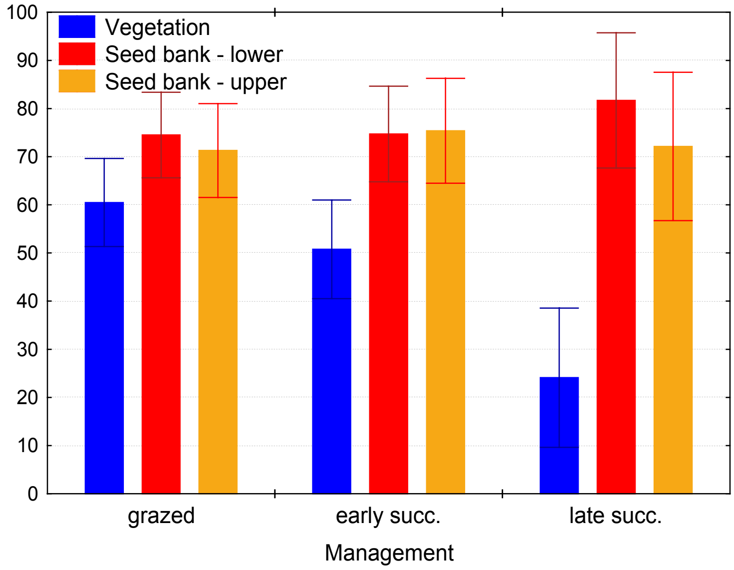


Fig. 7-9: Impact of management on relative abundance (percentage of total cover or percentage of all seeds, Mean ± SE) of 'characteristic species' of Boreal Baltic Coastal meadows (BBCM) in the seed bank horizons and aboveground vegetation.

A similar, but weaker pattern was observed for the relative species number of ‘characteristic species’ of BBCM, which was higher in the lower horizon (48.5%) than in the vegetation (40.6%) and intermediate in the upper horizon (46.8%, F=3.86, p<0.05, Tukeys Post-Hoc-test p=0.09). Relative species number in the vegetation decreased from 45% in grazed to 39% in early and 32% in late successional sites. It also decreased slightly in the upper horizon (grazed: 49%, early successional: 47%, late successional: 42%), but in contrast increased slightly in the lower horizon (grazed: 46%, early successional: 50%, late successional: 52%). However, the interaction management* vegetation/seed bank horizon was insignificant (F=0.65, p=0.63, factor management: F=0.3, p=0.75, 2-factorial ANOVA with vegetation/seed bank horizon as within-factor, data log-transformed).

The total number of ‘characteristic plant species’ of BBCM was 16 in the vegetation, and 11 in the seed bank. Most species missing in the seed bank were rare (*Salicornia europaea*) in or even absent (*Spergularia salina, Carex glareosa*) from the vegetation of the matched seed bank-vegetation data set. Only *Blysmus rufus* and *Ophioglossum vulgatum* were rather frequent in the vegetation (but see discussion on methods for *Ophioglossum vulgatum*, see 8.4.1).

Fig. 7-10 illustrates that the seed bank was more strongly dominated by few species than the vegetation. *Juncus gerardii* dominated the seed bank of grazed and early successional sites, and *Juncus gerardii* and *Eleocharis uniglumis* dominated the seed bank of late successional sites. Thus, these species are primarily responsible for the overrepresentation of BBCM species in the seed bank of successional sites. The next most common species in the seed bank differed between management classes: in grazed sites, *Juncus articulatus* was the second, in early successional sites *Agrostis stolonifera* and *Glaux maritima* were second and third, while in late successional sites, *Galium palustre* was the third.

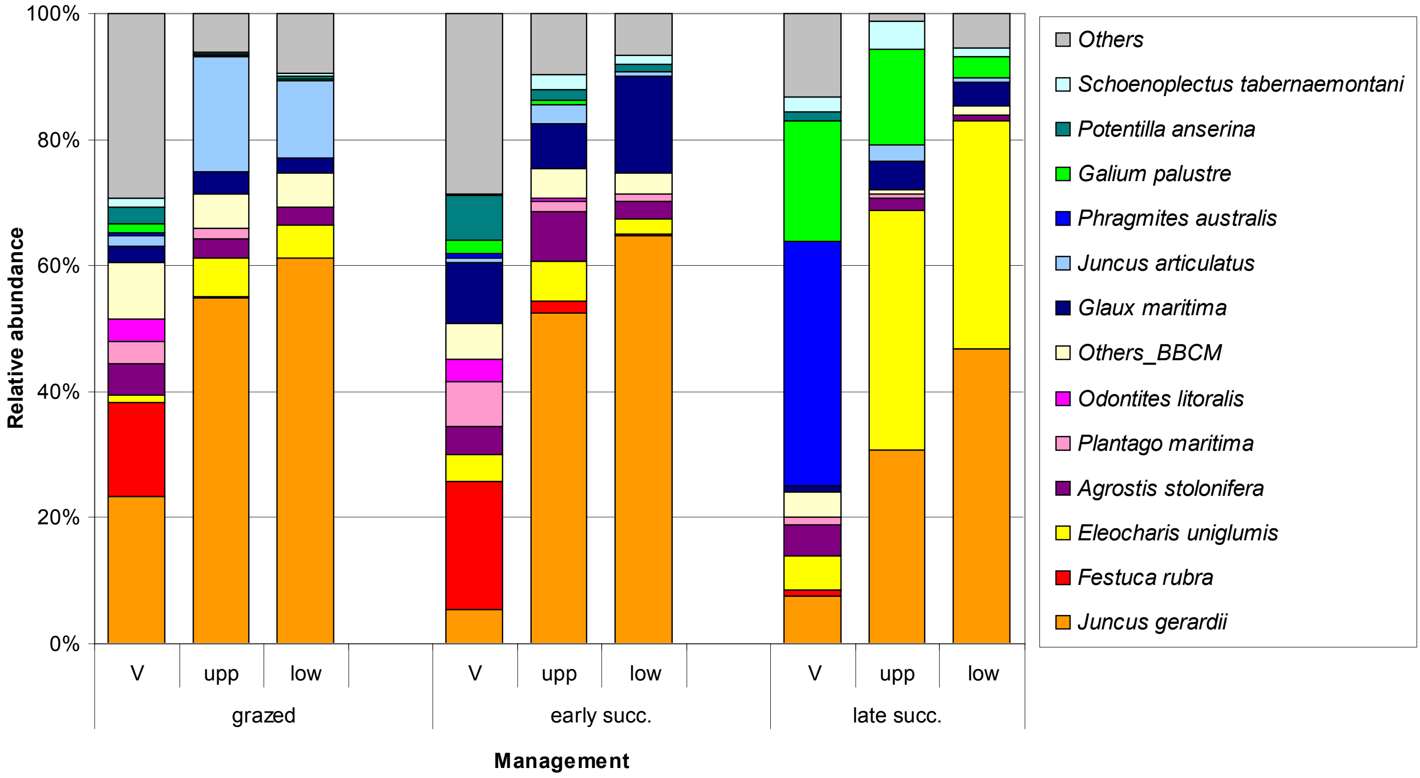


Fig. 7-10: Impact of management on the mean relative abundance (percentage of cover/seeds) of the most common species in the seed bank horizons and aboveground vegetation. 'Characteristic species' of BBCM in yellow-red-colours, all other species in blue-green colours. V: aboveground vegetation, upp: upper seed bank horizon (0-5 cm), low: lower seed bank horizon (5-10 cm), early/late succ.: early or late successional sites.

7.3.4 Similarity index

Similarity between aboveground vegetation and seed bank was not significantly affected by management (Sørensen: F=0.55, p=0.60, Bray-Curtis: F=1.05, p=0.39). However, there was a (weak) trend showing that Bray-Curtis-Similarity was highest in grazed and lowest in early successional sites (Table 7-11).

Table 7-11: Bray-Curtis and Sørensen-Similarity between vegetation and seed bank (horizons): Mean of each management class (calculated as mean of 5 subplots of 25 m²). whole: whole seed bank (upper and lower horizon pooled), upper/lower: upper/lower horizon separately. N = 5 for grazed, n = 4 for early successional and n = 2 for late successional sites.

	Bray-Curtis-Similarity			Sørensen-Similarity		
	grazed	early succ.	late succ.	grazed	early succ.	late succ.
V-whole	0.34	0.20	0.28	0.51	0.51	0.49
V-upper	0.34	0.23	0.29	0.53	0.54	0.48
V-lower	0.31	0.15	0.17	0.30	0.33	0.35
upper-lower	0.73	0.64	0.68	0.44	0.52	0.49

The Sørensen-Index indicated a lower similarity between vegetation and lower horizon than between vegetation and upper horizon or the two seed bank horizons (F=12.14, p<0.001, interaction management*vegetation/seed bank horizon: F=0.37, p=0.83, 2-factorial ANOVA with vegetation/seed bank horizon as within-factor). The Bray-Curtis-Similarity-Index indicated a higher similarity between the two horizons than between vegetation and upper or lower horizon, respectively (F=63.02, p<0.001, interaction management*vegetation/seed bank horizon: F=0.24, p=0.91, 2-factorial ANOVA with vegetation/seed bank horizon as within-factor).

7.3.5 Spatial heterogeneity

Spatial heterogeneity was significantly higher in the seed bank than in the aboveground vegetation (F=8.72, p<0.01), but was not significantly affected by management (F=0.13, p=0.88). However, the graph illustrates that spatial heterogeneity of the vegetation increased from grazed to early and late successional sites, while heterogeneity remained the same in both seed bank horizons (Fig. 7-11, interaction management* vegetation/seed bank horizon: F=0.81, p=0.54). Thus, the difference between vegetation and seed bank disappeared in the course of succession.

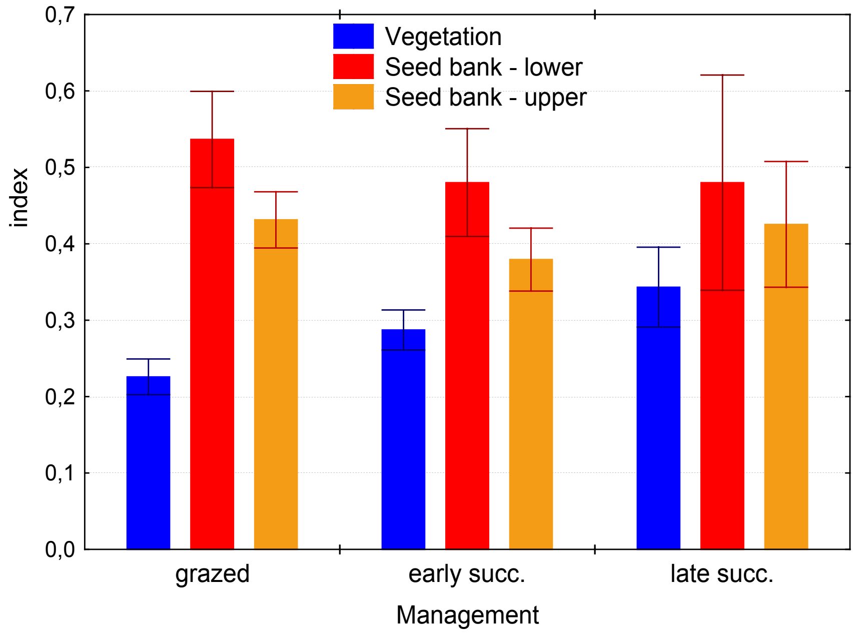


Fig. 7-11: Impact of management on spatial heterogeneity of vegetation and both seed bank horizons (Mean ± SE, Heterogeneity index = 1 - Sørensen-Index, which is based on presence-absence data only).

7.3.6 Longevity

For 37 species, a longevity index could be calculated (table 7-12). 3 species were classified as strictly persistent (LI = 1), 7 species had high longevity (LI > 0.66 and < 1), 5 intermediate (LI between 0.33 and 0.66), 6 low persistence (LI < 0.33 and > 0) and 16 were classified as strictly transient (LI = 0). Eleven of these species could not be classified by the data of the Thompson database alone. Five of them were assessed to have high (*Eleocharis uniglumis, Centaurium littorale, Schoenoplectus tabernaemontani*) or intermediate longevity *(Trifolium fragiferum, Carex distans).*

Nine of the classified species were characteristic for BBCM. Four of them had high longevity (*Eleocharis uniglumis, Juncus gerardii, Centaurium pulchellum, Centaurium littorale), Carex nigra* had intermediate longevity, two species had low longevity *(Triglochin maritimum, Plantago maritima*) and two were classified as transient *(Odontites litoralis, Festuca rubra* agg.).

Table 7-12: Longevity of all species that could be classified by using the Estonian data. Index ranges between 1 (strictly persistent) and 0 (strictly transient). LI_int: internal longevity index calculated from the separate classifications at all Estonian sites with at least 3 seeds per horizon according to Bekker et al. (1998a) – but with sites instead of records – for all species with at least 5 records or 3-4 unanimous records (see Bekker et al. 1998b), LI_B (=LI_Bekker): Longevity index calculated according to Bekker et al. (1998a) using data of the database given by Thompson et al. (1997) for all species with at least 5 records or 3-4 unanimous records (see Bekker et al. 1998b). LI_B+int: Longevity index calculated from the records in the Thompson database and the internal classifications (for each site). Ltp: long-term persistent, stp: short-term persistent, t: transient. BBCM: Characteristic species of habitat type 1630 (Boreal Baltic Coastal Meadows) are marked. *: These species were not classified, because their seeds or spores could not be detected for methodological reasons (see chapter 8.4.1).

	Number of sites					Number of records					Number of records					Charact.
Species	t	stp	ltp	total	**LI_int**	t	stp	ltp	total	**LI_B**	t	stp	ltp	total	**LI_B+int**	BBCM
Eleocharis uniglumis	0	10	1	11	1.00	1	0	0	1		1	10	1	12	0.92	x
Juncus bufonius agg.	0	4	4	8	1.00	7	26	24	57	0.88	7	30	28	65	0.89	
Juncus gerardii	0	9	3	12	1.00	1	3	1	5	0.80	1	12	4	17	0.94	x
Glaux maritima	1	4	7	12	0.92	2	2	2	6	0.67	3	6	9	18	0.83	
Centaurium pulchellum	1	3	5	9	0.89	0	2	1	3	1.00	1	5	6	12	0.92	x
Carex flacca	2	5	2	9	0.78	8	6	2	16	0.50	10	11	4	25	0.60	
Centaurium littorale	2	5	2	9	0.78	0	0	1	1		2	5	3	10	0.80	x
Agrostis stolonifera	3	8	1	12	0.75	23	14	8	45	0.49	26	22	9	57	0.54	
Juncus articulatus	2	6	0	8	0.75	6	8	13	27	0.78	8	14	13	35	0.77	
Schoenoplectus tabernaemontani	2	3	2	7	0.71						2	3	2	7	0.71	
Trifolium fragiferum	4	3	0	7	0.43	1	0	0	1		5	3	0	8	0.38	
Atriplex prostrata	3	1	1	5	0.40	0	4	2	6	1.00	3	5	3	11	0.73	
Carex nigra	5	2	1	8	0.38	11	4	3	18	0.39	16	6	4	26	0.38	x
Carex distans	6	3	0	9	0.33						6	3	0	9	0.33	
Potentilla anserina	8	2	2	12	0.33	9	4	1	14	0.36	17	6	3	26	0.35	
Triglochin maritimum	8	3	0	11	0.27	2	1	0	3		10	4	0	14	0.29	x
Plantago maritima	8	2	0	10	0.20	3	1	0	4		11	3	0	14	0.21	x
Galium palustre	8	2	0	10	0.20	11	2	3	16	0.31	19	4	3	26	0.27	
Leontodon autumnalis	9	2	0	11	0.18	13	3	2	18	0.28	22	5	2	29	0.24	
Trifolium repens	5	1	0	6	0.17	30	20	25	75	0.60	35	21	25	81	0.57	
Molinia caerulea	7	1	0	8	0.13	9	5	3	17	0.47	16	6	3	25	0.36	
Festuca rubra agg.	11	0	0	11	0.00	32	12	2	46	0.30	43	12	2	57	0.25	x
Odontites litoralis	10	0	0	10	0.00	0	0	2	2		10	0	2	12	0.17	x
Carex panicea	9	0	0	9	0.00	7	3	1	11	0.36	16	3	1	20	0.20	
Trifolium pratense	9	0	0	9	0.00	24	6	17	47	0.49	33	6	17	56	0.41	
Lotus corniculatus	8	0	0	8	0.00	22	6	9	37	0.41	30	6	9	45	0.33	
Phragmites australis	8	0	0	8	0.00	9	0	0	9	0.00	17	0	0	17	0.00	
Elymus repens	7	0	0	7	0.00	23	10	3	36	0.36	30	10	3	43	0.30	
Vicia cracca	7	0	0	7	0.00	18	1	1	20	0.10	25	1	1	27	0.07	
Blysmus rufus	5	0	0	5	0.00						5	0	0	5	0.00	
Rhinanthus angustifolius	5	0	0	5	0.00	6	0	0	6	0.00	11	0	0	11	0.00	
Centaurea jacea	4	0	0	4	0.00	15	4	0	19	0.21	19	4	0	23	0.17	
Angelica palustris	4	0	0	4	0.00						4	0	0	4	0.00	
Festuca arundinacea	4	0	0	4	0.00	10	4	0	14	0.29	14	4	0	18	0.22	
Blysmus compressus	3	0	0	3	0.00						3	0	0	3	0.00	
Carex disticha	3	0	0	3	0.00	5	2	1	8	0.38	8	2	1	11	0.27	
Succisa pratensis	3	0	0	3	0.00	11	2	1	14	0.21	14	2	1	17	0.18	
Frangula alnus (seedling)	3	0	0	3	*	3	0	0	3	0.00	6	0	0	6	0.00	
Ophioglossum vulgatum	3	0	0	3	*					*	3	0	0	3	*	x

The mean longevity index differed significantly between socio-ecological species groups (LI-Bekker+intern, see Table 7-13). The mean longevity of ruderal species (0.72) was significantly higher than that of grassland (0.28), indifferent species (0.38) and fen species (0.31). The other species groups did not differ significantly from either of these groups. Salt marsh species (0.50) and flood meadow species (0.49) had comparatively high mean longevity indices, whereas forest species had the lowest longevity index (0.05, but represented only by two species). The mean longevity index (LI-Bekker+intern) of all characteristic species of BBCM (15 species included) was slightly (but not significantly) higher (0.51) than the mean longevity index of all (90) other species of 0.40 (F=1.74, p=0.19).

Table 7-13: Mean (± standard deviation) seed longevity indices of the species in the aboveground vegetation and/or the seed bank, separated in socio-ecological species groups (see general methods). Test of significant differences between the species groups with 1-factorial ANOVA (F, p). ***: p<0.001. A, b: significant differences following Post-Hoc-test (HSD for unequal n). LI_Bekker+intern: all internal classifications (for each site with at least 3 seeds per horizon) were added to the records of the database of Thompson et al. (1997), and the longevity index was calculated from the combined data set (for all species with at least 5 records or 3-4 unanimous records).

	F	p	total n in LI calc.	Reed bed	Fen	Salt marsh	Ruderal	Flood meadow	Grassland	Forest	indiff	no info
total n in vegetation/seed bank			147	16	10	15	20	10	41	4	16	15
LI_Bekker+intern	5.60	***		ab	a	ab	b	ab	a	ab	a	
n			105	9	8	11	17	7	36	2	15	
Mean			0.41	0.42	0.31	0.50	0.72	0.49	0.28	0.05	0.38	
SD			0.30	0.29	0.27	0.33	0.23	0.20	0.25	0.07	0.29	

8 Discussion

8.1 Abiotic characteristics

The sites of the four management classes did not differ in any of the measured or estimated abiotic characteristics, except for the phosphate content of the soil, which was significantly lower in late successional sites. This is consistent with investigations of managed, abandoned and restored Estonian salt grasslands by Sammul et al. (2008). However, they also found higher contents of N, C and Mg, lower pH values, higher organic matter content, a deeper A-horizon and consequently a much higher carbon stock in abandoned, reed dominated sites.

It is possible that the phosphate uptake and storage of *Phragmites australis* is higher than that of other species, either just because of the higher plant biomass, or because of more efficient uptake and a longer storage within the large, long-lived, clonal plant. Drizo et al. (1997) showed that the presence of *Phragmites* contributed significantly to the phosphorus removal from sewage water in constructed wetlands. Sollie & Verhoeven (2007) observed an uptake of phosphorus by *Phragmites* in shallow lakes, significantly reducing phosphate peaks in the surface water of littoral zones.

Sammul et al. (2008) found that long-term abandonment with reed encroachment was connected with accumulation of organic matter and nitrogen, resulting also in a deeper/thicker A-horizon and much higher carbon stock. This ‘natural’ eutrophication persisted also after five years of restorative grazing. They assume that this process hampers restoration success, since it is not as quickly reversed as changes of vegetation structure.

An explanation for the fact that no significant differences in soil parameters were found (except for phosphate) might be that the process of internal eutrophication takes a long time, and that the period of abandonment prior to restoration was much shorter in the presented study (mostly 10-15 years, max 25 years) than in Sammul’s sites (30-50 years, per. comm. M. Sammul). Furthermore, my study sites had a thinner organic layer (3-15 cm) with a lower organic matter content (7-27%, mean of 15.7%) than Sammul’s with an organic layer of 10-13 cm and an organic matter content of 35-47%. The nitrogen content was half of Sammul’s (0.7% versus 1.3-1.5%), and the pH was slightly higher (mean of 6.3 versus 5.6-6.1). Thus it is possible that in their peatier sites, the nutrient level in general was higher and accumulation of nutrients may play a more significant role than in my study sites.

8.2 Vegetation changes during progressive secondary succession

8.2.1 Species richness and management

In the investigated Estonian salt grasslands, species numbers did not differ between the management classes on any of the investigated spatial scales (1, 25, 625 m²). Apparently, no species are lost in the course of succession until the investigated ‘late’ stage, or their loss must have been compensated by the appearance of other species (see below). Furthermore, the quite variable species number of the different sites shows that species richness in these salt grasslands seems to be influenced more strongly by other factors than management (see below).

It was shown that species number in ‘late’ successional sites decreased with increasing cover of reed, thus it can be expected that more species will be lost during later succession when reed beds become denser and more uniform. Tyler (1969b) described that geolittoral reed beds in Sweden were often so thinly spaced that the typical vegetation of the primary zonation could still develop, whereas in dense stands, colonisation of shore meadow plants was prevented – resulting in very low species numbers. Species richness as well as the number of rare fen plant species in (freshwater/terrestrial) reed beds was inversely related to the degree of reed dominance (Wheeler & Giller 1982, Wheeler & Shaw 1991). Sammul et al. (2008) found that species numbers in abandoned Estonian salt grasslands were significantly lower than in continuously managed salt grasslands. Their abandoned sites were reed dominated and abandoned already for 30-50 years, thus supporting the assumption that species numbers will further decrease in the course of succession.

Other studies in salt grasslands and salt marshes showed that the impact of management on species richness is not straight forward. While most results indicated a higher richness in moderately grazed salt grasslands (Dupré & Diekmann 2001, Puurmann et al. 2002) and salt marshes (Bakker et al. 1993, 2003), Jutila (1997, 1999, 2001) found lower species numbers in grazed sites, especially in the geolittoral zone. The impact on species richness depends also on the grazing intensity, in accordance with the Intermediate Disturbance Hypothesis (Connell 1978): under a high-density grazing regime, structural diversity is lower (Doody 2001), grazing sensitive species disappear (e.g. Härdtle 1984) and many species cannot reproduce by seeds. Märtson (1996) also found significant differences in species numbers between different management regimes, with highest species numbers at mown sites (13.3/m² versus 8/m² at grazed and 7/m² at ungrazed sites).

Kaljuste (2004a,b) found more species in grazed than in ungrazed coastal meadows in the West Estonian Matsalu National Park, but argued that the differences were caused by different habitats (grazed plots were mostly drier than ungrazed plots), and not by grazing alone. In his study, the average number of species per m² was 17-18 at ungrazed and 24-25 at grazed plots. The species numbers are higher than in the presented data because his transects were running from flooded saline meadows up to suprasaline communities and very species-rich dry alvar meadows. In contrast, the presented study was confined to the – relatively species poor – regularly flooded lower salt grasslands. Roosaluste (2002) reported a mean species number/m² of 9.6 in the Festucetum rubrae community in the suprasaline zone – which is close to the values found in the presented study – and lower numbers in all other communities of seashore meadows. The species numbers found by Märtson (1996) varied from 6.4 m² in the lower to 10.9/m² in the upper geolittoral, also comparable to the results of the presented study.

As already indicated by Kaljuste's results, species richness is strongly affected by environmental factors, especially in salt grasslands with various abiotic/environmental stress gradients. These factors also interact with the impact of grazing.

8.2.2 Species richness and environmental factors

The variability of species richness between sites was high (in all management classes), thus other factors than management seem to influence species richness. According to regression analyses, these factors were primarily connected to elevation and salinity, as well as elevation range and pH (with a lower percentage). Elevation range indicates variability in elevation on small scales that is either caused by natural microtopography or by hillock structures created by grazing animals. Differences in cover and litter, mostly caused by management, contributed to the variation with a lower percentage (7%), thus played a minor role compared to the aforementioned gradients.

That species richness increases with increasing elevation is a well-known pattern in salt grasslands observed also by Märtson (1996) and Puurmann et al. (2002) in Estonia and by Jutila (1997) in Southern Finland (up to an elevation of 70 cm). The less extreme site conditions (flooding, salinity, erosion, ice scouring) exclude less species from these higher elevations. A negative correlation between species richness and soil salinity was also found by Garcia et al. (1993) in Mediterranean salt marshes. Tyler (1969b) described for Swedish salt grasslands that distinct patterns of microtopography – hillock structures with up to 20-30 cm differences of level – formed through interplay between cattle trampling in summer and freezing of the soil in winter. In such hillock structures, the zonation is repeated on a microscale, resulting in very high small-scale species richness.

Märtson (1996) and Puurmann et al. (2002) demonstrated that Estonian coastal meadows on calcareous soils in transition to terrestrial ecosystems were especially species-rich. Jutila (1997) found on average 11.5 species on 1 m² of Finnish seashore meadows (in a transect analysis with very different communities from the water line up to the forest edges). The local species pool in her study area is smaller due to acidic soils in contrast to calcareous soils in Estonia.

8.2.3 Vegetation structure and changes in species composition in the course of succession

Vegetation structure was clearly affected by management: the vegetation as well as the litter layer was higher in early and late successional sites. Strongly reduced light availability in dense grass swards (Schrautzer & Jensen 2006) or reed beds (Kotowski & van Diggelen 2004: to less than 1%, Ekstam 2007) enhances light competition and may also inhibit germination and establishment (Tilman 1993, Goldberg & Werner 1983, Spackova et al. 1998, Jensen & Gutekunst 2003). Especially annual and biennial species might be negatively affected by this process. These had a lower cover in late successional sites, which was also visible in the significant decrease of the annuals *Odontites litoralis*, *Centaurium littorale* and *C. pulchellum*.

That annual species benefit from gap formation due to grazing has also been reported by Bakker (1989), Gibson et al. (1987) and Bullock et al. (1994). In contrast, Jutila (1997) did not confirm this impact of grazing for all her study transects at the Finnish coast. She found large differences between transects which she attributed to the degree of exposure of the coastal sites, and concluded that disturbances by the fluctuating water table and erosive forces of waves, ice and wind are more important than disturbances by cattle. The sites closest to the open sea and most severely affected by these disturbances were richest in species and also annuals. It has also been suggested that the land uplift at the Finnish coast offers competition free sites for plants (Ericson 1980, Jutila 2001).

The mentioned changes in vegetation structure caused also changes in species composition. Management and the associated changes in vegetation structure are correlated to the first axis in the ordination diagram (also correlated with pH and phosphate), illustrating that they are more important for species composition than environmental variables such as salinity which is correlated to the second axis (along with mean Ellenberg value of nitrogen). Furthermore, the changes in species composition were visible in shifts between socio-ecological species groups: reed bed species increased in cover, while salt marsh species decreased. Also the frequency of several species significantly changed.

The higher frequencies of *Plantago maritima, Leontodon autumnalis, Odontites litoralis, Festuca rubra* and *Glaux maritima* in grazed sites agree with the results of Jutila (1999) from Southern Finland. *Phragmites australis* and *Galium palustre* were more frequent (and had higher cover) in ungrazed sites, as also found by Jutila (1999, 2001). Tyler (1969b) in contrast assessed *Odontites litoralis* and *Centaurium littorale* as sensitive to heavy grazing, while I found that both species decreased in late successional sites. In Tyler's study, both species profit from moderate grazing, and Scherfose (1993) likewise assessed them as being favoured by grazing.

The decrease of the annual *Centaurium pulchellum* after abandonment is also in good accordance with the results of Härdtle (1984) from the German Baltic coast, as well as the increase of *Phragmites australis, Bolboschoenus maritimus* in the lower and *Elymus repens* in the upper geolittoral. Burnside et al. (2007) showed that abandonment of western Estonian salt grasslands was indicated by species like *Phragmites australis* and *Elymus repens* (as well as woody species such as *Juniperus communis, Frangula alnus* or *Pinus silvestris*), corresponding also to the results of the presented study.

Jutila (1999) found that *Eleocharis uniglumis* (also Kauppi 1967) and *Elymus repens* were favoured by grazing, while in my sites, both species increased in early and late successional sites. Rebassoo (1975) describes that the Eleocharetum uniglumis community has increased in Estonia in recent decades while the influence of grazing decreased. Dahlbeck (1945) also found that grazing hindered the development of the association in the Øresund region. Tyler (1969b) mentioned *E. uniglumis* as being rather indifferent to grazing. According to Scherfose (1993), *Eleocharis uniglumis* is only favoured by low-density grazing, while grazing in the investigated salt grasslands sometimes could be described as high density, which may explain different assessments by the mentioned authors.

Festuca rubra was assessed to be suppressed by grazing by Härdtle (1984) and Scherfose (1993), but Burnside et al. (2007) classified *Festuca rubra* as grazing indicator (which decreases after abandonment). I found that *Festuca rubra* had a slightly higher cover in early successional sites than in grazed sites and only decreased when reed became dominant (in late successional sites). Thus it seems that it depends on the studied length of the successional trajectory, whether *F. rubra* is classified as decreasing or not.

The cover of characteristic species of BBCM decreased in late successional sites. Five of the 16 species of this group significantly decreased (*Plantago maritima, Odontites litoralis, Centaurium littorale, C. pulchellum, Festuca rubra*, see above), and two of these species increased in the course of succession (*Eleocharis uniglumis, Bolboschoenus maritimus*).

While the abundance of several species differed between successional stages, species numbers did not differ significantly. Also analyses of species groups showed that changes in abundances were more pronounced than in number of species. This agrees with the conclusion of Bakker (1989) and Bakker et al. (2003) that a change in species abundance precedes a change in species number.

8.3 Vegetation changes during retrogressive succession (restorative grazing)

The observed changes in the course of progressive secondary succession were largely reversed in sites of restorative grazing, thus in the course of retrogressive succession. Here, the vegetation was much lower than in late successional sites, but still higher than in grazed sites. The litter layer was similar to grazed sites, and the vegetation cover was even lower than in grazed sites (as observed by Sammul et al. 2008). In the ordination diagram, restored sites were found – fairly widespread – in the middle between late successional and grazed sites. Changes of species' cover or frequencies were reversed – except for *Phragmites australis* and *Elymus repens*. *Phragmites australis* was eaten by the cattle and thus reduced in cover and height, but still occurred frequently in restored sites.

This indicates that restoration measures take more time than (the investigated) 2-4 years until the original vegetation composition is re-established. Kaljuste (2004a, b) estimates for Estonian salt grasslands that restoration needs as much time as the preceded abandonment phase. Also Sammul et al. (2008) state that five years of restoration were enough to create a vegetation structure (and small-scale species richness) relatively similar to that of continuously managed Estonian salt grasslands, but not yet similar species composition.

For abandoned back-barrier salt marshes in the Netherlands, Bakker (1989) found that the resumption of grazing reversed the changes in the vegetation after abandonment within 5 to10 years at relatively high stocking rates. Mainly because of removal of the tall grass *Elymus athericus*, species richness increased again in high marshes, whereas it decreased in low marshes due to the destruction of vegetation and topsoil by trampling (Bakker 1989). The increasing richness was caused mainly by species of the lower salt marsh re-establishing in the higher marsh (Bakker et al. 1985, Bakker et al. 1997). For brackish marshes at the Dollard estuary at the North Sea coast, Esselink et al. (2002) showed that abandonment of the drainage system reinforced the spread of lower marsh species into the higher marsh.

8.4 Impact of succession on the seed bank

8.4.1 Discussion of methods

The sample volume of 4 l per site exceeds by far the suggested volume for determining seed bank species composition in grasslands from Hutchings (1986) of 1 to 1.2 litre.

Species with a seed density in all sites of at least 7.5 seeds/m² are detected with a chance of 95%, assuming a Poisson distribution of the seeds in the soil (compare Thompson et al. 1997 and Strykstra et al. 1998). In Table 8-1, the detection level is given per management class.

Table 8-1: Minimal seed density of a species to be detected with a chance of 95%, assuming a Poisson distribution of the seeds. Calculated as minimal detectable seed density = ln20/(n*A) with n = number of cores and A = area of each core (15.9 cm²) or A = volume of each core (159 ml) as described in Thompson et al. (1997).

	number of cores	minimal detectable seed density/m²	minimal detectable seed density/l
all sites	250	7.53	0.08
all grazed sites	175	10.76	0.11
all early successional sites	95	19.83	0.20
all late successional sites	30	62.79	0.63

Species richness may have been underestimated because germination conditions may not have been favourable for all species. The ‘cold treatment’ (winter directly after sampling and between the two summers of seedling emergence and identification) should have been able to release dormancy for most species. According to Ter Heerdt et al. (1996), the seedling emergence method usually detects more than 90% of the species present in the soil samples of grasslands. The high number of species found in the presented study also suggests that not too many species should have been missed.

Roberts (1981, s. Thompson et al. 1997) suggested that two years of seedling emergence – as applied in the presented study – would be reasonable for seed bank analyses. Thompson et al. (1997) argue that with longer germination phases, moss cover increases and may inhibit germination, which occurred also in my samples. Species, whose seedlings are difficult to determine such as grasses and sedges, may have been underestimated in the seed bank. However, the long germination and identification period allowed the determination of at least a part of these seedlings to species level.

Seed bank was sampled in November. Thus seed production of the last summer and autumn should have largely been included and transient seeds were detected in the seed bank, too. This is the reason why seeds present only in the upper layer were classified as transient (as described in Thompson et al. 1997). Seed density estimates should then be (relatively) higher than e.g. in Jutila's study (1998, 2002) who sampled the seed bank in early summer/June (after spring germination, but before seed production, thus determining primarily persistent seeds).

For the calculation of the longevity index of species groups, it should be taken into account that only comparatively few data are available for salt marshes (Bakker et al. 2002).

If vegetation and seed bank are compared, it has to be taken into account that some species could not contribute to the seed bank or their contribution was missed for methodological reasons, since their seeds or spores were lost with sieving or are difficult to germinate. This applies to pteridophytes (*Ophioglossum vulgatum*, *Equisetum* spec.), orchids (*Dactylorrhiza* spec*., Epipactis palustris*, see also Thompson et al. 1997*)* or other species occurring in the vegetation only as seedlings (such as *Frangula alnus* in grazed sites). However, these species were not excluded from the analysis of the matched vegetation and seed bank data set to avoid inconsistencies between the various analyses (of vegetation alone and of seed bank + vegetation). There is no 'common standard' in the literature: This handling corresponds with that of Bossuyt & Hermy (2004), but Bekker et al. (1999) have decided differently, and even excluded all species with low frequencies in the vegetation or seed bank (resulting in an analysis of 37 of 59 species found in total). This is one aspect why we should be very careful with direct comparisons of e.g. figures of seed bank-vegetation similarities from different studies.

Furthermore, for all comparisons between vegetation and seed bank, it has to be considered that the seed bank was not sampled on the complete area of the vegetation relevé (25 m^2), but only on 80 cm^2. However, since the seed bank sample was mixed from several cores, seed input from the whole plot may have been included – with the mentioned bias against species with low seed densities.

In salt grasslands, dispersal by flooding water can import seeds to a site where the species is not present in the vegetation. In this case, the species (being present in the upper seed bank horizon, but not in the vegetation) is classified as short-term persistent following the seed bank classification key by Thompson et al. (1997), which would lead to an overestimation of its persistence. This is the reason why Wagner et al. (2003) modified the Thompson classification key by preferring the vertical distribution over the criterion of 'a species being present in the seed bank but absent from the vegetation' for the floodplain meadows that they studied. However, since a species was only classified as 'present' with at least 3 seeds in each layer, it is unlikely that this misclassification has happened often. Still, it becomes clear that the classification of seed persistence derived from the comparison of vegetation and seed bank and the depth distribution of seeds has its shortcomings and should only be used with considerable caution. Direct measurements of seed persistence by burial experiments are more reliable, but represent rather the upper limit of persistence (Jensen 2004), since factors depleting the seed bank are usually excluded in burial experiments (predation, transport to the surface resulting in germination).

8.4.2 General characteristics of the seed bank

Species richness

Compared to other seed bank studies of salt grasslands, quite many species were found in the seed bank (78 taxa), nearly the same number as in the vegetation of the same plots (85), and two thirds (67%) of the taxa number found in the vegetation of all sites (117). A high number of species is considered as one precondition for the seed bank to be useful in restoration (Blomqvist et al. 2003).

Chang et al. (2006) found 21 and Wolters & Bakker (2002) 29 species in seed banks of salt marshes on the Dutch island Schiermonnikoog. Ungar & Woodell (1993) recorded only 7 species in two British salt marshes. Grandin (2001) counted 38 taxa (including seed banks of mature forests) at the Swedish East coast, Jerling (1983) detected only 13 species in the same region. In contrast, Jutila (1998a) recorded 82 species at the Finnish coast (about 50% of the species number of the vegetation), and Bossuyt et al. (2005) found 85 species in the seed banks of Belgian salt marshes (more than in the vegetation, including many species from several grassland types and forest edges or clearings). Ludewig (2009) detected 45 species in seed banks of Baltic salt grasslands in Western Germany.

These large variations reflect on the one hand differences in species richness of the studied plant communities (e.g. between species-poor salt marshes of the North Sea and species-rich coastal meadows in the Northern Baltic). On the other hand, comparisons of species richness are complicated by differences in sampling effort, which determines the probability to detect rare species and species with a highly patchy distribution (Thompson et al. 1997).

Seed density

In this study, a much higher seed density (upper: 35,085 seeds m^{-2}, lower: 15,468 seeds m^{-2}, both: 50,553/m^2) was found than in several other studies which were also conducted in salt marshes (Jerling 1983, Hartman 1988, Bossuyt et al. 2005, Ungar & Woodell 1983, Chang et al. 2001). However, the results of Jutila (1998a), Grandin (2001) and Ludewig (2009) from the Baltic Sea coast as well as of Wolters & Bakker (2002, for some communities) and Marañon (1998) are in the same order of magnitude. Jerling (1983) even recorded 140,000 seeds/m^2 at the Swedish Baltic Sea coast. These studies have all in common that annuals and/or *Juncus gerardii* are the dominating species. I also found that these species which produce large quantities of small (persistent) seeds were dominating the seed bank. Thus the general assumption by Adam (1990) that seed densities were low in salt marshes does not apply to the studied Estonian salt grasslands.

According to Bossuyt & Honnay (2008), very high seed densities in ‘marshes’ (about 13,000 seeds/m^2, ‘marshes’ comprise salt and freshwater marshes incl. flood meadows) compared to grassland and forest (below 4,000 seeds/m^2) indicate that most marsh species produce long term persistent seeds.

Soil profile – similarity between aboveground vegetation and seed bank

A decreasing similarity between the seed bank and vegetation with increasing soil depth was also found by Milberg (1995), Grandin & Rydin (1998) and Wagner et al. (2003) in semi-natural grasslands. One reason for this pattern is that the seed bank of upper soil layers is usually more quickly depleted after a species has disappeared from the vegetation, whereas it persists longer in the lower layer. Furthermore, seeds from recent colonisers appear earlier in the upper than in the lower layer, because it takes time for seeds to penetrate to lower layers (Bekker et al. 1998a).

Individual species

The dominant species in the seed bank were quite similar to other studies, especially those from Baltic salt grasslands. *Juncus gerardii* was also among the most abundant species in the studies of Jerling (1983) and Grandin (2001) from Sweden,, of Jutila (1998a,b, 2002) from Southern Finland, and of Ungar & Woodell (1996) from South Wales, Wolters & Bakker (2002) and Chang et al. (2006) from the Dutch Wadden Sea island Schiermonnikoog. Ungar & Woodell (1993) found *Juncus gerardii* dominant in April, but missing in the autumn seed bank, which was not confirmed by the presented results from sampling in November. *Juncus articulatus*, the second most abundant species in the presented study, was also frequent in Grandin's study (2001) and in dune slack seed banks (Bekker et al. 1999).

In Jerling's study (1983), *Eleocharis uniglumis*, typical for the lower geolittoral of low salinity areas, was totally missing in the seed bank although common in the vegetation. This was traced back to specific germination requirements. Jutila (1998a, b), however, found the species frequently in the seed bank and classified it as persistent, in agreement with the presented internal longevity index of 1. *Glaux maritima* was frequently recorded by Jutila (1998a, b), Wolters & Bakker (2003) and Chang et al. (2006), *Agrostis stolonifera* by Jutila (1998a), Chang et al. (2006) and Bekker et al. (1999), but only with low abundance by Jerling (1983).

Centaurium littorale was common in the study of Jutila (1998a) and Grandin (2001). Bekker et al. (1999) proved a persistence of at least 40 years of seeds of *Centaurium littorale* and *Carex flacca* in the seed bank of dune slacks, which was confirmed by Grootjans et al. (2001) for *Carex flacca*. In contrast to my results, Jutila (1998a) did not detect *Centaurium pulchellum, Leontodon autumnalis* and *Carex panicea* in the seed bank, although they were regularly present in the vegetation. However, Chang et al. (2006) found *Centaurium pulchellum* in the salt marsh seed bank on the Dutch island Schiermonnikoog.

The species that were present in the seed bank, but not in the vegetation, mostly had high longevity indices (LI-Bekker, calculated with data from Thompson et al. 1997): e.g. *Juncus bufonius* agg. (0.88), *Poa annua* (LI=0.89, also found by Jutila (1998a) in the seed bank, but not in the vegetation), *Poa pratensis* (0.58), *Rorippa palustris* (1) and *Linaria vulgaris* (0.43).

8.4.3 Changes after abandonment

The seed bank seems to change relatively little after abandonment: neither species number in the seed bank nor seed density did change. Spatial heterogeneity did not change in the seed bank while it increased in the vegetation of successional sites. In the ordination (PCA), seed bank samples showed less separation between management classes than vegetation relevés. In contrast to their decline in the vegetation, the relative abundance of salt marsh species did not decrease in the seed bank in the course of succession. Only four species significantly changed in seed density after abandonment: *Centaurium littorale* decreased in late successional sites, the other three were increasing (*Glaux maritima* in early successional sites, *Galium palustre* and *Eleocharis uniglumis* in late successional sites).

In contrast to these results, however, seed bank changes follow vegetation succession in some respect: similarity between vegetation and seed bank did not significantly change, and reed bed species showed the same increase during succession in the seed bank as in the vegetation (both in relative species number and in relative abundance).

Density

Jutila (1998a) found a significantly larger and richer seed bank in ungrazed salt grasslands, and ascribed this to the taller vegetation of ungrazed sites retaining more sediment and litter (Grumblat 1987, Andresen et al. 1990) that may also contain seeds. Chang et al. (2008) experimentally proved that dense, more rigid vegetation types retained more seeds (in a field and a flume study).

Jensen (1998), Falinska (1999) and Wagner et al. (2003) reported a peak of seed density in early successional wet grassland sites followed by a decline, while Amiaud & Touzard (2004) found no changes in seed density (after only 3 years of succession), as in the presented study.

Species number

Ungar & Woodell (1996) found highest species numbers in lightly grazed, and lowest in heavily grazed salt marshes in Southern Wales, while ungrazed salt marshes were intermediate. Also Jutila (1998a) discussed that species richness of the seed bank under grazing impact may follow the hump-shaped optimum curve as postulated by the Intermediate Disturbance Hypothesis (Connell 1978). Studies on the impact of grazing on species richness of the seed bank in other grassland types gained different results: While in some studies species numbers were higher at grazed sites (Donelan & Thompson 1980, Gibson and Brown 1991), other studies revealed the opposite to be true (McDonald et al. 1996, Bakker et al. 1996b).

Seed bank-vegetation similarity

Ungar & Woodell (1996) reported a higher similarity between seed bank and vegetation for heavily grazed than for ungrazed and lightly grazed salt marshes. In contrast, Jutila (1998a) found a higher similarity between vegetation and seed bank in ungrazed than in grazed salt grasslands in Southern Finland.

Jensen (1998), Amiaud & Touzard (2004) and Wagner et al. (2003) found that similarity of seed bank and vegetation was higher in managed than in abandoned wet grasslands, since species from earlier successional stages persist in the seed bank of abandoned sites. The same accounts for French chalk grasslands studied by Dutoit & Alard (1995). The presented results show the same decreasing trend in Bray-Curtis-similarity for early successional sites, but not in Sørensen-similarity. This pattern can be caused by dominant species in early successional sites that contribute little to the seed bank such as *Festuca rubra,* which decreases the values of Bray-Curtis-similarity (which takes abundances into account), but not those of Sørensen-similarity (based on presence-absence only).

When comparing results of different studies on seed bank-vegetation similarity, we have to keep in mind that the outcome of the analysis also depends on the measure of (dis)similarity and on sampling effort. Indices are either based on abundances or presence-absence data. Some authors excluded species with low abundances (1, 2, 3 seeds only etc.) or pooled species difficult to distinguish. Others assessed 'similarity' from distances in multivariate ordination space. Calculations can be based on the whole data set or on separate subsets or sites (as I did for sites). The higher the number and volume of samples, the higher is the probability to detect rare species. This results in higher similarity, if these species are also present in the vegetation, or in lower similarity, if they are not.

8.4.4 Seed banks as a source for restoration?

The comparatively numerous and species-rich seed bank found in this study, in which characteristic species are over-represented compared to the vegetation (particularly in early and late successional sites) indicate a rather high potential of the seed bank to contribute to the restoration of typical salt grassland communities.

This is in contrast to the conclusions from other seed bank studies, be it for dune slacks (Bakker et al. 2005b), calcareous grasslands (Dutoit & Alard 1995, Bakker et al. 1996a) or fens (Maas & Schopp-Guth 1995, Matus et al. 2003). Why do the results of the presented study differ from these findings?

Potential of the seed bank

Dominance: target or non-target species

In other studies, the low potential of the seed bank is derived from the **dominance of non-target species** in the seed bank, for example in dune slacks (e.g. Bossuyt et al. 2005) or fens (e.g. Maas & Schopp-Guth 1995). In these studies, high densities of seeds from nutrient rich plant communities were found dominating the seed bank. For instance Maas & Schopp-Guth (1995) reported that the proportion of fen species in the seed bank declined to less than 4% ten years after intensification of agricultural use and to less than 1% in arable fields on fen soils. Since the proportion of non-target species increased dramatically, these authors do not recommend using the seed bank for restoration purposes after more than 5 years of degradation.

Bossuyt et al. (2005) documented for dune slacks, that species from nutrient rich habitats dominated the seed bank. They conclude that germination from the seed bank would rather hamper the establishment of target species due to competitive exclusion. In this study, target species were poorly represented in the seed bank, and similarity between seed bank and vegetation was low. In contrast, in the salt marshes which they studied as well, similarity of seed bank and vegetation was higher because of a higher contribution of typical salt marsh species.

Bakker & Berendse (1999) also confirm that similarity of seed bank and vegetation was higher in salt marshes than in most other grassland and heath communities. Following the meta-analysis of Bossuyt & Honnay (2008), similarity (Jaccard-Index) of (freshwater and salt) marshes was intermediate between grasslands (with highest similarity) and forest (with lowest similarity). Also Hopfensperger (2007) calculated from 131 studies (worldwide) that Sørensen-similarity in wetlands, including salt marshes and salt grasslands, was higher than in forests and slightly lower than in grasslands.

In (i.a. fen) grasslands, dominating non-target species are e.g. *Juncus bufonius* or *Juncus effusus* (Jensen 1998, Bakker & Berendse 1999) which produce extremely high numbers of small seeds with a high persistence in the soil. *Juncus effusus* is considered as a problem species in agricultural use and in nature conservation of wet meadow communities, since it has a low nutritional value

(Klapp 1965), occurs as a disturbance indicator tending to become dominant (Merchant 1993, Dierschke & Briemle 2002, Bockholt et al. 2006), and decreases the habitat value of meadows for breeding meadow birds (Starkmann 2002). The dominance of *Juncus* species is a common phenomenon in European seed banks of different habitats: Bossuyt & Honnay (2008) showed that *Juncus* species were among the most abundant species in more that 50% of 102 European seed bank studies, and in almost 90% of the included (fresh and salt) marsh studies (see also Bekker et al. 1997).

In the study presented here, the most dominant species was *Juncus gerardii*. However, this species is one of the characteristic species of BBCM (and salt grasslands in general) and is considered as being valuable in different respects: It provides a forage resource for migrating, moulting and breeding geese (Fox et al. 1998, van der Graaf et al. 2007), extensive areas with low vegetation (dominated by *Juncus gerardii* and *Agrostis stolonifera*) are important as preferred breeding habitats for wading birds (Kaljuste 2004b, Burnside et al. 2007), and additionally have a high fodder value for cattle (Köster et al. 2004).

In contrast to seed banks of fens or dune slacks, seed banks of salt marshes and salt grasslands are thus usually dominated by (some of their) typical – and thus target – species (Jerling 1983, Ungar & Woodell 1993, 1996, Jutila 1998a, Grandin 2001, Wolters & Bakker 2002, Bossuyt et al. 2005, Chang et al. 2006, Ludewig 2009). Only Hutchings & Russell (1989) reported a species *(Urtica dioica*) considered as atypical for salt marshes in substantial numbers in a salt marsh seed bank. However, they failed to retain seeds of *Juncus, Spergularia* and *Inula* because of their sieving technique, and they sampled *Salicornia* only inefficiently. Since these species form a major part of the seed bank in other salt marsh studies, it is likely that the proportion of *Urtica dioica* relative to all seeds would have otherwise been much smaller.

The dominance of typical species in seed banks of salt marshes and grasslands is probably caused by the rather extreme abiotic conditions (salinity, flooding, in Estonia partly also desiccation in summer). These extreme conditions exclude on the one hand 'non-target' species from the aboveground vegetation. On the other hand, seeds of salt intolerant species may not retain their viability under conditions of salt stress (Ungar 2001). If seeds of salt-intolerant species of nutrient rich habitats (which potentially could outcompete typical salt grassland species) remain viable in the seed bank (Bossuyt et al. 2005), their presence should be less problematic than in other habitats since their germination and establishment would be hampered by salt stress (Jutila 1998b, Ungar 2001), at least in frequently flooded lower elevations (Wolters & Garbutt 2006).

In addition, dispersal of these non-target species into salt grasslands and marshes is also rather unlikely, because salt grasslands and marshes are not often directly adjacent to other eutrophic grassland types, and because dispersal vectors such as wind or (tidal) water usually do not connect them with these habitats. All these factors restricting the presence of non-halophytes in seed bank or vegetation may be less important in Estonian salt grasslands with their gradual transitions to non-saline habitats and a much lower salt content in water and soil (except for in salty patches, Kauppi 1967, Siira 1970, Puurmann & Ratas 1998) than in salt marshes e.g. at the North Sea. Nonetheless, the presented study indicates that there is no real 'risk' emerging from the dominance of non-target species in the seed banks of Estonian salt grasslands.

Interaction with restoration measures

In other habitats, restoration measures can either be a chance to activate the seed bank of target species (Bekker et al. 1999), or can be responsible for a low potential or even a ‘risk’ coming from the seed bank. In fens and dune slacks e.g., restoration is often carried out in combination with top soil removal to remove excess nutrients. With this measure, the seed bank can largely be removed or decreased, either that of the target species (Grootjans et al. 2001, Bakker et al. 2005b) or that of non-target species (Verhagen et al. 2001, Hölzel & Otte 2003, Rasran et al. 2007). Top soil removal may also activate non-target species such as *Juncus effusus* (Bakker & Berendse 1999). These aspects are not relevant for salt grasslands, since restoration of salt grassland does usually not imply top soil removal.

Persistence of target species

A further reason why many authors consider the potential of the seed bank for restoration as low, is that they mostly report **low (or no) persistence of target species**. That here, the opposite conclusion is drawn may result from actual differences between habitats regarding seed persistence, but additionally problems in evaluating seed persistence.

Characteristic species of BBCM and salt marsh species in general showed comparatively high persistence, as also reported by Bossuyt et al. (2005). The average longevity index of the ‘salt marsh species’ (LI-B+int=0.50, see Table 7-13) was higher than that of most target alliances of low productive grasslands on sandy soils (0.23-0.45, except for Ericion tetralicis with 0.71, Verhagen et al. 2001) or that of the fen flora of North-western Germany (0.3-0.4 for species groups with high habitat specificity such as Molinietalia, Phragmitetea, Scheuchzerio-Caricetea, but 0.53 for ‘others’, Jensen 2004). Mean longevity was somewhat lower than that of arable weed communities which are well known for producing many persistent seeds (Caucalidion and Fumario-Euphorbion with 0.64 and 0.70 respectively, Bekker et al. 1998b). Some salt grassland species proved to persist for decades or even centuries: *Centaurium littorale* and *Carex flacca* survived in the seed bank for at least 40 years (Bekker et al. 1999, Grootjans et al. 2001). Grandin (2001) found *Centaurium littorale* and *Juncus gerardii* in the seed bank of mature forest on a land uplift seashore and concluded that they persisted for several centuries.

Without human interference in the form of management (grazing/mowing), salt grassland species would be restricted at the Baltic Sea to wave-exposed sites and early successional stages on newly created land (Jeschke 1987), which are subject to frequent disturbances. Species occurring in habitats characterised by disturbances such as flooding, sedimentation, erosion and ice scouring in general are favoured by the production of a large number of long-lived seeds (van der Valk & Davis 1978, Grime 2001, Bossuyt & Honnay 2008) waiting in the soil for favourable conditions for germination.

This is also the reason why Bossuyt & Honnay (2008) conclude that the seed bank may be useful for restoration in particular for plant communities depending on disturbance, and that marsh species adapted to recurring draw-down cycles (van der Valk & Davies 1978) are the exceptions from the rule that restoration via germination from the seed bank may be successful only in the first 5 years after degradation.

However, the mean longevity index of 0.5 also illustrates that only a part of the salt marsh and characteristic BBCM species belongs to these early successional and persistent species, and that not all species are likely to have a high potential of re-establishing themselves from the seed bank.

The estimation of low persistence of target species in other studies may also result from **methodological reasons:** the classification key of Thompson et al. (1997) applied by most authors (e.g. McDonald et al. 1996, Bekker et al. 1997, 1998b, 1999, 2000, Wolters & Bakker 2002, Matus et al. 2003, Blomqvist et al. 2003) defines a species as 'transient' if it is present in the aboveground vegetation, but absent from the seed bank. However, the absence of a species from the seed bank samples may easily result from a seed density below the detection level, which strongly depends on sampling effort. Due to practical limitation, only a small percentage of the total area (of the vegetation study) is sampled, which results in an underestimation of species richness and of seed density of individual species (Bossuyt & Honnay 2008) and in particular underestimates the presence and persistence of less frequent (and rare) species, which are often target species of nature conservation and restoration. Jensen (2004) showed that, when longevity is calculated only from 'real seed bank counts', or even derived from burial experiments, estimated persistence is much higher, and that most species of the Northern German fen flora are able to accumulate short-term or even long-term persistent seed banks. Thus, seed banks may play a more important role in conservation and restoration of wet grasslands than concluded by other authors. Consequently, he recommends to refrain from applying the mentioned classification criterion 'absent = transient'.

In addition, a patchy distribution of the seed bank contributes to an underestimation of persistence. Moreover, the germination requirements of particular species may not be fulfilled in seed bank studies, since *inter alia* stratification, heating, flooding and sampling period may affect the outcome of germination trials (Bossuyt & Honnay 2008).

Species 'lost' from the vegetation

A further indication of a 'high potential' of the seed bank for restoration is to find **(many) species that are absent from the vegetation** (Blomqvist et al. 2003, Bakker et al. 2005b). Since only few species were lost from the aboveground vegetation during the studied succession from grazed to the 'late successional' stage, not many 'lost' species in the seed bank could be detected. A few species (such as *Centaurium littorale, C. pulchellum)* decreased in the vegetation and were over-represented in the seed bank of early successional sites. These species also increased in frequency in the vegetation after the introduction of restorative grazing, indicating a re-establishment from a (at least short-term) persistent seed bank.

The fact that the 'late successional' sites were still quite species-rich can be attributed to the rather low age of these successional sites of 10-15 years. When succession continues, reed will become denser, and consequently species richness will decrease (see negative correlation to reed cover, Fig. 7-2). In this situation, the need for the 'reserve' of a long-term persistent seed bank is not that high (yet), because only few species are lost in the course of succession. However, only two thirds of all characteristic species of BBCM were represented in the seed bank, quite many of them with low numbers, in particular in late successional sites (Fig. 7-10). In absolute species numbers, each seed bank sample contains less characteristic species (and less species in total) than the vegetation. The overrepresentation of characteristic species in the seed bank was mainly due to the dominance of *Juncus gerardii* and, in late successional sites, *Eleocharis uniglumis*. Thus, it can be concluded that the seed bank of the studied sites has a high potential for re-establishment of characteristic species, but not necessarily for restoration of high species richness.

Realised contribution: germination and establishment from the seed bank

To what extent the **potential** of the seed bank is realised as a **contribution** of the seed bank to re-establishment of typical species, depends on many other factors. In general, only a small fraction of the seed bank will contribute to seedling germination and establishment. Jutila (2003) showed that in Finnish salt grasslands, 2.2-2.5% of the seeds in the seed bank germinated in the field and that the species number of seedlings in the field was much lower than in the sampled seed bank. Willems & Bik (1998) stressed the importance of appropriate conditions for germination and establishment for restoration success.

In particular, species accumulating a persistent seed bank require light as a germination trigger (Baskin & Baskin 1989), thus buried seeds need a disturbance that opens the soil and the vegetation canopy and 'activates' the seed bank. Trampling by grazing animals may create such small disturbances serving as 'safe sites' for germination and establishment (Grubb 1977, Pickett & White 1985). However, Stammel & Kiehl (2004) showed that single hoof-prints in wet peat soils of fen meadows did not enhance recruitment of seedlings because of an unfavourable microclimate (dark, wet). The authors also pointed out that an accumulation of many hoof-prints or hoof-prints in different soil conditions may give rise to different results. Estonian salt grasslands (in most cases) have no deep peat layers, thus abiotic conditions in hoof-prints differ from those in fens. Microclimatic conditions should be more favourable in (shallower) hoof-prints. In general, germination is often not gap-dependent in nutrient-poor grasslands (such as the fens studied by Stammel & Kiehl (2004)) because the vegetation per se is not very dense (Zobel et al. 2000). However, in particular in abandoned salt grasslands, very dense canopies may develop – thus here, gap-dependence for germination is more likely.

In addition, also other animals may contribute to soil disturbances and thereby enhance seedling recruitment, such as grubbing wild boar (Kotanen 1995, Lavorel et al. 1998) or rabbits (Edwards et al. 2000). Indeed, high numbers of seedlings were observed at wild boar grubbing sites in salt grasslands and brackish reed beds. Another factor which may play a role in disturbing the soil and decreasing competition in more exposed sites near the coast line is erosion by waves or ice scouring (Cramer & Hytteborn 1987). Jutila (1997) recorded at the most exposed shore transects high species richness and in particular many annual and biennial species that are indicative of disturbances and rely upon a persistent seed bank.

Appropriate restoration measures should thus ensure favourable conditions for germination and establishment from the seed bank, such as creating gaps and (patches with) a low canopy with low competition of the established vegetation. The results of the presented vegetation analysis suggest that this was (at least partly) fulfilled in the restorative grazing sites. The percentage cover was lower in restored sites, and the litter layer in restored sites was thinner than in early and late successional sites. However, vegetation was still higher than in grazed sites, mainly because *Phragmites australis* was still present with a high frequency, but low cover and bitten down by cattle to an average vegetation height of 32 cm. That grazing opens the canopy, reduces litter accumulation and thereby enhances establishment of seedlings in salt marshes, was also shown by Bakker et al. (1985) and Bakker & de Vries (1992).

Possibly, germination from the seed bank could be enhanced by technical restoration measures such as rotovation or litter-stripping, if a thick litter layer is present (as observed in most early and late successional sites) that may inhibit germination (Jensen & Gutekunst 2003). In a restoration project in Southern Finland, rotovation was applied to cut or break the reed rootstocks (Huolman & Priha 2007). Milberg (1994) showed in a study on restoration of overgrown wet grasslands in Sweden that several long-term persistent species increased their cover or re-colonised after rotovation. Litter-stripping proved to enhance establishment of *Calluna vulgaris* from the seed bank in heathland restoration (Mitchell et al. 1998, 1999). Litter-stripping can also reduce the effect of nutrient accumulation (Mitchell et al. 1999), which occurs after abandonment of wet grasslands (Müller et al. 1992) and was also observed in long-term abandoned Estonian salt grasslands (Sammul et al. 2008).

Results of a field experiment at one of the investigated 'late successional' sites (on Vormsi island) also indicated that soil disturbances initiated re-establishment of target species that were not present in the vegetation prior to the disturbance such as *Centaurium littorale* and *C. pulchellum* from a persistent seed bank (M. Berg, pers. comm.). The species richness of the vegetation also increased after the disturbance treatments.

In contrast to studies of the seed bank composition, the contribution of the seed bank to germination and (re-)establishment has as yet not been studied so often. Brown (1998) reported that, in spite of a large seed bank, establishment from the seed bank was limited in mature vegetation, and that only a subset of the species present in the seed bank became established. Vinther & Hald (2000) reported that species which (re-)established after the reintroduction of grazing of a fen-meadow had a higher seed persistence than the species present before restoration started.

Bakker et al. (2005b) found that the seed bank did not affect changes in vegetation composition directly after restoration measures in a dune slack, although the seed bank was identified to have a large potential by being species-rich, by containing many 'lost' species and by target species being overrepresented compared to the aboveground vegetation. In contrast, the majority of new establishment originated from the seed rain. However, he also stated that this result was influenced by relatively deep soil removal, which removed large proportions of the seed bank. Where sod cutting was more superficial, the influence of the seed bank was estimated to be greater (Bekker et al. 1999).

In contrast, Kalamees & Zobel (2002) found that the seed bank was an important source for re-colonisation of small gaps (accounting for 44% of the seedlings). Their findings are confirmed by Pakeman & Small (2005) who reported for a Scottish acidic grassland that 43% of the regeneration of gaps after one year had been derived from the seed bank, and 57% from the seed rain (wind and endozoochorous dispersal). That all the regeneration was accounted for from the seed rain in the study of Edwards & Crawley (1999) in acidic grasslands in England, is probably because their experiment was carried out with as little soil disturbance as possible, which avoided activating the seed bank. Furthermore, Pakeman & Small (2005) showed that re-established vegetation in gaps with a seed bank differed more from the surrounding vegetation than in gaps with seed rain. Thus there are greater chances to gain species from earlier successional stages from the seed bank, than from the seed rain. In an Estonian flood-plain meadow, experimental soil disturbances increased the number of seedlings by a factor of 3.7 and doubled the seedlings' species number. Since disturbances were created in spring and seedlings were counted before the main seed dispersal period, most of these seedlings were derived from the seed bank, indicating a high importance of the seed bank for gap re-colonisation (Wanner 2003).

In a field experiment on the re-colonisation of gaps in a German Baltic salt grassland, 87% of the seedlings originated from the seed bank and only 13% from seeds dispersed by water or wind. After an exceptionally long period of summer flooding (of several weeks), however, vegetative ramets had higher survival rates than seedlings and thus were – under these special weather conditions – finally quantitatively more important for the re-colonisation of gaps than the seed bank. Nevertheless, the seed bank seedlings contributed a higher number of species than vegetative re-growth. Thus the seed bank may still be relevant for species richness of salt grasslands (Ludewig 2009).

Other pathways for re-establishment: The (potential) role of seed dispersal

The importance of the seed bank for restoration depends also on other potential sources for re-establishment of target species. In other terrestrial habitats, dispersal of target species is often regarded as the major bottleneck, in particular if habitats are fragmented, e.g. in small nature reserves surrounded by intensively used agricultural land (Verhagen et al. 2001). Dispersal limitation is aggravated by the disappearance of important vectors of long-distance dispersal from the present landscape – such as large animals or flooding water (Poschlod & Bonn 1998, Bruun & Fritzboger 2002).

In contrast, regular flooding provides a potential vector for short- and long-distance dispersal in salt grasslands (Koutstaal et al. 1987, Huiskes et al. 1995). In addition, birds (ducks, geese, shorebirds) resting or feeding on salt grasslands and often migrating long distances may also contribute to seed dispersal (Green et al. 2002, Charalambidou et al. 2003). Seeds of several salt marsh species were capable of floating for weeks whilst mostly maintaining their germination capacity (Koutstaal et al. 1987), suggesting a potentially good dispersal capacity. Thus, dispersal should be less limited in coastal ecosystems which are in general also less fragmented, as emphasised by Metzing (2005). He nevertheless exempts parts of the Baltic salt grasslands from this general rule due to their fragmentation.

For re-establishment of salt marsh target species after de-embankment, Wolters & Bakker (2002) expect a much higher contribution from seed dispersal by tidal water than from a long-term persistent seed bank. However, their study revealed that seeds were transported by tidal waters mainly over short distances, thus restoration success depends on the distance to potential seed source areas (Wolters et al. 2005). There are also empirical salt marsh studies showing that dispersal is limiting the recruitment of seedlings (Hutchings & Russell 1989, Lindig-Cisneros & Zedler 2002) and species richness (Rand 2000).

Since salt grasslands are still quite widespread in Western Estonia, resulting in short distances from restoration sites to seed source areas, and are well connected by dispersal vectors such as flooding water and (migrating) birds, it can be concluded that dispersal should not be limiting.

Conclusions on the impact of restorative grazing and on the restoration potential of the soil seed bank from a nature conservation point of view are integrated in chapter 11 (conclusion for nature conservation management.

9 A method for classifying coastal marshes of the German Baltic Sea for the European Water Framework Directive

9.1 Introduction

The Water Framework Directive (WFD) of the European Union aims at achieving a ‘good ecological status’ of all surface water bodies by 2015. This applies also to coastal waters, including the intertidal zone. The ecological status must be classified into 5 classes from ‘high’ to ‘bad’ using biological, physico-chemical and hydro-morphological quality elements. The classification of coastal waters is primarily based on three ‘biological quality elements’: benthic invertebrates, phytoplankton and macroalgae and angiosperms (‘other aquatic flora’). These are supported by physico-chemical and hydro-morphological quality elements, inter alia ‘structure and condition of the intertidal zone’ (WFD, European Commission 2000).

Only recently, the term ‘angiosperms’ has been taken to include not only seagrasses, but also salt marsh plants (CIS Coast 2003, CIS Wetlands 2003). As a consequence, several classification methods have been developed which consider salt marshes as part of the coastal or transitional water bodies (e.g. Brys et al. 2005 for Belgium, Dijkema et al. 2005 for the Netherlands, and Best et al. 2007 for Great Britain). For the German North Sea coast, a common classification method is now under development (Stock pers. comm.), consulting the work of Arens (2006), Adolph et al (2007) and Stiller (2005a, 2005b).

However, all these approaches refer to tidal waters including the intertidal zone which is explicitly considered within the water body in the directive and in several guidance documents of the Common Implementation Strategy (CIS Coast 2003, CIS Wetlands 2003, CIS Monitoring 2003). So far, no WFD classification approach exists for non-tidal coastal marshes, nor has the relevance of non-tidal coastal marshes for the implementation of the WFD been discussed.

Thus, the following research questions will be considered:

- Should coastal marshes of the Baltic Sea be regarded as relevant for the ecological status of coastal waters and consequently for the Water Framework Directive? If yes, why?
- How can the ecological status of coastal marshes of the German Baltic coast be classified? A draft outline of a classification method will be presented.
- How does management influence ecosystem functions of Baltic coastal marshes? (chapter 10.4)

9.2 Coastal marshes as part of the coastal water bodies

For non-tidal coastal waters such as the Mediterranean and Baltic Sea, the guidance document on Monitoring (CIS Monitoring 2003) proposes the term ‘mediolittoral zone’ as an equivalent to the ‘intertidal zone’, which comprises communities that are dependent on flooding by sea water.

At the Baltic Sea, coastal marshes form an important part of these irregularly flooded communities on shallow, wind-protected coasts. In this paper, ‘coastal marshes’ is used as a generic term for both salt marshes and brackish reed beds. Salt marshes have developed in most areas due to centuries of grazing or mowing (Schmeisky 1974, Dijkema 1990), while brackish reed beds form without grazing. At the south-western Baltic, coastal marshes are largely developed as coastal peatlands.

The formerly extensive coastal marshes along the Eastern German Baltic Sea coast (federal state of Mecklenburg-Vorpommern) have been reduced by more than 80% due to diking and drainage (Herrmann & Holz 1997). Coastal marshes are not only sensitive to alterations of their flooding regime and morphology by drainage and construction of dikes, but also to eutrophication (Jeschke 1987, Krisch 1989, Adam 2002, Boorman 2003) and chemical pollution by heavy metals, organic substances or oil (Vestergaard 1979, 2002, Van Bernem et al. 1994, Boorman 2003, Schuldt & Borgwardt 2005). While eutrophication and chemical pollution are also indicated by other quality elements of the WFD classification (e.g. phytoplankton and seagrass, which are probably more sensitive to eutrophication than – naturally eutrophic – coastal marshes), hydro-morphological alterations of the coastal zone such as diking and drainage are more directly indicated by the status of coastal marshes.

Since coastal marshes are wetlands, they must be included in the coastal water body, if they ‘are directly influencing the status of the related water body’ (CIS Water Bodies 2003) and if ‘the structure and condition of such wetlands is relevant to the achievement of the objectives for a surface water body’ (CIS Wetlands 2003).

Coastal marshes (especially coastal peatlands) can affect the status of coastal waters, particularly relating to eutrophication. They have a potential for nutrient retention if intact and regularly flooded, whereas they can contribute to nutrient load if peat is mineralised due to drainage. However, quantitative studies on the function of coastal peatlands of the Baltic Sea are currently lacking (Trepel & Kluge 2001). The significance of coastal marshes as a nutrient sink or source depends on the ratio of water area and coastal marsh area. It can be particularly high for small, enclosed water bodies surrounded by large (former) coastal peatlands (such as the lagoons in Mecklenburg-Vorpommern or the Schlei fjord in Schleswig-Holstein). Hence, this area ratio should be taken into account when classifying the ecological status of the water bodies.

We conclude that coastal marshes can potentially influence the status of coastal waters and should therefore be generally considered as part of the coastal water bodies. Further, coastal marshes are particularly likely to reflect morphological alterations of coastal waters. Therefore they can complement the other quality elements in an integrated assessment of the ecological status of coastal waters.

9.3 Scale of classification: reference conditions

The scale for the classification of the WFD is related to the ‘reference conditions’, that are defined in the Directive as ‘undisturbed conditions’ with ‘no, or only very minor, anthropogenic alterations’, under which ‘the values of the biological quality elements […] show no, or only very minor, evidence of distortion’. The term ‘disturbance’ in this context is confined to ‘anthropogenic alterations’. As mentioned above, anthropogenic alterations to coastal marshes may be changes of hydromorphology and hydrodynamics as well as input of nutrients and pollutants.

In general, (agricultural) grazing can also be considered an anthropogenic factor and at the Baltic sea coast, large areas of salt marshes have developed from brackish reed beds during the last 500 years as a consequence of grazing (Jeschke 1987: ‘anthropo-zoogenic salt marshes’, Dijkema 1990). So far, it is not known whether salt marshes and brackish reed beds differ in their ability to retain nutrients or form coastal peat. Therefore the impact of grazing is not considered as either positive or negative in the sense of the WFD in this paper.

Thus, only anthropogenic alterations of hydromorphology and -dynamics will be defined as ‘disturbances’ to coastal marshes in the context of the WFD. We define a coastal marsh under reference conditions as an area exposed to natural flooding regime where either salt marshes or brackish reed beds have become established that are subject to no or only very minor anthropogenic alterations.

The classification method for coastal marshes of the Baltic Sea is based on vegetation parameters (as part of the quality element ‘angiosperms’) and uses hydromorphological parameters further to support the assessment based on vegetation. Hydromorphological parameters reflect alterations of the flooding regime more directly than the coastal marsh vegetation. In some cases, halophyte species are known to persist in the vegetation for years or even decades after the construction of a dike and the cut-off from regular flooding.

The proposed draft classification method for coastal marshes results from a project that focused on coastal marshes at the Baltic Sea coast of the federal state of Schleswig-Holstein. Within the frame of the project, the present situation of coastal marshes in Schleswig-Holstein was analysed using existing (mainly digitally available) data. Results of this analysis were used to derive class boundaries for hydromorphological parameters. They should therefore not be in the same way applied to coastal marshes in Mecklenburg-Vorpommern without considering adaptations to local conditions. The general classification method, however, is designed to be applied for the whole German Baltic Sea coast. The consideration of local differences has to be one aspect of a field trial in the future (see ‘perspectives’ below).

9.4 Hydromorphological parameters

Three hydromorphological parameters were selected: flooding dynamics, intensity of drainage and restriction of flooding. To derive class boundaries, ten coastal marsh sites along the Schleswig-Holstein Baltic coast were selected reflecting the whole gradient of degradation from natural flooding to completely diked and drained areas. GIS-based information, aerial photographs and site visits were used to assign these sites to the five WFD classes of ecological status for each of the three parameters separately. From this classification, class boundaries for the three parameters were derived.

9.4.1 Flooding dynamics

Creeks and salt pans are the products of natural flooding dynamics. The parameter is assessed by using GIS-available data of the most recent biotope mapping and is indicated by the total number of the biotope types ‘near-natural saline small water body’ and ‘tidal creek/tideway’ (LANU 2003) of a site per km² (see Tab.). For the ten sites in Schleswig-Holstein, the number of these biotope types ranged from 0 (Großer Binnensee) to 88/km² (Graswarder).

It remains unclear whether the indicator ‘creeks and salt pans’ is applicable for sites totally covered by reed beds. Creeks are described as a characteristic feature of (mostly grazed) salt marshes, but less of brackish reed beds. This may be a result of the fact that microrelief is facilitated by grazing and open vegetation, or that creeks may just not be visible in reed beds. Further, the existence and number of creeks, salt pans and other small water bodies also depends on the type and age of the site. Young sites of beach ridge systems have a more varied microtopography than older sites, especially than more uniform extensive coastal peatlands.

Further on, only larger creeks may have been mapped, while most creeks in Baltic salt marshes are rather small. Therefore, during a field trial it must be determined whether it is necessary to complement the digital mapping results during field visits.

9.4.2 Intensity of drainage

The density of ditches and the existence of pumping stations to lower the ground water table determine the intensity of drainage. To assess the density of ditches (km/km^2), digital data of the local water boards was used. At the ten selected sites, the density of ditches ranged from 0 (Schleimünde, Bottsand) to 7.85 km/km^2 (Reesholm). The proposed class boundaries are presented in Tab. 9-1. For the class boundary between ‘good’ and ‘moderate’ status, information on the degree of ditch maintenance has to be requested from the local water boards.

9.4.3 Restriction of flooding

Flooding by salt or brackish water is an essential ecological factor for coastal marshes. Today, flooding is often restricted by dikes or dams. If a site is separated from the sea by a dike, some salt water influence may still be possible from saline ground or seepage water unless the site is additionally drained by a pumping station. Thus, the five classes are defined as given in Tab. 9-1. The parameter can be classified using digital data of the nature conservation and coastal defence authorities (in Schleswig-Holstein: State Agency for Nature and Environment = Landesamt für Natur und Umwelt, Agency for Rural Areas = Amt für ländliche Räume).

Tab. 9-1: Hydromorphological parameters and indicators - Description of the five ecological status classes according to the WFD. The number of creeks and salt pans is derived from GIS-available data of the most recent biotope mapping (total number of the biotope types ‘near-natural saline small water body’ and ‘tidal creek/tideway’ (LANU 2003) of a site per km^2). For assessing the density of ditches, digital data of the local water boards is used. Information on dikes is obtained from digital data of the nature conservation and coastal defence authorities (in Schleswig-Holstein: State Agency for Nature and Environment, Agency for Rural Areas).

Parameter	Flooding dynamics	Intensity of drainage	Restriction of flooding
Indicator Status	Number of creeks and salt pans (no/km^2)	Density of ditches (km/km^2)	Dikes
high	Very many, > 10 /km^2	No ditches	No dikes
good	Many, 7 < to ≤ 10 /km^2	Only few old, not maintained ditches or ditches with impoundments, ≤ 1 km/km^2	Dike removed
moderate	Existing, 4 < to ≤ 7 /km^2	Only few maintained ditches, ≤ 1 km/km^2	Dikes/dams with tubes (no regulation of water in-/outflow possible), dike with breach
poor	Few, 1 < to ≤ 4 /km^2	Moderate length of ditch system, 1 < to ≤ 3 km/km^2	Dike with sluice
bad	Very few to none, ≤ 1 /km^2	Dense ditch system, 3 km/km^2	Dike with pumping station

9.5 Vegetation parameters

9.5.1 Normative definitions of the WFD for angiosperms

The WFD gives the following normative definitions for the ecological status of the quality element angiosperms (WFD Annex V, table 1.2.4):

High status: *All disturbance-sensitive angiosperm taxa associated with undisturbed conditions are present. The level of angiosperm abundance is consistent with undisturbed conditions.*

Good status: *Most disturbance-sensitive angiosperm taxa associated with undisturbed conditions are present. The level of angiosperm abundance shows slight signs of disturbance.*

Moderate status: *A moderate number of the disturbance-sensitive angiosperm taxa associated with undisturbed conditions are absent. Angiosperm abundance is moderately disturbed and may be such as to result in an undesirable disturbance to the balance of organisms present in the water body.*

Based on the definition of ‘disturbances’ given above, ‘disturbance sensitive taxa’ are defined here as all characteristic plant species adapted to natural flooding and natural (locally varying) levels of salinity of flooding water and soil (halophytes).

9.5.2 Quantity: Coastal marsh area

„Abundance of angiosperms’, in this case coastal marsh vegetation, is dependent on the area of this habitat type. Therefore, areal extent is a basic parameter in all existing classification methods for salt or coastal marshes, and those being developed at present (Brys et al. 2005, Dijkema et al. 2005, Arens 2006, Adolph et al. 2007, Best et al. 2007, Stock for German North Sea coast, pers. comm.). The classification methods differ mainly in the way the value for the reference area is derived: either by predictive modelling or from historical data, and if the latter, the historical reference time differs.

We decided not to use a historical reference, because

- for times with ‘no anthropogenic alteration’ (of hydromorphology), no adequate data or maps are existing
- any reference time based on data availability would be arbitrarily chosen
- such an approach would be too static: coastal dynamics and formation of new coastal marshes since a historical reference point would be ignored.

Instead, we developed a simple way of predictive modelling of the ‘**potential coastal marsh area**’. The most dramatic anthropogenic alteration of Baltic coastal marshes is the loss of area by diking and drainage. Therefore, the reference area is the area that would be covered by coastal marshes if today all these anthropogenic alterations of flooding dynamics were removed (‘potential natural status’). The potential coastal marsh area includes coastal areas

- that would be regularly flooded if no dikes and other coastal defence structures existed (‘potential flooding area’) and
- that are suitable for coastal marsh communities, i.e. the sites have to be sheltered (‘potential coastal marsh area’).

At the German Baltic Sea coast, the mean high water is about 1.2 m at the outer coast (long-term mean for Schleimünde and Marienleuchte, Warnemünde, Sassnitz, Koserow) and occurs at 1.3 days/year on average (KfKI 2003). The elevation limit of halophyte vegetation was found at an average elevation of 0.7 m by Krisch (1990), but at 1 m by Paulson & Raskin (1998) and Seiberling et al (2004).

Therefore, we delimited the 'potential flooding area' for Schleswig-Holstein as being at 1 m above sea level, being flooded several times a year and characterised by halophytic vegetation. This area was generated using GIS. With the elevation data of the digital terrain model (scale 1:25,000), 3D-models were constructed. By use of these models, 1-m-elevation lines were generated. From these 'potential flooding areas', areas of lagoons and small water bodies as well as beaches and dunes – all unsuitable for coastal marsh formation – were subtracted to obtain the 'potential coastal marsh area'.

The '**present coastal marsh area'** was calculated for each water body from the digital results of the most recent biotope mapping for the Habitats Directive (habitat types: salt grasslands, salt and brackish reed beds, brackish tall forbs, other types of brackish grasslands, LANU 2003) and the HELCOM-mapping of coastal biotopes.

The metric for the classification is the ratio of present coastal marsh area to potential coastal marsh area for each water body. The class boundaries are preliminarily set as follows: High – 80-100%, good – 60-79%, moderate – 40-59%, poor – 20-39%, bad – 0-19%.

9.5.3 Quality: Zonation

Another parameter in all existing WFD-classification methods for salt marshes is the zonation of the vegetation (Brys et al. 2005, Dijkema et al. 2005, Stiller 2005a, Arens 2006, Adolph et al. 2007, Best et al. 2007, Stock pers. comm.). The background of the Dutch classification (Dijkema et al. 2005) is the model of a dynamic equilibrium of salt marsh zones under reference conditions. Pioneer, lower, middle and higher salt marsh zones are seen as a successional series, being built up by sedimentation, then destroyed by erosion and followed by new accretion.

The concept of cyclic processes and a dynamic equilibrium cannot be easily transferred to the Baltic Sea coast. Coastal peatlands cannot grow above certain heights (except under conditions of sea level rise), and hence are not subject to (cyclic) succession. Beach ridges are created by active coastal dynamics of abrasion and sedimentation, but abrasion takes place at nearby cliffs. Thus, a dynamic equilibrium exists not within a system of younger and older salt marsh stages (= vegetation zones), but within a larger-scale coastal landscape system.

Still, zonation can be used as a characteristic feature and classification parameter for Baltic coastal marshes. The classification should be focused on the effects of anthropogenic alterations such as dikes in front of or behind the coastal marsh on the zonation. Since many factors (salinity, flooding frequency, moisture, local freshwater input, exposure, relief, substrate, grazing etc.) act together at the Baltic Sea coast, many species occur at differing elevations depending on local conditions. Thus species cannot generally be assigned to one elevational zone and lower and upper salt marsh cannot in all cases be clearly delimited. The delimitation of elevational zones is further complicated by the small vertical range of the zonation (Dijkema 1990).

For these reasons, only two vegetation zones are distinguished here: The '**pioneer zone**' is characterised by active dynamics (by flooding, erosion, ice scouring, trampling etc.) and therefore colonized by pioneer species, often with a high percentage of open soil. These areas comprise, if existing,

- a zone around the mean water line, in transition from mud flat to coastal marsh, or
- areas strongly affected by flood water and other soil disturbances (such as trampling). They are often low-lying and salt accumulating areas as creeks, depressions, salt pans or their margins.

All higher elevations with halophyte vegetation are summarized as the '(**lower and upper) coastal marsh zone**'.

Coastal marshes that are not anthropogenically altered are characterized by gradual transitions to terrestrial habitats such as dunes, dry or fresh grassland types, fens, swamps, coastal heathlands and forests. By diking, many coastal marshes are reduced in their extent and cut off, so that upper salt marshes and natural transitions are missing. Therefore the existence or lack of such transitions is included in the classification.

Further, freshwater indicator species are also used since the occurrence of species like e. g. *Hippuris vulgaris* or *Ranunculus aquatilis* in the pioneer zone indicates that salinity is decreased by a dike that prevents flooding or reduces flooding frequency. However, these can be used as indicators only in sites with higher salinity of flooding water, i. e. west of the Darß sill (except for sites at the Inner Schlei or at oligohaline lagoons) and without natural structures that restrict flooding frequency (beach ridges etc.). At sites with low salinity, these species belong to the characteristic communities (Fukarek 1961).

Each site is classified by the lower value of the two criteria (zonation and freshwater indicators, see Tab. 9-2). The assessment is carried out for each site separately.

Tab. 9-2: Zonation of the vegetation – Description of the five ecological status classes according to the WFD to be assessed in the field. 'Pioneer zone' comprises a zone around the mean water line, in transition from mud flat to coastal marsh as well as other disturbed areas strongly affected by flooding water, trampling etc, as creeks, depressions and salt pans. All higher elevations with halophyte vegetation are summarized as the '(lower and upper) coastal marsh zone'.

Ecological status	Zonation[1]	Freshwater indicators[2] (e.g. *Hippuris vulgaris, Ranunculus aquatilis*)
high	Pioneer zone and coastal marsh zone developed completely consistent with relief. Gradual transition to terrestrial habitats.	No freshwater indicators in the pioneer zone
good	Pioneer zone and coastal marsh zone nearly developed completely consistent with relief, i.e. elevational gradient within the coastal marsh zone noticeable (but can also border on a dike)	No freshwater indicators in the pioneer zone
moderate	Pioneer zone and coastal marsh zone existing. No gradual transition to terrestrial habitats (e.g. upper part cut off by a dike).	Freshwater indicators in the pioneer zone
poor	Only one zone existing	Freshwater indicators in the pioneer zone (if pioneer zone existing)
bad	No zone existing	---

1: If sites are very small because of natural relief, the pioneer zone can be missing without negative assessment, especially at narrow margins along the coast line (< 10 m width)

2: Only for sites with higher salinity of flooding water (i.e. west of the Darß sill, not in the Inner Schlei or at oligohaline lagoons) and without natural structures that restrict flooding frequency (beach ridge etc.)^

9.5.4 Quality: Plant species composition

Above, halophytes have been defined as 'disturbance-sensitive taxa' in the context of the WFD. Reference conditions are described as 'all disturbance-sensitive angiosperm taxa associated with undisturbed conditions are present.' Since many ecological factors interact in determining which taxa could occur at a specific site without anthropogenic disturbances, it is not possible to prescribe a specific target species list for each individual site. This approach would also be too static and not allow for natural changes, and would be not practical with a high number of sites.

With our selective list of characteristic species (Tab. 9-3), we allow for the diversity of site conditions. To keep the classification method as simple as possible, we present one list for the whole German Baltic Sea coast, differentiating between salinity levels for some species only. Whether more differentiation is necessary must be determined through a field trial in the future.

Tab. 9-3: Characteristic species of coastal marshes of the German Baltic Sea to be used for assessing the species composition as part of the WFD-classification method. Our own selection, compiled after: Jeschke (1987), Dijkema (1990), Berg et al. (2004).

Pioneer zone (including creeks, salt pans, depressions)	**Lower and upper coastal marsh zone**	**Restriction**
Agrostis stolonifera agg.		low salinity[2]
Schoenoplectus tabernaemontani		low salinity[2]
Aster tripolium	*Armeria maritima*	
Atriplex prostrata agg.	*Aster tripolium*	
Bolboschoenus maritimus	*Bolboschoenus maritimus*	
Cotula coronopifolia	*Carex distans*	
Juncus maritimus	*Carex extensa*	
Phragmites australis	*Centaurium litorale*	
Puccinellia distans	*Centaurium pulchellum*	
Salicornia europaea	*Festuca rubra*	
Spergularia media	*Glaux maritima*	
Spergularia salina	*Juncus gerardii*	
Suaeda maritima	*Juncus maritimus*	
	Leontodon autumnalis	
	Lotus tenuis	
	Phragmites australis	
	Plantago maritima	
	Puccinellia maritima	
	Spergularia media	
	Trifolium fragiferum	
	Triglochin maritimum	
	Artemisia maritima	only western part[1]
	Limonium vulgare	only western part[1]
	Agrostis stolonifera agg.	low salinity[2]
	Blysmus rufus	low salinity[2]
	Eleocharis uniglumis	low salinity[2]
	Elymus repens	low salinity[2]
	Hordeum secalinum	low salinity[2]
	Oenanthe lachenalii	low salinity[2]
	Triglochin palustre	low salinity[2]

1: The species *Limonium vulgare* and *Artemisia maritima* are only characteristic in the western part (up to the Wismar bight) and occur sporadically to the western part of Rügen.

2: These species are characteristic for coastal marshes of low salinity, i.e. east of the Darß sill and the inner coastal waters of Mecklenburg-Vorpommern, in the western part at lagoons and inner coastal waters (e.g. inner Schlei) or at sites where flooding dynamics is restricted e.g. by a beach ridge.

Tab. 9-4: Species composition – Description of ecological status classes (characteristic species of coastal marshes see Tab. 9-3). The frequency of species has to be assessed in the field during 'structured walks' using the 'DAFOR scale' (Kent & Coker 1992, JNCC 2004, see Tab. 9-5).

Ecological status	**Pioneer zone** [1] (incl. Salt marsh creeks, salt pans, depressions)	**Coastal marsh zone**	**Additional metric cover** [2]
high	At least 1 species abundant, 2 other frequent, 1 other rare	At least 2 species abundant, 3 other frequent, 2 other occasional	Species together sum up to at least 75% of cover
good	At least 1 species abundant, 2 other frequent	At least 2 species abundant, 3 other frequent	Species together sum up to 50-74% of cover
moderate	At least 1 species abundant, 1 other frequent	At least 1 species abundant, 2 other frequent	Species together sum up to 25-49% of cover
poor	At least 2 species frequent	At least 2 species frequent	Species together sum up to at least 10% of cover
bad	Less than 2 species frequent	Less than 2 species frequent	Species together sum up to 0-9% of cover

1: Especially in the pioneer zone the frequency may be (depending on the scale) dependent on the total cover which can be low – this has to be taken into account!

2: Whether an additional metric 'cover' is necessary has to be proven in a field trial – in general we aim at using as few and simple metrics as possible. Also the numbers are preliminary.

The frequency of species should be estimated with a scale and a procedure that allows a simple, quick overview of large areas in the field and results in broad, but reproducible estimates that are independent of the person in charge. Based on the method described in the 'Common Standards Monitoring Guidelines for Salt marsh Habitats'(JNCC 2004) vegetation composition (presence of species + dominance > 50%) should be recorded on at least 20 stops at 1 m²-plots during 'structured walks' across the site. To avoid subjectivity when selecting stops, the route and stops should be selected in advance on a map or aerial photo. With these data, the frequency of the species can be estimated using the following scale (Tab. 9-5).

Tab. 9-5: Frequency classes 'DAFOR scale' (Kent & Coker 1992, JNCC, 2004)

Dominant	Species appears at most (>60%) stops and it covers more than 50% of each sampling unit
Abundant	Species occurs regularly throughout a stand, at most (>60%) stops and its cover is less than 50% of each sampling unit
Frequent	Species recorded from 41-60% of stops
Occasional	Species recorded from 21-40% of stops
Rare	Species recorded up to 1-20% of stops

9.6 Water bodies for which coastal marshes should be considered in the WFD-classification

Coastal marshes should be included in the WFD-classification only if their potential impact is relevant to the quality of the coastal water body. This depends *inter alia* on the ratio of water area to coastal marsh area. Hence, we propose to assess the ecological status of coastal marshes for all water bodies in Schleswig-Holstein that are not heavily modified and in which the potential coastal marsh area (see above) comprises

- at least 10% of the total area of the water body (total area = water area + potential coastal marsh area) or
- at least 250 ha.

These include eleven water bodies: all three water bodies of the Schlei fjord, three water bodies around Fehmarn island (Fehmarn Rund, Fehmarn Belt, Orther Bucht), the coasts of Ostholstein

(Putlos, Grömitz, Neustädter Bucht) and the Probstei. Following this procedure, 11,027 of 12,085 ha of potential coastal marsh area (91.2%) in Schleswig-Holstein would be integrated into the WFD-classification of the coastal waters.

9.7 Combining parameters to an overall assessment

When strictly interpreting the formal requirements of the WFD, hydromorphology of coastal marshes would account for a part of the hydromorphological quality element ('structure and condition of the intertidal zone'), while the coastal marsh vegetation would be summarized with seagrasses and macroalgae in the quality element 'macroalgae and angiosperms'. The hydromorphological quality element would only 'support' the biological quality elements, i.e. would only be relevant for high status (European Commission 2000, CIS REFCOND 2003). Here we will refrain from this very formal interpretation to allow for a more integrative ecological understanding: because hydromorphology and vegetation of coastal marshes are closely linked and together indicate the same pressures on coastal waters, we recommend summarising both to an integrative classification. This would result in a coastal marsh classification indicating the pressure on and status of this zone of the coastal water body.

Two components are classified for each water body, hydromorphology and vegetation. The latter is composed of two aspects: quantity of vegetation (area) and quality of vegetation (zonation and species composition). In Fig. 9-1, an overview is given of how the single metrics are combined to an overall assessment.

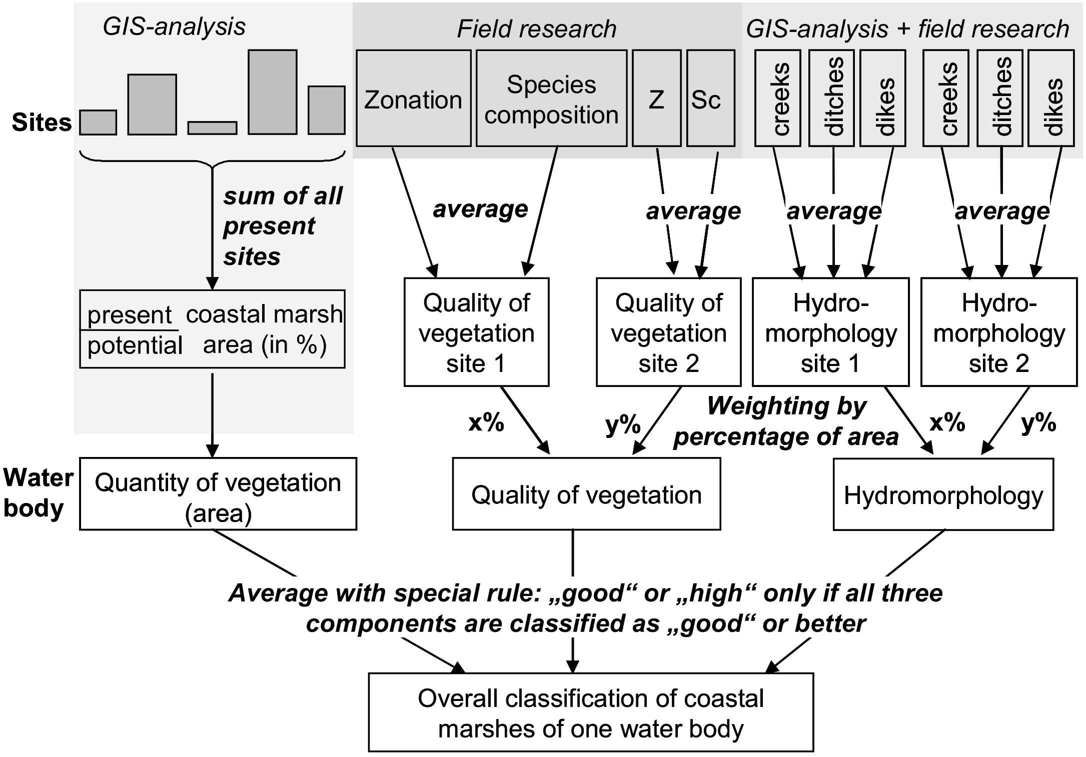


Fig. 9-1: Combination of all parameters to an overall assessment of the ecological status of coastal marshes per water body. x,y: Percentage of area of site 1 and 2 related to total area of present coastal marshes of a given water body.

The quantity of vegetation (area) is analysed using GIS for each water body as described above. Zonation and species composition are assessed in the field for each site separately, and the results are averaged to determine the 'quality of vegetation' of the respective site. The classifications of all sites in a water body are combined by weighting the individual results by the areal percentage of the sites to the ‘quality of vegetation’ of all coastal marshes of a given water body.

The same applies to the classification of hydromorphology: the values of all parameters assessed by GIS-analysis and/or in the field for a specific site are averaged to a classification of the hydromorphology of the site. In a second step, the classification of all sites in a water body are averaged weighted by the percentage of area to a classification of hydromorphology of all coastal marshes of a given water body.

In the last step, the three classifications of hydromorphology, quantity and quality of vegetation are combined to the overall classification of coastal marshes in a water body. This is done by calculating the mean of the three classifications with the restriction that the status ‘good’ can only be achieved if all three parameters are assessed as being of ‘good’ or ‘high’ status. This special rule makes sure that the coastal marshes of a water body cannot be at ‘good’ status if one of the three parameters is not ‘good’. On the other hand this special rule makes it still possible to improve the overall status, even in the case of the parameter ‘area’ being in ‘bad’ status, without creating large new coastal marshes. By reducing hydromorphological alterations in the present coastal marsh areas, the quality of vegetation as well as the hydromorphology could be improved, which could raise the overall classification from ‘bad’ to, in the best case, ‘moderate’. If in contrast the ‘one out – all out’ rule were applied for the three parameters, the water body would remain in the class ‘bad’ as long as the coastal marsh area was not enlarged to at least 60% of the potential area. The present coastal marsh area must not be reduced in any case.

9.8 Monitoring

In contrast to the Wadden Sea area, no consistent monitoring data set exists so far on the status of coastal marshes at the Baltic Sea. Thus, an initial area-wide monitoring of all coastal marsh sites should be conducted to be used as a quantitative baseline for detecting future long-term changes (CIS Monitoring 2003). To limit the efforts of future monitoring cycles, a representative number of sites per water body should be sampled. Sites that are part of the Natura 2000 monitoring network should be included to use the data efficiently.

Since most coastal marshes are part of protected areas, they have to be included in the operational monitoring (WFD Annex V, 1.3.5). As a general rule of the WFD, the operational monitoring of angiosperms should be carried out at least every three years ‘unless greater intervals would be justified on the basis of technical knowledge and expert judgement.’ (WFD Annex V, 1.3.4). Coastal marshes largely consist of perennial plants, thus climatic between-year fluctuations are not very pronounced. Therefore, a greater monitoring interval of six years is considered to be sufficient. Only in cases where hydrodynamics have changed substantially should the monitoring be carried out more often, at least every three years. Generally, monitoring of vegetation should be carried out during the growing season between July and September.

All parameters proposed for the classification should be monitored. Some of the hydromorphological parameters (dikes, ditches) are classified according to GIS-based information. During a field trial or during the first monitoring cycle it should be determined whether these data are correct, up-to-date and detailed enough. For future monitoring cycles it should be sufficient to only check for changes.

9.9 Perspectives

Since the proposed classification method has been developed without any fieldwork, a field trial is needed as a feasibility test before applying it to the whole German Baltic coastline. After checking the results for plausibility, class boundaries and species lists may have to be modified. Coastal marshes of Schleswig-Holstein as well as Mecklenburg-Vorpommern should be included to make the method suitable for all varieties of coastal marshes along the German Baltic coast.

Further, 'Atlantic salt marshes' are listed in the Annex I of the EU-Habitats Directive as a habitat type of community importance (European Commission 1992). Thus, their status also has to be monitored according to the Habitats Directive. It should be examined how the classification of 'ecological status' (WFD) and of 'favourable conservation status' (Habitats Directive) could be combined and particularly how the monitoring procedure can be harmonized to use synergies in the best and most efficient way. This implies selecting monitoring sites, harmonizing monitoring intervals and timing, and developing common detailed monitoring methods.

To improve the knowledge on the relevance of coastal marshes for coastal water quality, studies on the nutrient balance of intact and drained coastal peatlands should be carried out. Further, the nutrient balance of grazed and ungrazed coastal marshes should be analysed to assess the impact of management on the capacity for nutrient retention.

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The only changes were made in formulating the research questions. This chapter is the summary of a project report to the State Agency for Nature and Environment Schleswig-Holstein (Landesamt für Natur und Umwelt Schleswig-Holstein) in 2007 (*Wanner, A. & H. Rudolphi (2007): Salzrasen und -röhrichte an der Ostsee in der Bewertung von Küstengewässern nach der Wasserrahmenrichtlinie (WRRL): Prüfung der Tauglichkeit und Vorschlag für ein Bewertungsverfahren. Abschlussbericht an das Landesamt für Natur und Umwelt Schleswig-Holstein, 99 S.*).

The first author contributed to this article by (i) justifying the integration of salt grasslands to the WFD-classification, (ii) developing the overall classification method, (ii) selecting the vegetation parameters, (iv) developing the proposal for combining the parameters and the monitoring scheme and (v) formulating the article. The overall contribution of the first author to this article was approx. 90%. The second author developed the hydromorphological classification parameters (described in 9.4) and carried out GIS-analyses of existing data. The third author supervised the project, contributed to fruitful discussions and to formulation of the final version of the article.

10 Conclusions for nature conservation management

In the following, conclusions for nature conservation management are drawn from the results of this thesis (primarily parts 1 and 2). The impact of abandonment on the seed bank and vegetation changes after restorative grazing were only studied in Estonia (part 2). Nevertheless, these findings may also be valuable for nature conservation and restoration of salt grasslands in other parts of the Baltic Sea region – always taking the described regional differences into account. Therefore, the conclusions from a nature conservation point of view of the study in Estonia (part 2) from a nature conservation point of view are integrated into this final chapter (10.2.3, 10.2.4). The potential impact of management on ecosystem functions, a crucial issue for classifying the ecological status of coastal marshes for the Water Framework Directive (part 3), is also addressed (10.4).

10.1 Two general concepts for nature conservation in coastal ecosystems

Two alternative concepts can be distinguished in nature conservation (and restoration): the ‘wilderness’ concept of letting ‘nature do the job’ and avoiding any human interference, versus the ‘biodiversity’ concept of a management aiming at ‘target communities’ including a high species-richness by maintaining or creating a high variation in abiotic conditions (Kiehl & Stock 1994, Bakker et al. 1997).

For the Wadden Sea salt marshes of the North Sea coast for example, both concepts are relevant: According to the criteria of the International Union for the Conservation of Nature (IUCN), National Parks (IUCN-category II protected areas) are ‘large natural or near natural areas set aside to protect large-scale ecological processes’ (along with the complement of species and ecosystems characteristic of the area, Dudley 2008) and National Parks mainly follow the ‘wilderness’ concept. Especially in the National Parks of the German Wadden Sea coast, wilderness is the overriding concept for conservation of salt marshes (Kiehl & Stock 1994, Stock et al. 1999). In contrast, in the Netherlands (and in Denmark) the ‘biodiversity’ concept is followed and most of the area is managed (*inter alia* by different grazing regimes) according to precise nature conservation targets (Bakker et al. 1997).

However, the European Habitats (European Commission 1992) and Birds Directives (European Commission 1979) rather follow the ‘biodiversity’ concept, and the ‘favourable conservation status’ is measured relative to a specific (historical) reference status. The European Habitats Directive includes a large number of ‘semi-natural’ habitats which have only developed in the cultural landscape and depend on either (close-to) traditional land use or nature conservation management which tries to mimic at least the essential components of the traditional land use.

Since most National Parks and protected areas are also designated as ‘Sites of Community Importance’ (according to the Habitats Directive) and/or as ‘Special Protected Areas’ (according to the Birds Directive), a conflict between both concepts and target systems may arise, which is also highly relevant for the conservation and management of salt marshes and salt grasslands (e.g. Hälterlein 2002, Lutz et al. 2003). Berger (2003) and Oppel & Stock (2004) discussed controversially whether it is acceptable to let a species go extinct (locally) in a National Park.

Conflicts between the ‘wilderness concept’ of National Parks and the targeted conservation of species and habitats also arise in National Parks of the Baltic Sea. One example is the protection of coastal breeding birds against predation: In the German National Park ‘Bodden Landscape of Vorpommern’, it is discussed whether hunting as a human interference should be stopped or be allowed to secure the achievement of 'favourable conservation status' of Bird species according to the Birds Directive (Stodian 2004). It is also relevant for the question of management of salt grasslands versus abandonment and succession to brackish reed beds (Dücker 1996). The conflict between the conservation of the semi-natural habitat type Baltic salt grasslands and the 'natural' habitat type reed beds can also not be solved by the Nature Conservation Laws of the federal states Schleswig-Holstein and Mecklenburg-Vorpommern, which categorise both as 'protected habitat types' (LNatG M-V 2002, LNatSchG S-H 2007).

Baltic salt grasslands of the Southern Baltic coast are in most cases 'secondary' ecosystems that developed from natural brackish reed beds after the start of livestock grazing (Jeschke 1987, see introduction). In Estonia, salt grasslands are often regarded as 'primary' (e.g. Rebassoo 1975, Rannap et al. 2004) and moderate grazing as 'natural' (Sammul et al. 2008), in the sense that the land surface newly emerging from the sea due to the isostatic land rise has never been anything else but salt grassland – and has been grazed from the beginning. Nevertheless, the long-term persistence of these semi-natural ecosystems is dependent on any kind of disturbance preventing the dominance of reed. Apart from livestock grazing, this can be wave-action, erosion, ice scouring or grazing and grubbing of other (wild) animals (as discussed above, 5.4.5).

In the Western Baltic, there is a transition towards conditions closer to those of the North Sea coast, where high salinity prevents the dominance of *Phragmites australis*, allowing the persistence of salt grasslands also without livestock grazing at least for several years up to decades. The probability that salt grasslands persist without management increases with increasing salinity further up north, and also depends on the soil type of salt grassland (see 5.4.5). Thus, it becomes clear that – at least partly – different management strategies are appropriate along the different sections of the salinity gradient.

Both concepts of nature conservation can compete and result in conflicts. Even within the biodiversity approach, many different species groups with different ecological needs might require different management strategies. Hence, it is essential to agree on the general concept and on specific nature conservation targets before it is possible to recommend an 'optimal' management of Baltic salt grasslands.

Before drafting the conclusions from this study's findings on the impact of successional processes on the vegetation of salt grasslands along these sections of the gradient, the impact of management and succession on the 'botanical nature conservation targets', and further on other common target species groups as well as on other protected commodities of nature conservation and environmental protection will shortly be highlighted.

10.2 Consequences of management on the vegetation

So far, the impact of management on different aspects of biodiversity of salt grassland vegetation has been discussed (see 5.4, 5.5). However, not only the diversity of the vegetation is relevant as a 'botanical nature conservation target', but also the 'quality' of species. Two 'quality' aspects of the vegetation were studied in this thesis (see 4.7).

10.2.1 'Characteristic' species

Characteristic species of '*Salicornia* and other annuals colonising mud and sand' (type 1310), 'Atlantic Salt Meadows' (Type 1330) and 'Boreal Baltic Coastal Meadows' (type 1630) according to the Habitats Directive decreased in late successional sites. The decrease was more pronounced in cover, but was also visible in plant species' frequencies. The scale of observation also played a role, since differences between management classes were smaller on larger scales.

Also Bakker et al. (2003a) found that even if species density (species number per area) decreases with succession, none of the typical salt marsh species occurs exclusively on grazed sites. Thus, it is unlikely that any plant species would go extinct if large (or all) areas of salt grasslands were abandoned. There would always be (small) sites, where primary succession of salt grasslands would take place and provide habitat for these early successional species (as long as natural processes of sedimentation and erosion are possible, see Dücker 1996 for Baltic salt grasslands. Also Tüxen suggested that the salt grassland communities Puccinellietum maritimae, Juncetum gerardii, and Artemisietum maritimae should maintain their status as part of the 'potential natural vegetation' (which would appear after a sudden cessation of any human impact, Ellenberg 1996). He believes that these communities always existed in small patches or narrow zones due to disturbances by coastal dynamics and 'natural' grazing of wild herbivores causing quick successions (R. Tüxen in the discussion of Schmeisky 1977). Vestergaard (1998) stressed as well, that most species today characterising grazed salt grasslands were present already before human impact on Baltic coastal vegetation started, due to erosion, primary succession and herbivory by wild animals.

There were also regional differences in the relative percentage and cover of characteristic species: they had a lower percentage and cover in Estonia. This difference increased with increasing spatial scale: it was not visible in relative species number on a 1 m² scale. Regarding cover, it was only visible on the 625 m² scale. The scale effect was stronger in Estonia, illustrating that the higher environmental heterogeneity allowed more 'non-characteristic' species to coexist in particular at larger scales.

10.2.2 Red List species

The analysis of Red List species in Schleswig-Holstein and Mecklenburg-Vorpommern showed that rare and endangered species occurred not only in grazed, but also in early and late successional sites. Some Red List species decreased and disappeared sooner (e.g. *Trifolium fragiferum, Sagina maritima* in early successional sites) or later (e.g. *Puccinellia maritima, Salicornia europaea, Suaeda maritima, Centaurium pulchellum* in late successional sites) in the course of succession, whereas others newly established in early (e.g. *Oenanthe lachenalii, Althaea officinalis*, *Ophioglossum vulgatum, Odontites litoralis*) or late successional sites (e.g. *Apium graveolens, Inula britannica*). Some species showed a maximum frequency in early successional sites. Thus, they were favoured by the cessation of grazing in the first phase, but decreased again after reed became dominant (e.g. *Limonium vulgare, Artemisia maritima, Aster tripolium, Armeria maritima*). This species turn-over was connected to an overlap of 'early successional' and 'late successional' Red List species in Schleswig-Holstein, which created a peak of Red List species in early successional sites.

An initial increase in species richness, called 'charming phase of succession' by Ekstam & Forshed (1992), was also described by Schreiber & Schiefer (1985) for the succession of grasslands of the Black Forest and by Rosén (1985) for alvar grasslands on Öland (Sweden). This charming phase is usually followed by a decline in species richness (Jensen & Dierßen 1999).

The overall lower number of Red List species in Mecklenburg-Vorpommern compared to Schleswig-Holstein results from several species missing in the Mecklenburg-Vorpommern dataset: species with a predominantly western distribution (such as *Limonium vulgare, Cochlearia anglica*) and/or species characteristic for salt grasslands of higher salinities, which become less frequent with decreasing salinities (such as *Salicornia europaea, Suaeda maritima).* Some species were recorded by chance in single sites in Schleswig-Holstein, but not in those of Mecklenburg-Vorpommern (such as *Althaea officinalis, Plantago coronopus, Apium graveolens).*

Some of the occurring rare and endangered plant species are characteristic for grazed salt grasslands, while others are characteristic for rather open brackish reed beds (where reed has not reached maximum dominance yet, or which are kept open by occasional grazing or other disturbances), such as *Oenanthe lachenalii* (see Krisch 1992). The relative number of Red List species, however, decreases when reed becomes strongly dominant. Nevertheless, Vestergaard (2002b) stressed that also the terrestrial reed bed (= overgrown salt grassland) in south-eastern Denmark is the biotope for several red- and yellow listed species.

These results show that the same management regime may not favour all rare and endangered plant species. Thus, the nature conservation target ‘protection of rare and endangered plant species’ can only be fulfilled if a variety of management regimes or at least grazing intensities is applied on a regional scale.

Rarity and degree of threat are widely accepted criteria for setting nature conservation targets in the sense of the ‘biodiversity concept’ and more traditional approaches of species’ protection (Usher & Erz 1986). However, it is difficult to compare absolute or relative numbers of Red List species between studies using different red lists – this is why not all four regions were compared with respect to the occurrence of Red List species. The national Red Lists of Denmark (Stoltze & Pihl 1998) and Estonia (Nature Conservation Committee 1998) included only very few of the species of the presented dataset, which made a statistical analysis impossible. A comparison between these national lists and the Red List for German Baltic coastal areas would have also ‘compared apples and oranges’, since obviously the criteria when a species is rare (or endangered) were set after different criteria.

For Schleswig-Holstein and Mecklenburg-Vorpommern, it was decided to use the ‘Red List of vascular plants of the German Baltic coast’ (Berg et al. 1996) for the following reasons: The Red List of Schleswig-Holstein (Mierwald & Romahn 2006) has been updated more recently, but it classifies salt grassland species for the whole federal state. Since the Wadden Sea salt marshes predominate in area, classifications of rarity and the degree of threat rather apply to the situation there than to the Baltic coast, where remnant salt grasslands are much smaller and more fragmented, resulting in a possibly higher threat. Furthermore, some halophyte species are rare at the Schleswig-Holstein Baltic coast because of the lower salinity, but not at the North Sea coast. In addition, at least two regions (Schleswig-Holstein and Mecklenburg-Vorpommern) could be compared by using the list published by Berg et al. (1996).

10.2.3 Impact of restorative grazing of Estonian salt grasslands

As shown in part 2 (7.2, 8.2), restoration of Estonian salt grasslands from reed-dominated ‘late’ successional stages (after 10-25 years of abandonment) by the reintroduction of cattle grazing is very promising. Species (groups) that declined during progressive secondary succession increase again. Most species that increased in the abandonment phase decreased again. However, dominant late successional species such as *Phragmites australis* and *Elymus repens* still remain frequent (see 7.2.3). Although vegetation changes are reversed, 2-4 years are obviously not enough to restore the vegetation of salt grasslands. This is confirmed by Kaljuste (2004a, b) who estimates that restoration takes as long as the preceded abandonment phase. Also Sammul et al. (2008) state that species composition and soil properties need more than five years to be restored. In Wadden Sea salt marshes, vegetation of abandoned salt marshes returned to the initial succession stage 5 to 10 years after the resumption of grazing (Bakker et al. 1997).

The presented results on the initial changes after introduction of restorative grazing suggest that restoration of Estonian salt grasslands should be possible also merely by grazing. Furthermore, personal observations in some of the study sites between 2004 and 2008 showed that reed has completely disappeared in belts of tens of metres. This is in contrast to the statement of Esselink et al. (2000, 2002) that the process of reed invasion in brackish marshes and grasslands was practically irreversible by grazing alone, which is also resumed by Bakker & Piersma (2005).

However, Esselink (2000, 2002) refers to the situation of a nature reserve at the Dollard, where the grazing seasons starts relatively late (Esselink, pers. comm.). It was shown that the timing of grazing or mowing is essential for negatively affecting *Phragmites australis*: only in spring and early summer, when storage carbohydrates are mobilised from rhizomes and buds, reed could be reduced by grazing (Van Deursen & Drost 1990) or mowing (Güsewell 2003). Later, reed was no longer eaten by cattle or horses, and late mowing did not affect reed negatively, since (most) storage carbohydrates had already been transferred to belowground storage organs (Van Deursen & Drost 1990, Güsewell 2003).

Van Deursen & Drost (1990) showed in a Dutch nature reserve under (partly) slightly brackish conditions that re-introduction of grazing management had broken the reed dominance within four years, and that reed beds in some parts had been replaced by *Agrostis stolonifera*. Furthermore, lateral spread of reed was stopped, and large parts of the original reed bed stands were cut back to lower height (of 30-80 cm). Anyhow, grazing was then in equilibrium with the production of reed: grazing could prevent further spread, but could not further reduce the vitality of reed. Due to the late start of the grazing season in early June, reed was eaten by cattle only during a period of five weeks. The authors further suggest that horses may have a heavier impact on reed than cattle, since they caused a stronger reduction of leaf area in July and August.

Jeschke (1983) stated that, if no other means of utilisation is possible, reed stands can be removed by burning in late winter followed by grazing of young cattle in spring, as soon as the reed resprouts. With this combination of measures, the reed vanishes already after two years and salt grassland species, first of all *Agrostis stolonifera*, begin to establish. Also Lundberg (1996) stresses for brackish salt grasslands in southern Norway that reintroduction of cattle grazing can be an effective management tool for the restoration of species-rich salt marsh vegetation from brackish reed beds.

It is essential to maintain a moderate to high grazing pressure for a longer period to further repress late successional dominant species. A combination with mowing, crushing or burning of reed as presented by Rannap et al. (2004) and Huolman & Priha (2007) may accelerate the process, especially if it is difficult to reach the grazing intensity necessary to open up the dense reed in the beginning. However, the effect of such technical measures will soon be invisible again if grazing pressure is not sufficient afterwards.

10.2.4 Potential of the seed bank for restoration

The seed banks of the studied Estonian salt grasslands have a high potential for the restoration of characteristic vegetation, but will not necessarily enhance species richness. In contrast to other habitats, there is also no ‘risk’ in activating the seed bank, since there are no ‘weed’ or ‘problem’ species in the seed bank that could out-compete target species. Indications for an establishment from a persistent seed bank were found for some species (*Centaurium pulchellum, C. littorale*). At least for the studied sites, which were abandoned rather recently, seed limitation (be it from the seed bank or from seed dispersal) is not very likely. Thus, restorative grazing may activate the seed bank and contribute to the re-establishment of characteristic plant species, but is more crucial as a measure to decrease the dominance of the highly competitive, dominant species such as *Phragmites australis* (or *Elymus repens, Festuca arundinacea*, *Juniperus communis* etc.).

The relation of target versus non-target species in the seed bank is different if ‘restoration’ of salt grassland means de-embankment of former salt grasslands which have (nearly) completely lost typical salt grassland plant species decades beforehand. In such embanked salt grasslands or salt marshes, indeed only low seed densities of few halophyte species were found in the seed bank (Folkowski & Seiberling 2002, Wolters & Garbutt 2006). However, even then these few seeds may represent a valuable potential for restoration of some species (Folkowski & Seiberling 2002).

10.3 Consequences of management on some animal groups

The described changes during vegetation succession do not affect only the vegetation, but also have consequences for other species groups which rely on a certain vegetation structure for their breeding, feeding or roosting habitat or on the presence of certain (flowering or fruiting) plant species as a food source. One of the most important motivations for nature conservation or restoration in coastal areas is often the habitat value of salt grasslands for birds.

10.3.1 Birds

Herbivorous birds such as geese and ducks favour a low sward dominated by grasses such as *Puccinellia maritima* or *Festuca rubra* which is created by rather high levels of livestock grazing pressure (Adam 1990, Doody 2008, see 5.4.5).

Other nesting or staging waders and meadow birds have somewhat different habitat demands regarding vegetation structure. In general, they prefer open grasslands of either short vegetation (e.g. oystercatcher, *Haematopus ostralegus* or Baltic dunlin, *Calidris alpina schinzii*) or higher, more varied vegetation as shelter against predators such as redshanks (*Tringa totanus*, Norris et al. 1997, Doody 2008, Thorup 2008) or passerines (Doody 2008). According to Doody (2008), the decline of dunlins during the 20th century is clearly connected to changes in the management (primarily grazing regime) on salt marshes and inland wet meadows. Apart from factors related to the migration and wintering sites, inappropriate grazing (referring to grazing pressure and grazing too early during the breeding season) has also contributed to the decline of ruffs (*Philomachus pugnax)* at a local and regional level (Widemo 2007). The mentioned bird species Baltic dunlin, ruff and avocet (*Recurvirostra avocetta*) were selected as target species in the LIFE-project Baltcoast (2005-2011).

Apart from changes of the vegetation structure, abandonment also increases the food availability for bird species feeding on seeds or insects, and higher vegetation may provide shelter against predation. Additionally, livestock grazing and trampling also presents a risk of damage to nests (Hälterlein et al. 2003).

Bakker et al. (2003a, b) conclude that the taller vegetation structure after abandonment or a decrease of stocking rates has negative consequences for winter and spring staging geese, but positive effects on some breeding birds. Hälterlein (2002) and Hälterlein et al. (2003) summarise that abandonment in general has a positive impact on breeding bird diversity and density, even when the reduction of management may have contributed to a decrease for individual species (such as lapwing, *Vanellus vanellus*). They conclude that the 'wilderness' concept of the National Park is therefore compatible with the obligation for bird protection.

Ottvall & Smith (2006) summarise for Baltic salt grasslands on the Swedish island Öland that grazing management is an important tool to conserve the abundance of waders (represented in their study by redshank, oystercatcher, lapwing and ringed plover, *Charadrius hiaticula*). However, they also stress that the relationship between grazing intensity and breeding density is non-linear: In their study, cattle grazing had a positive effect creating suitable nest sites for different wader species. In contrast, Norris et al. (1998) found a negative relationship between grazing intensity and redshank densities, indicating that sheep grazed salt marsh vegetation too short to be suitable for redshank nesting. Thus a more varied vegetation structure seems more beneficial for most wader species.

Regarding management effects on bird communities, results from North Sea salt marshes are only comparable to the vegetation succession of grazed salt grasslands to 'early successional stages' (still dominated by salt grassland species). The further course of succession towards brackish reed beds characterises a more fundamental shift of a potential bird habitat from 'meadow' to 'reed bed'.

In a study of grazed and abandoned salt grasslands in Estonia, grazing promoted short grass and sedge communities and Waders and grassland associated passerine bird species. Abandonment led either to the development of reed communities providing habitat for reed birds, or – under drier site conditions – to the development of scrubs and associated scrub bird species. The bird species diversity was significantly lower in the reed communities than in salt grasslands (Phillips 2007). Associated with land use changes (see chapter 2), bird communities at the southern coast of Matsalu Bay have witnessed a pronounced shift in the last decades: while in 1957-1960, waders contributed with more than 60% to the total number of birds, their proportion declined to about 20% in 2001-2003, also gulls and ducks declined. Reed, bush and open landscape passerines strongly increased, 'winners' from the overgrowth of meadows were passerines like reed bunting (*Emberiza schoeniclus*), sedge warbler (*Acrocephalus schoenobaenus*) and whinchat (*Saxicola rubetra*, Kuresoo & Mägi 2004).

Also Esselink et al. (2000) stress that brackish reed beds have a high habitat value for reed breeding birds (such as bearded tit *Panurus biarmicus*, sedge warbler Savi's warbler *Locustella luscinoides*, included in the Dutch Red List), which should not be ignored. Pehrsson (1988) proposed a several-year long rotation between cattle-grazed and ungrazed sites as the best measure to promote bird species foraging on *Bolboschoenus maritimus* seeds such as mallard (*Anas platyrhynchos*) and teal (*Anas crecca*). Esselink et al. (2002) conclude that tall and short vegetation in coastal marshes represent different ornithological values, both with a high conservation value.

10.3.2 Amphibians

Also some amphibian species live in salt grasslands or coastal lagoons and have specific habitat requirements related to management. For instance, the endangered natterjack toad (*Bufo calamita)* requires warm, shallow, open pools (with a salinity of up to 4 psu, Bast & Dierking 1996) on upper salt grasslands with adjacent open, sun exposed terrestrial habitats with short vegetation or minimally vegetated ground mostly of sandy soil (Rannap 2004, Doody 2008). It looses its habitat to its competitors (*Bufo bufo, Rana temporaria, Rana arvalis*), if shallow ponds are grown over with dense vegetation after abandonment (Rannap 2004). In Estonia, the number of natterjack toad populations has decreased from 123 in the first half of the 20th century to 14 isolated populations (4 of which were in coastal meadows) in 2004 due to land use changes such as amelioration and fertilisation, but also abandonment (Rannap 2004, Rannap et al. 2007). The green toad (*Bufo viridis)* also breeds in fresh and brackish water (Bast & Dierking 1996). On coastal areas of the Baltic region, it occurs on open, grazed coastal meadows. It has witnessed a steady decline during the 20th century for the same reasons as the natterjack toad (Briggs 2004, LIFE Baltcoast 2009). Consequently, natterjack toad is one of the target species for e.g. the EU LIFE projects 'Boreal Baltic coastal Meadow Preservation in Estonia' (2001-2004) and of the LIFE-project Baltcoast (2005-2011, together with the green toad, *Bufo viridis*).

10.3.3 Invertebrates

It has also been shown that population densities, species richness and community diversity of invertebrates initially increased after abandonment of North Sea salt marshes (in the Leybucht), because (intensive) grazing reduces species living in or on upper parts of the vegetation or which are sensitive to trampling by cattle (Andresen et al. 1990). Phytophagous invertebrates in salt marshes and grasslands are highly specialised to specific host plants or even plant parts, and are therefore even more sensitive to grazing of salt marshes than their host plants (Meyer & Reinke 1998a). A high number of phytophagous insects lives e.g. on *Limonium* ssp. (Doody 2008). Fully developed *Aster tripolium* provides habitat and food for 22 insect species, whereas under intensive grazing only two species occur (Heydemann 1983/84). This is why a higher diversity and density of phytophagous insects was found in ungrazed and moderately grazed salt marshes than in intensively grazed salt marshes (Meyer & Reinke 1998b). Livestock grazing changes the structure of the whole food web: The loss of specialised phytophagous insects is juxtaposed to a shift to grass feeding herbivores and an increase in detritophagous and microphytophagous invertebrates (feeding on algae of open soils, Reinke & Meyer 1999). Trampling by grazing livestock also negatively affected soil dwelling invertebrates (such as the detritophagous amphipod *Orchestia gammarellus,* Reinke & Meyer 1999, Kockel et al. 2004; or the larvae of the herbivorous beetle *Phyllobius vespertinus,* Reinke & Meyer 1999).

However, abandonment may also have negative consequences on invertebrate diversity in the long run: since high rates of sedimentation in abandoned salt marshes promote the immigration of species from the higher salt marsh and adjacent grasslands, halotopophilous species and communities may eventually disappear (Andresen et al. 1990). In western France, halophilic spider species decreased in abundances and densities after the invasion of *Elymus athericus* (Pétillon et al. 2005).

At the Baltic Sea coast, vegetation changes even more profoundly after abandonment if brackish reed beds develop (see 4.3 to 4.7). Therefore, the reaction of invertebrates may also differ from the described patterns at the North Sea coast. Mathiak & Müller-Motzfeld (2004) described that different halobiont, halophilic and halotolerant ground beetle species characterised brackish reed beds, pioneer communities and grazed salt grasslands in Mecklenburg-Vorpommern, while Red List species (excluding the halophilic or halotolerant species) generally reacted negatively to grazing. Species richness, number of individuals and total biomass of ground beetles strongly decreased with increasing management intensity (grazing and/or mowing, Kockel et al. 2004). The abundance of amphipods was much lower in grazed than in abandoned or natural salt grasslands (Kockel et al. 2004). At the Schleswig-Holstein Baltic Sea coast (Sehlendorfer Binnensee), more individuals of more species of ground beetles were found in ungrazed brackish reed beds and tall forb communities (*Althaea officinalis*) than in grazed salt grasslands (Heller et al. 2000). Spiders were less numerous, but more species rich in ungrazed conditions, and fungus gnats (Sciarids) occurred with only one species under grazed, but several species and more individuals under ungrazed conditions. The reaction to grazing of some spider species was opposite to their reaction at the North Sea coast, indicating that results from the North Sea may not be easily transferred to the Baltic (Heller et al. 2000).

As these examples may have already illustrated, the diversity of different species groups is often not correlated. For example, Pärt & Söderström (1998) studied whether 'botanically valuable' semi-natural grasslands in Sweden also harboured a high diversity of birds, but could hardly detect any correlations. In a further study on the correlation of species richness of six taxa groups (plants, birds, butterflies, bumblebees, ground beetles and dung beetle) some of these groups were positively, others negatively correlated, so that Vessby et al. (2002) conclude that one species group cannot necessarily indicate 'biodiversity' as a whole. Consequently, different species groups cannot always be protected with the same management in a specific area.

10.4 Consequences of management on ecosystem functions

Salt grasslands are not only important as habitats for numerous plant and animal species, they do also support ecosystem functions related to water balance, sedimentation and erosion processes and biogeochemical cycles. Particulate matter and nutrients can be deposited in salt grasslands by sedimentation and peat formation, and various transformation processes take place in the soil and in flooding water. Thus, salt grasslands and salt marshes can play an important role in the nitrogen-, phosphorous- and possibly silica balance of coastal waters (Mitsch & Gosselink 2000, Struyf et al. 2006).

Peat formation and sedimentation are also important for the function of salt grasslands for coastal protection due to their contribution to the attenuation of wave height and dissipation of wave energy, as shown for macro-tidal salt marshes (Möller et al. 1999). Wave height attenuation was highest in September to November, when salt marsh vegetation was fully developed, indicating that vegetation structure plays an important role in the dissipation of wave energy (Möller & Spencer 2002). Thus, management may also affect the coastal protection function of salt marshes and salt grasslands. Possible differences in the effect of Baltic salt grasslands and brackish reed beds with their different vegetation structures on wave attenuation are currently being studied by the University of Greifswald.

In addition, salt marshes and salt grasslands have an important function for nutrient retention. For the Patuxent River at the Chesapeake Bay, Merrill & Cornwell (2000) calculated that local fresh and oligohaline marshes may retain 35% of the nitrogen and 81% of the phosphorous input from the catchment area. Likewise, salt grasslands as well as brackish reed beds at the Baltic Sea function as natural buffer systems for nutrients (Boedecker & Knapp 1996), as well as beach ridges and dune systems on sandy soils (CIS Wetlands 2003). In particular coastal peatlands at the Southern Baltic coast are in general seen as nutrient sinks in the 'intact' or natural state of on-going peat formation (Jeschke 1995). By diking and drainage, they are transformed to a nutrient source as peat becomes aerated and decomposed. Therefore, diked and drained former coastal peatlands represent a considerable source of nutrient load in particular to semi-enclosed lagoon systems such as the 'Bodden' waters in Mecklenburg-Vorpommern (Jeschke 1995, LFG MV 2002). De-embankment of polders is therefore described as a possible measure to decrease the nutrient input from diffuse sources and to reach the goals of the Water Framework Directive (Quast et al. 2002), in particular if peat growth of coastal peatlands can be reactivated (Folkowski & Seiberling 2002). Shepherd et al. (2007) estimated that nitrogen (N) and phosphorous (P) fluxes from the Humber estuary into the North Sea could be reduced by more than 50% (for N) and 25% (for P), if all intertidal areas (tidal flats and salt marshes) of the Humber were restored (after a loss of more than 90% due to land reclamation during the last 300 years). The ecological function of nutrient retention of Baltic coastal marshes is the reason why this study suggests considering them as part of the coastal or transitional water bodies, and including them in the classification of 'ecological status' of coastal waters (part 3).

However, it is still largely unknown whether the function of nutrient retention and peat growth is enhanced or reduced by different management in the sense of grazing regimes, and whether or how salt grasslands or brackish reed beds differ in their nutrient retention efficiency. Nutrients are retained by sedimentation as well as by peat formation. Vegetation structure has been shown to affect sedimentation rates, since sedimentation depends on the flow velocity, which is slowed down by the vegetation (Leonard & Croft 2006). Therefore, sedimentation rates in intensively grazed salt marshes are usually lower than in moderately or ungrazed salt marshes (Andresen et al. 1990, Kiehl 1997, Stock et al. 1997, Bakker et al. 1997, Esselink et al. 1998, Neuhaus et al. 1999).

For the Southern Baltic coast, Jeschke (1987) emphasises that peat growth above the mean water line is possible only under the influence of trampling of livestock, and that abandonment – connected with the overgrowth and dysfunction of the natural drainage system – finally leads to the degeneration of salt grassland and the decomposition of organic matter (Jeschke 1983). Kockel et al. (2004) discussed that enhanced peat growth at grazed salt grasslands could also be indirectly caused by the reduced populations of amphipods as main decomposers. In contrast, Sammul et al. (2008) described for Estonian salt grasslands that abandonment enhances the accumulation of nutrients and the formation of peat. Also Vestergaard (1998) detected an increase in organic matter content and thickness of the organic layer after abandonment in all elevation classes (connected with a decrease in dry bulk density) in salt grasslands in south-eastern Denmark. Salt grasslands in this region mostly resemble those in Mecklenburg-Vorpommern (soil type, land subsidence). Hence, it is rather unlikely that the proposed differences in mechanisms and patterns of grazing impact on nutrient accumulation really exist. Instead, it has to be concluded that the impact of grazing and abandonment on nutrient accumulation and peat formation is still unclear.

Nitrogen can either be retained in the plant-soil-water system by sedimentation or peat growth, or it can be removed from the system by denitrification (Merrill & Cornwell 2000). The nitrogen retention rate by sedimentation depends on the sedimentation rate. For Dutch Wadden Sea salt marshes, a nitrogen retention by sedimentation of 43-200 kg N/ha*year on the islands (with 1-5 mm/year sedimentation) and 300-750 kg N/ha*year on the mainland (with 10-20 mm/a sedimentation) were calculated (Rozema et al. 2000). Sedimentation contributes only little to the formation of salt grasslands in the Baltic Sea, thus the major nitrogen deposition occurs through peat formation. For the de-embanked coastal peatland Karrendorfer Wiesen in Mecklenburg-Vorpommern, Lampe & Wohlrab (1996) estimated a nitrogen retention of 80 kg N/ha*year at a predicted peat growth of 1.5 mm/a.

Measured rates of denitrification strongly differ from 8 kg N/ha*year in salt marshes of the United Kingdom (Abd Aziz & Nedwell 1986b, after Rozema et al. 2000) to rates between 50 kg N/ha*year (White & Howes 1994, after Valiela et al. 2000) and 140 kg N/ha*year (Kaplan et al. 1979) in salt marshes of the United States. In a tidal wetland in the inner Randers Fjord at the Danish Baltic coast, denitrification rates of 150-200 kg N/ha*year were measured (Hoffmann 2008, see also Hoffmann et al. 2006).

Livestock grazing, as herbivory in general, affects nitrogen dynamics directly by the export of nitrogen by removal of aboveground plant material (Van Wijnen & Bakker 2000) which does not represent a high efflux from the salt marsh (Rozema et al. 2000). Grazing also affects nitrogen dynamics indirectly by influencing sedimentation and peat growth (see above), and by altering soil conditions which influence microbial processes, such as denitrification. Jensen et al. (1990) assume that soil compaction by grazing animals leading to more waterlogged soils may result in higher denitrification rates of salt marshes. That grazing increased denitrification rates was also shown for (non-saline) semi-natural grasslands by Frank et al. (2000) and Le Roux et al. (2003).

Because *Phragmites australis* reed beds are known to accumulate nutrients, contribute to peat formation and are widely used in constructed wetlands for wastewater treatment (Schieferstein 1997, Mitsch & Gosselink 2000, Succow & Joosten 2001, Meuleman et al. 2002), it is quite likely that brackish reed beds may fulfil the function of nutrient retention at least as efficiently as salt grasslands.

The removal of reed beds by restoring salt grasslands may even include a danger of releasing nutrients which accumulated in the reed and/or sediments, as described by Huhta (2007). Thus, the author recommends a careful assessment on possible chances and dangers of restorative measures, which should not in every case result in the decision for reed removal, but also for the maintenance of reed beds in cases where they buffer and retain nutrients of run-off waters.

Furthermore, large amounts of carbon are stored in salt marshes (Chmura et al. 2003, Andrews et al. 2006) and coastal peatlands (Succow & Joosten 2001). Carbon burial in saline wetlands is potentially a globally important sink for atmospheric CO_2 (Chmura et al. 2003, Choi & Wang 2004). The carbon storage efficiency depends on sedimentation rates or, in coastal peatlands, on peat growth rates. For the de-embanked coastal peatland Karrendorfer Wiesen in Mecklenburg-Vorpommern with a predicted peat growth of 1.5 mm/a., Lampe & Wohlrab (1996) estimated a carbon fixation of 5.1 t CO_2/ha*year. Especially in coastal peatlands, other processes may also influence the net carbon sequestration, such as the emission of CH_4 occurring under anaerobic conditions of permanently waterlogged soils (Succow & Joosten 2001, not included in the calculation of Lampe & Wohlrab 1996). Chmura et al. (2003) calculated a net carbon sequestration of coastal wetlands (salt marshes and mangroves) of 2.1 t CO_2/ha*year, and compared this to 0.2-0.3 t CO_2/ha*year for peatlands (see also Bromberg Gedan et al. 2009). Consequently, Chmura et al. (2003) suggest that coastal wetlands could even be more valuable carbon sinks per unit area than other ecosystems (such as peatlands), because the rates of carbon sequestration are higher and CH_4 emissions are lower.

Sedimentation as well as peat formation may be influenced by grazing, as described above. The higher the sedimentation rates and peat growth, the more carbon can be stored in salt grasslands. Morris & Jensen (1998) showed that grazing reduced the organic matter content in the sediments of Danish Wadden Sea salt marshes, since a part of the produced phytomass was removed by livestock. In general, Jones & Donnelly (2004) see a significant potential to increase the carbon sequestration in temperate grassland systems through grazing management, but also summarise that there are still uncertainties in estimating the actual impact of different grazing intensities.

10.5 Conclusions

The possible effects of salt grassland succession on different species groups and abiotic nature conservation targets (ecosystem functions) differs for the succession of grazed to 'early successional' stages (which can still be regarded as salt grasslands) and for the more fundamental changes brought about by the dominance of *Phragmites australis.* The overall evaluation of these changes from a nature conservation point of view is summarised in table 5-1.

Table 10-1: Summarised evaluation of the impact of abandonment on the nature conservation targets described above (10.2 to 10.4), separated for the succession from grazed to 'early successional' stages (still salt grasslands) and from 'early' to 'late successional' stages (brackish reed bed). **+**: positive reaction (increase of diversity/abundance of species group, increase of habitat suitability), **-**: negative reaction/decrease of diversity/habitat suitability, **=**: no changes. **?**: unclear. Evaluation based on results of the presented study for vegetation, and on literature review for other species groups and ecosystem functions (see 10.2 to 10.4).

Nature conservation targets		grazed → early succ.		early succ.→ late succ.	
Vegetation	Diversity	=		= / long-term (& mainly small scale): -	
	Characteristic species	=		-	
	Rare and endangered species	= (MV)	+ (SH)	= (MV)	- (SH)
Animal groups					
Birds	Geese	(-)		-	
	Waders/Meadow birds	+ (some -?)		-	
	Reed birds	=		+	
Rare/endangered amphibians	Natterjack and green toad	-		-	
Invertebrates**	Species characteristic/ specific for saline habitats	+ (long-term -?)		+?	
Ecosystem functions	Coastal protection (wave attenuation)	+?		+?/ ??	
	Sedimentation	+?		+ ?/ ??	
	Peat formation	+? (EST)	-? (SH/MV)	+? (EST)	-? (SH/MV)
	Nutrient retention	= ?		=?/??	
	Carbon storage	= ?		= ?	

Differences between regions: to graze or not to graze?

In general, this evaluation is similar for all study regions along the salinity gradient. What differs, is the speed and probability of the two successional steps (see 5.4.6), which results in differential conclusions for the different regions. Additionally, for precise decisions on nature conservation management, ecological facts and priorities on human interests would have to be balanced for each specific location (see below).

The table 10-1 illustrates that changes associated with the first successional step from grazed to 'early successional' stages can be evaluated as positive or neutral for most species groups and ecosystem functions, except for the habitat suitability for rare/endangered amphibians (*Bufo calamita, Bufo viridis*) and (possibly) geese. Most negative changes of 'salt grassland nature conservation targets' are associated with the fundamental change to brackish reed beds – which, however, include their own, rather different, habitat values. Most nature conservation targets related to salt grasslands may still be reached without grazing, as long as the dominance of reed is prevented. Since these 'early successional' salt grassland stages may persist at least for several decades in the western regions of the Baltic (Schleswig-Holstein and Denmark), grazing is not necessary in all cases.

The persistence of salt grasslands without grazing apparently depends on other disturbance factors and on the soil type, as described in 5.4.5, and should therefore be carefully monitored and evaluated before taking decisions on management and/or restoration. The long-term development beyond a period of 40-50 years, however, is still unknown. To maintain and monitor the development of some of these long-term ungrazed salt grasslands (such as a part of Graswarder) would thus be of great value merely from a scientific point of view.

In contrast, in the eastern regions (Mecklenburg-Vorpommern and Estonia), the second successional phase of increasing dominance of brackish reed beds is reached much faster. However, the decline of plant species diversity still depends on soil type, being slower or less severe in sites of the shallow soil type. Thus, the persistence of these 'early successional' stages is more transitional in the regions of lower salinity (especially when combined with high nutrient availability and low disturbance frequency). Hence, if Baltic salt grasslands are to be maintained, this would in most cases involve an appropriate grazing (or mowing) regime and restoration measures in abandoned areas.

However, the habitat values of brackish reed beds (see 10.2,10.3) should also be acknowledged (see Krisch 1989, Kieckbusch 1998, Esselink et al. 2000, 2002, Vestergaard 2002a). On a regional scale, both habitat types should be maintained in a certain balance, as also concluded by Polte in the Red List of threatened habitat types in Mecklenburg-Vorpommern (Berg et al. 2004). Vestergaard (1999) emphasised in his criteria of 'high botanical quality of salt marshes' (of the Baltic Sea coast) that a variety of seral (successional) stages from grazed salt grassland to ungrazed reed bed should be present.

In a 'management model' for the Natura 2000 habitat types 'Atlantic Salt Meadows' and 'Boreal Baltic Coastal Meadows' commissioned by the European Commission, Doody (2008) stressed that options are complex and different nature conservation targets need different management strategies. Related to grazing, decisions on reducing or re-introducing grazing by livestock have to be taken, depending on historical management and existing nature conservation interests. In this EU-report, the two geographically distinct habitat types ‘Atlantic Salt Meadows’ (1330) and ‘Boreal Baltic Coastal Meadows’ (1630) are summarised also in relation to management (Doody 2008).

Differences between the two Natura 2000 habitat types?

With regard to the presented results from four regions of the Baltic sea coast, it can be questioned whether the separation of the two EU habitat types 1330 and 1630 is justified, and if yes, if the same management and restoration guidelines can be applied to both types.

Sweden is the only country, where both ‘Atlantic Salt Meadows’ as well as ‘Boreal Baltic Coastal Meadows’ occur. Boreal Baltic coastal meadows differ from the Atlantic type in that they have a lower salinity and are much less influenced by tides (Doody 2008). The Swedish nature conservation authority gives an indicative salinity limit of 15‰ (Naturvårdsverket 1997), thus sites east of the southern mouth of the Sound (Öresund) are classified as ‘Boreal Baltic coastal Meadows’. According to the classification of the European Union, Denmark and Germany (and Poland) do not belong to the Boreal biogeographical region, but – related to the Baltic Sea coast – to the Continental biogeographical region, thus ‘Boreal Baltic Coastal Meadows’ do not occur there, irrespective of tidal amplitude and salinity. However, the mentioned Swedish criteria also apply to the German coast approximately east of Kiel. Thus, it can be suspected that there is rather a gradual transition than a clear border between both types.

The more profound differences between salt grasslands in Estonia and the other three regions were primarily related to the land rise and the soil type, not to salinity alone. However, differences in (speed of) successional processes, resulting in differential evaluation on the necessity of continuous grazing and/or quick restoration of grazing regimes were primarily related to salinity. The fundamental difference that ‘Atlantic salt meadows’ of high salinity regions stay (in most cases) salt grasslands even if not grazed, whereas ‘Boreal Baltic coastal Meadows’ and ‘Atlantic Salt Meadows’ approximately below the Swedish salinity limit of 15‰ transform rather quickly into brackish reed beds, should therefore not be underestimated.

How to graze and manage?

For more precise decisions on grazing management – depending on the specific targets – also the type of livestock (cattle, sheep, horses; Scherfose 1993, Rannap et al. 2004) and the grazing pressure (length of grazing season, livestock unit/ha) are important (Kiehl et al. 1996, Kiehl 1997, Kleyer et al. 2003, Doody 2008). In many cases, intermediate, moderate grazing of large complexes, resulting in a mosaic of intensively and lightly grazed patches and a high variety of vegetation structures and habitat for different species groups, might have the greatest nature conservation benefit (Doody 2008). Since both factors could not be investigated in this thesis, they will not be discussed further here.

Furthermore, nature conservation management of Baltic salt grasslands – also with regard to botanical nature conservation targets – does not only comprise grazing management, but also the maintenance or restoration of natural hydrology and submergence patterns as well as natural morphology (Vestergaard 1999).

How to decide on the management of specific Baltic salt grassland locations?

For precise decisions on the management (or restoration) of specific (former) salt grassland locations, various factors have to be taken into account to set priorities. These are, on the one hand, biological and geo-/hydromorphological facts which determine the suitability of a salt grassland location for a specific nature conservation target. On the other hand, socio-economic interests have to be weighed up against each other, including society's interest in nature conservation.

First, the importance of a specific salt grassland locality for different species groups and/or abiotic processes may vary depending on **biological and/or geo-/hydromorphological facts**, as the following examples may illustrate.

- For the actual or potential habitat value for geese, the location along the fly-way/ in a spring-staging area of e.g. brent geese may be relevant, as well as the size and shape of the area (see 5.4.5, 10.3.1).
- If the habitat properties needed by natterjack toads shall be restored, the present or historical importance as a natterjack breeding site may be relevant, as well as whether there are remnant populations in the vicinity able to immigrate to the restoration site. Otherwise, restoring habitat conditions would not be sufficient, but tadpoles or toads would have to be (re)introduced.
- The presence of specific rare or endangered plant or animal species with specific demands (such as for a certain vegetation structure or the presence of certain host plant species, but also for a high or low grazing pressure, an early or late start of grazing) can be a reason to decide for a specific grazing regime.
- For restoration projects, the distance to source populations of target species is an additional important factor which may determine the restoration success (Wolters et al. 2005a).
- The relevance of the coastal protection function depends on e.g. the position, shape and extension of a salt grassland area relative to a dike or to a settlement needing protection against flooding.
- A salt grassland site's potential for nutrient retention depends on its extension relative to the size and water resident time of the water body and on the nutrient load of the water body, as well as on the elevational profile of the salt grassland and the properties of the peat layer determining its peat growth potential.

Second, there is a need to consider the various possible **socio-economic interests**, as indicated in the following. Some of these interests are of higher relevance for projects on the restoration of natural flooding (de-embankment projects), at least until further research may have revealed a clearer picture on the impact of grazing on ecosystem functions of salt grasslands such as sedimentation, peat growth, nutrient retention and carbon storage (see 10.4).

Although the agricultural interest in using salt grasslands has decreased in the last decades, salt grasslands may still be economically important for grazing of cattle, sheep or horses. Vice versa, a conservation or restoration project may also gain higher acceptance or interest by the local population if it provides economic perspectives for local farmers. This may imply also changes of traditional agricultural use, such as e.g. the shift from dairy cattle to beef cattle in the Estonian Väinameri project, which was accompanied by the development of marketing strategies (Lotman et al. 2005).

Depending on the location, the coastal protection function of salt grasslands dissipating wave energy may be of primary importance (see 10.4). In areas of high tourist or recreational interest, the attractiveness of the landscape may be relevant for the decision of pro or contra grazing. On the Darß peninsula in Mecklenburg-Vorpommern, for example, tourists indicated their interest in and their willingness to pay for the maintenance of grazing to re-establish salt grasslands after de-embankment (Beil & Hampicke 2004). Nature conservation or restoration projects may also include the establishment of infrastructure for experiencing nature (such as bird watching facilities) on the one hand, and for guiding visitors to limit disturbances and damages on the other hand (Lotman et al. 2005).

In coastal areas suffering high eutrophication, the nutrient retention function of salt grasslands may be of importance (see 10.4). A management targeted at maximising nutrient retention may be of interest as a measure to fulfil the requirements of the Water Frameworks Directive. The carbon storage function may be enhanced in the framework of projects e.g. financed by Clean Development Mechanisms (primarily in developing countries) or as carbon credits (compensation measures for carbon emissions). So far, the nutrient retention and carbon storage potential has been included in cost-benefit analyses in the context of de-embankment of former salt marshes (Andrews et al. 2006, Shepherd et al. 2007).

From a scientific point of view, it would be valuable to leave some areas permanently ungrazed and without any other human impact, since the long-term succession is not known yet (see above). It would also be favourable to apply different grazing regimes in the same way for a longer period (management experiments) to better investigate their consequences on vegetation, animals and ecosystem functions (Bakker et al. 2003a).

Last but not least, the nature conservation interest with respect to salt grasslands, as formulated above (10.2, 10.3), implies the conservation of different plant and animal groups, ‘biodiversity’ as a whole and of natural processes.

Finally, within the field of nature conservation, **priorities** within the different possible **nature conservation targets**, as described above, have to be set. The biological and geo-/ hydromorphological facts should be taken into account and may help to set priorities, because in a specific location, some targets will have better chances of success than others. Nevertheless, a decision on the aims cannot be taken by scientific knowledge alone – just describing the facts – but has to be preceded by a subjective decision on values and norms of the society (compare Hume 1740/1978, Moore 1904/1970, see introduction).

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Annex 1

Species traits of all species in the complete vegetation data set. Occurrence in the four regions: DK: Denmark, SH: Schleswig-Holstein, MV: Mecklenburg-Vorpommern, EST: Estonia; life cycle: a: annual, b: biennial, p: perennial; socio-ecological species groups (see methods 3.3.2); Red List category for German Baltic coast (Berg et al. 1996); Characteristic species of habitat types 1310, 1330, 1630 (EC 2007, see methods 3.3.2), prior: priority species of Annex II of the EU-Habitats Directive; CSR-strategy types after Grime (derived from Frank & Klotz 1990).

Name	occurrence in				life cycle	socio-ecol. species group	Red List Baltic	EU-habitat types			CSR-Klotz
	DK	SH	MV	EST				1310	1330	1630	
Achillea millefolium	x	x	x	x	p	grassland					C
Agrostis gigantea				x	p	grassland					CSR
Agrostis stolonifera	x	x	x	x	p	flood meadow			x	x	CSR
Alopecurus pratensis				x	p	grassland					C
Althaea officinalis		x			p	flood meadow	3				CS
Angelica archangelica ssp. *litoralis*	x				p	ruderal					CS
Angelica palustris				x	p	grassland				prior.	CS
Anthoxanthum odoratum	x				p	indifferent					CSR
Anthriscus sylvestris					p	grassland					C
Apium graveolens		x			b	flood meadow	1				CS
Armeria maritima	x	x	x		p	salt marsh	3		x		CSR
Artemisia maritima	x	x	x		p	salt marsh	3		x		CS
Aster tripolium	x	x	x	x	b	salt marsh	3				CS
Atriplex littoralis	x			x	a	salt marsh			x		S
Atriplex pedunculata	x				a	salt marsh	1		x		S
Atriplex prostrata	x	x	x	x	a	ruderal			x		S
Blysmus compressus				x	p	indifferent	3				CSR
Blysmus rufus				x	p	salt marsh	1		x	x	CSR
Bolboschoenus maritimus	x	x	x	x	p	reed bed				x	CS
Briza media				x	p	grassland					CSR
Bupleurum tenuissimum	x				a	flood meadow	1	x			S
Caltha palustris		x		x	p	grassland					CSR
Calystegia sepium					p	ruderal					C
Cardamine pratensis				x	p	indifferent					CSR
Carex distans	x	x		x	p	indifferent	3				CS
Carex disticha				x	p	reed bed					CSR
Carex elata				x	p	reed bed					CS
Carex extensa		x			p	salt marsh	2		x		S
Carex flacca	x			x	p	indifferent					CSR
Carex flacca x panicea				x	p	not classified					CSR
Carex glareosa				x	p	not classified				x	
Carex nigra				x	p	fen/small sedge				x	S
Carex otrubae	x		x		p	forest (edge)					CS
Carex panicea				x	p	fen/small sedge					CSR
Carex viridula var. *viridula*	x	x		x	p	indifferent	2				S
Centaurea jacea			x	x	p	grassland					C
Centaurium littorale	x			x	a	salt marsh	2			x	S
Centaurium pulchellum	x	x	x	x	a	ruderal	2			x	SR
Cerastium holosteoides	x	x			p	grassland					CR
Cicuta virosa (juv.)				x	p	reed bed					CS
Cirsium arvense		x	x	x	p	ruderal					C
Cirsium vulgare			x	x	b	ruderal					CR
Cochlearia anglica		x			b	salt marsh	3				CS
Cochlearia danica	x				b	salt marsh	3	x			SR
Cochlearia officinalis	x				b	salt marsh	2				SR
Convolvulus arvensis		x			p	ruderal					CR
Cotula coronopifolia		x			a	flood meadow	P				
Dactylorhiza majalis				x	p	grassland					CSR
Danthonia decumbens	x				p	grassland					CS
Deschampsia cespitosa				x	p	indifferent					C
Eleocharis palustris				x	p	reed bed			x		CS
Eleocharis uniglumis	x	x	x	x	p	reed bed	*		x	x	CSR

Name	occurrence in DK	SH	MV	EST	life cycle	socio-ecol. species group	Red List Baltic	EU-habitat types 1310	1330	1630	CSR-Klotz
Elymus repens	x	x	x	x	p	ruderal			x		C
Empetrum nigrum	x				p	grassland					CSR
Epilobium palustre				x	p	reed bed					CSR
Equisetum pratense				x	p	forest (edge)					CSR
Eriophorum vaginatum				x	p	fen/small sedge					CS
Eupatorium cannabinum		x			p	ruderal					C
Festuca arundinacea	x	x	x	x	p	flood meadow					C
Festuca rubra agg.	x	x	x	x	p	salt marsh	3/*		x	x	C
Filipendula ulmaria				x	p	grassland					C
Filipendula vulgaris				x	p	grassland					CSR
Frangula alnus (juv.)				x	p	forest (edge)					C
Fraxinus excelsior (juv.)				x	p	forest (edge)					C
Galeopsis spec.			x	x	a	not classified					
Galium aparine				x	a	ruderal					CR
Galium boreale				x	p	grassland					CSR
Galium palustre	x		x	x	p	reed bed					CSR
Galium uliginosum				x	p	grassland					CSR
Galium verum	x			x	p	grassland					CSR
Glaux maritima	x	x	x	x	p	salt marsh			x		S
Heracleum mantegazzianum	x				p	indifferent					C
Hierochloe odorata				x	p	grassland					CS
Holcus lanatus	x	x			p	grassland					C
Hypochaeris radicata				x	p	grassland					CSR
Inula britannica					p	flood meadow	3				CSR
Inula salicina				x	p	grassland					CS
Juncus articulatus	x			x	p	fen/small sedge					CSR
Juncus gerardii	x	x	x	x	p	salt marsh	3		x	x	S
Juncus maritimus		x	x		p	salt marsh	*				CS
Juncus ranarius		x	x	x	a	ruderal					R
Juniperus communis				x	p	indifferent					C
Lathyrus palustris				x	p	grassland					CSR
Lathyrus pratensis				x	p	grassland					C
Lathyrus spec.				x	p	not classified					CSR
Leontodon autumnalis	x	x	x	x	p	grassland					CSR
Lepidium latifolium		x			p	flood meadow	P				C
Limonium vulgare	x	x			p	salt marsh	3				S
Linaria vulgaris		x			p	ruderal					CSR
Linum catharticum				x	a	grassland					SR
Lolium perenne		x			p	grassland					C
Lotus corniculatus	x	x	x	x	p	grassland					csr
Lotus tenuis	x		x		p	flood meadow					CS
Lycopus europaeus				x	p	reed bed					CS
Lysimachia thyrsiflora				x	p	reed bed					CS
Lysimachia vulgaris				x	p	indifferent					CS
Medicago lupulina				x	a	grassland					CSR
Melilotus altissimus		x		x	b	ruderal					CR
Mentha aquatica				x	p	reed bed					CS
Molinia caerulea	x			x	p	indifferent					CS
Odontites litoralis	x		x	x	a	salt marsh	3			x	
Oenanthe lachenalii	x	x	x		p	flood meadow	2				
Ophioglossum vulgatum	x	x		x	p	grassland	2				
Parnassia palustris				x	p	fen/small sedge					CSR
Pedicularis palustris				x	b	fen/small sedge					
Peucedanum palustre				x	p	reed bed					CS
Phleum pratense				x	p	grassland					C
Phragmites australis	x	x	x	x	p	reed bed					CS
Pinus sylvestris	x			x	p	indifferent					C
Plantago coronopus	x	x			b	salt marsh	3				S
Plantago lanceolata				x	p	grassland					CSR
Plantago major				x	p	ruderal					CSR
Plantago major ssp. *winteri*		x		x	p	not classified	3				
Plantago maritima	x	x	x	x	p	salt marsh	*		x	x	S
Poa annua				x	a	indifferent					R

	occurrence in							EU-habitat types			
Name	DK	SH	MV	EST	life cycle	socio-ecol. species group	Red List Baltic	1310	1330	1630	CSR-Klotz
Poa pratensis	x		x	x	p	grassland					C
Poa trivialis				x	p	grassland					CSR
Potentilla anserina	x	x	x	x	p	flood meadow			x		CSR
Potentilla erecta			x		p	grassland					CSR
Primula farinosa				x	p	fen/small sedge					CSR
Puccinellia maritima	x	x	x		p	salt marsh	3		x		SR
Radiola linoides	x				a	ruderal					SR
Ranunculus acris				x	p	grassland					C
Ranunculus repens		x		x	p	indifferent					CSR
Ranunculus sceleratus	x				a	ruderal					SR
Rhinanthus angustifolius				x	a	indifferent					S
Rumex crispus	x	x	x	x	p	flood meadow					C
Sagina maritima	x	x			a	salt marsh		x			SR
Sagina nodosa	x			x	p	flood meadow	2	x			CSR
Salicornia europaea	x	x	x	x	a	salt marsh	3	x			S
Schoenoplectus tabernaemontani				x	p	reed bed					CS
Scorzonera humilis				x	p	grassland					CSR
Selinum carvifolia				x	p	grassland					CS
Sesleria caerulea				x	p	fen/small sedge					CS
Sium latifolium				x	p	reed bed					CS
Sonchus arvensis	x			x	p	ruderal					CR
Sonchus asper	x	x	x		a	ruderal					CR
Sonchus oleraceus				x	a	ruderal					CR
Sonchus palustris		x	x		p	ruderal					CS
Spergularia media	x	x	x		p	salt marsh			x		S
Spergularia salina	x	x	x	x	a	salt marsh				x	S
Stellaria alsine				x	p	fen/small sedge					CSR
Stellaria graminea	x				p	indifferent					CS
Suaeda maritima	x	x		x	a	salt marsh		x			S
Succisa pratensis				x	p	grassland					CSR
Taraxacum officinale agg.	x			x	p	not classified					CSR
Thalictrum flavum		x			p	grassland					C
Trifolium fragiferum	x	x	x	x	p	flood meadow	3				CSR
Trifolium pratense	x		x	x	p	grassland					C
Trifolium repens	x	x	x	x	p	grassland					CSR
Triglochin maritimum	x	x	x	x	p	salt marsh	3		x	x	S
Triglochin palustre	x		x	x	p	fen/small sedge	3				S
Urtica dioica					p	ruderal					C
Valeriana officinalis				x	p	grassland					C
Vicia cracca	x	x		x	p	grassland					C
Betula spec. (juv)				x	p						
Carex spec.		x			p						
Cerastium spec.	x										
Chenopodium spec.		x			a						
Dactylorhiza spec.				x	p						
Epilobium spec. (juv.)				x	p						
Rumex spec. (juv.)			x								
Sonchus spec. (juv.)		x									
Poaceae		x									
unknown		x		x							

Annex 2

Mean cover (%) of all species on the 625 m²-plots, mean per region and management class, sorted by occurrences in the regions. EST: Estonia, MV: Mecklenburg-Vorpommern, SH: Schleswig-Holstein, DK: Northern Denmark. G: grazed, ES: early successional, LS: late successional.

Region	all	EST	EST	EST	EST	MV	MV	MV	SH	SH	SH	DK	DK	DK
Management		G	ES	LS	R	G	ES	LS	G	ES	LS	G	ES	LS
in all regions														
Festuca rubra agg.	28.04	15.4	47.4	13.2	13.2	8.4	47.4	35.8	18.0	38.8	38.0	10.8	68.0	15.2
Phragmites australis	26.25	2.3	3.6	78.0	25.2	2.8	1.6	88.0	1.4	1.4	78.0	0.6	-	68.0
Plantago maritima	10.90	12.0	10.8	5.2	5.2	5.2	4.4	3.6	29.4	21.2	1.6	21.6	12.8	8.2
Juncus gerardii	17.90	31.6	20.2	6.4	25.8	26.8	15.2	7.6	20.4	16.4	12.0	26.8	12.8	5.2
Agrostis stolonifera	13.88	14.6	9.6	10.4	18.0	53.0	13.2	8.4	20.2	10.8	4.0	4.4	8.4	5.2
Glaux maritima	6.75	11.1	10.4	5.2	4.0	4.0	5.2	4.4	11.6	5.2	7.2	8.4	5.2	4.0
Triglochin maritimum	4.84	7.1	6.4	4.0	5.2	6.4	4.0	2.4	4.0	7.6	2.4	4.0	5.2	3.2
Aster tripolium	3.27	1.7	1.8	1.4	1.4	3.2	6.8	3.0	2.4	7.0	2.8	3.8	4.0	3.8
Atriplex prostrata	2.66	0.4	1.6	1.6	2.0	3.0	3.2	3.2	3.0	2.4	6.4	2.4	3.0	3.2
Potentilla anserina	3.84	5.6	7.2	5.2	3.2	2.4	5.6	2.6	3.6	4.6	2.0	2.0	1.6	3.6
Bolboschoenus maritimus	3.25	0.4	2.8	3.0	1.8	2.2	16.0	3.0	0.8	3.0	4.0	0.8	3.2	2.4
Salicornia europaea	1.03	0.4	-	-	0.8	0.6	-	-	4.4	3.0	-	3.2	0.6	0.6
Spergularia salina	1.25	0.9	0.6	-	0.6	3.2	0.6	0.6	4.0	1.6	0.8	3.0	0.6	-
Elymus repens	5.76	1.0	13.2	10.8	3.2	2.2	16.4	6.8	1.6	1.6	2.4	0.8	3.6	13.2
Lotus corniculatus/tenuis	1.40	2.7	2.8	2.0	1.2	2.4	1.6	0.8	0.8	1.0	0.8	0.8	0.8	0.0
Centaurium pulchellum	1.37	3.0	0.8	0.8	3.4	-	0.6	0.8	0.8	1.4	-	3.2	1.6	0.8
Trifolium repens	0.84	1.1	2.4	1.4	0.2	0.8	0.6	1.2	1.4	0.8	-	0.8	-	-
Leontodon autumnalis	1.87	3.9	4.0	3.2	3.8	1.6	0.8	1.4	0.8	-	0.8	1.6	0.8	0.8
Trifolium fragiferum	0.60	2.6	0.8	-	0.4	0.8	-	-	1.6	-	-	0.8	-	-
Vicia cracca	1.58	1.6	3.0	1.6	2.4	-	-	0.8	-	0.8	-	0.8	3.6	6.0
Carex viridula var. *viridula*	0.72	1.1	1.4	-	2.4	-	-	0.8	-	0.8	-	0.6	0.6	1.4
Eleocharis uniglumis	2.52	3.6	6.4	13.2	3.2	-	2.8	0.8	0.8	-	-	0.8	-	0.8
Festuca arundinacea	1.49	2.3	3.2	4.0	2.4	0.8	2.4	2.4	-	-	0.8	-	-	0.8
Achillea millefolium	0.55	0.6	-	1.2	1.4	-	0.8	1.6	0.8	-	-	-	-	0.8
Rumex crispus	0.31	-	0.6	0.8	-	-	0.6	0.6	-	0.6	-	-	-	1.0
in three regions														
Carex distans	1.97	3.4	4.0	3.6	5.2	-	-	-	0.8	1.6	0.8	1.6	2.4	1.6
Suaeda maritima	0.52	0.4	-	-	-	-	-	-	1.6	1.4	-	3.4	-	-
Ophioglossum vulgatum	0.54	0.4	1.0	1.6	1.4	-	-	-	-	0.2	0.8	-	0.8	0.8
Sonchus arvensis	0.52	0.3	2.0	-	1.6	-	-	0.8	-	-	-	-	0.8	1.4
Trifolium pratense	1.19	3.0	3.8	2.8	2.4	-	0.6	0.6	-	-	-	-	0.8	0.8
Triglochin palustre	0.55	1.3	0.6	1.6	1.6	1.2	-	-	-	-	-	0.6	-	-
Poa pratensis	0.48	-	-	0.8	0.8	-	0.8	0.8	-	-	-	0.8	-	2.4
Odontites litoralis	1.69	4.0	4.0	1.6	3.2	-	0.6	1.2	-	-	-	2.4	2.4	1.6
Galium palustre	1.54	2.7	4.0	4.0	3.2	-	0.8	3.2	-	-	-	-	-	1.6
Juncus ranarius	0.18	0.4	0.8	-	-	0.4	-	-	0.6	-	-	-	-	-
Plantago major ssp. *winteri*	0.15	-	-	-	0.6	-	-	0.6	0.8	-	-	-	-	-
Cirsium arvense	0.55	-	-	0.6	-	-	0.8	1.2	0.8	0.8	3.2	-	-	-
Puccinellia maritima	4.54	-	-	-	-	4.8	-	-	19.4	4.4	-	23.8	8.4	-
Sonchus asper	0.76	-	-	-	-	-	2.6	2.0	-	-	4.2	-	-	1.4
Oenanthe lachenalii	0.54	-	-	-	-	-	1.8	2.4	-	0.4	1.4	-	0.4	0.8
Artemisia maritima	3.58	-	-	-	-	-	0.8	0.8	7.6	15.6	0.8	2.0	17.4	3.0
Spergularia media	1.25	-	-	-	-	1.6	-	-	3.8	2.4	0.8	4.0	2.0	2.2
Armeria maritima	1.48	-	-	-	-	0.8	-	0.6	0.6	1.6	7.6	4.0	3.2	1.4
Holcus lanatus	0.28	-	-	-	-	-	-	0.8	0.8	-	-	0.6	0.8	0.8
in two regions														
Molinia caerulea	1.00	2.7	4.0	2.4	2.4	-	-	-	-	-	-	-	0.8	-
Carex flacca	0.93	2.7	4.0	0.8	3.2	-	-	-	-	-	-	-	-	0.6
Juncus articulatus	0.90	2.7	2.2	0.8	3.6	-	-	-	-	-	-	-	0.8	0.8
Centaurium littorale	1.06	3.9	2.2	0.8	2.4	-	-	-	-	-	-	1.8	0.8	0.8
Taraxacum officinale agg.	0.52	1.1	1.4	1.8	1.6	-	-	-	-	-	-	0.6	-	-
Galium verum	0.36	0.9	0.8	0.8	1.4	-	-	-	-	-	-	-	-	0.6
Pinus sylvestris	0.06	-	-	-	0.2	-	-	-	-	-	-	-	0.2	0.4
Sagina nodosa	0.16	0.4	-	-	-	-	-	-	-	-	-	-	0.8	0.8
Atriplex littoralis	0.31	-	0.4	-	-	-	-	-	-	-	-	0.4	0.6	2.8
Cirsium vulgare	0.04	-	-	-	0.4	-	0.2	-	-	-	-	-	-	-
Centaurea jacea	0.46	1.3	1.4	0.8	1.6	-	0.6	-	-	-	-	-	-	-
Lathyrus pratensis	0.10	-	-	0.8	-	-	-	0.6	-	-	-	-	-	-
Galium aparine	0.09	-	0.6	-	-	-	-	0.6	-	-	-	-	-	-
Schoenoplectus tabernaemontani	0.79	1.7	2.8	3.2	1.4	-	-	0.8	-	-	-	-	-	-
Mentha aquatica	0.22	0.9	-	0.8	0.2	-	-	0.8	-	-	-	-	-	-
Agrostis gigantea	0.16	1.0	-	-	-	-	-	0.8	-	-	-	-	-	-
Ranunculus repens	0.21	0.6	-	-	1.2	-	-	-	0.8	-	-	-	-	-
Melilotus altissimus	0.19	1.4	-	-	-	-	-	-	-	0.6	-	-	-	-
Caltha palustris	0.04	-	-	0.4	-	-	-	-	-	-	0.2	-	-	-
Juncus maritimus	1.13	-	-	-	-	0.8	2.0	4.8	-	7.6	-	-	-	-
Sonchus palustris	0.40	-	-	-	-	-	0.8	-	-	0.8	3.8	-	-	-
Eupatorium cannabinum	0.09	-	-	-	-	-	-	0.6	-	-	0.6	-	-	-
Carex otrubae	0.10	-	-	-	-	-	0.6	-	-	-	-	-	-	0.8
Plantago coronopus	0.06	-	-	-	-	-	-	-	-	0.2	-	-	-	0.6
Sagina maritima	0.25	-	-	-	-	-	-	-	1.2	-	-	0.8	0.6	0.8
Cerastium holosteoides	0.27	-	-	-	-	-	-	-	0.6	0.8	-	0.6	0.8	0.8
Limonium vulgare	1.34	-	-	-	-	-	-	-	2.2	4.8	-	3.2	5.6	2.2
only in EST														
Carex panicea	1.03	4.3	3.0	2.4	2.4	-	-	-	-	-	-	-	-	-
Blysmus rufus	0.97	2.7	3.0	1.6	4.6	-	-	-	-	-	-	-	-	-
Carex nigra	0.87	4.0	1.6	0.8	3.6	-	-	-	-	-	-	-	-	-
Angelica palustris	0.66	2.1	3.2	1.2	1.4	-	-	-	-	-	-	-	-	-
Selinum carvifolia	0.51	1.0	0.8	2.2	2.4	-	-	-	-	-	-	-	-	-
Rhinanthus angustifolius	0.42	1.6	2.2	1.2	-	-	-	-	-	-	-	-	-	-
Blysmus compressus	0.34	0.6	0.8	2.4	0.6	-	-	-	-	-	-	-	-	-
Valeriana officinalis	0.31	0.4	1.2	0.8	1.6	-	-	-	-	-	-	-	-	-
Inula salicina	0.27	1.0	1.4	0.8	-	-	-	-	-	-	-	-	-	-
Galium boreale	0.25	1.0	0.8	0.6	0.6	-	-	-	-	-	-	-	-	-

Region	all	EST	EST	EST	EST	MV	MV	MV	SH	SH	SH	DK	DK	DK
Management		G	ES	LS	R	G	ES	LS	G	ES	LS	G	ES	LS
Lathyrus palustris	0.21	0.1	0.8	1.2	0.6	-	-	-	-	-	-	-	-	-
Pedicularis palustris	0.16	-	-	1.4	0.8	-	-	-	-	-	-	-	-	-
Frangula alnus (juv.)	0.21	1.9	-	-	0.2	-	-	-	-	-	-	-	-	-
Filipendula ulmaria	0.16	0.4	-	0.8	0.8	-	-	-	-	-	-	-	-	-
Hierochloe odorata	0.16	0.6	-	0.6	0.8	-	-	-	-	-	-	-	-	-
Sesleria caerulea	0.19	1.9	-	-	-	-	-	-	-	-	-	-	-	-
Juniperus communis	0.15	0.7	-	0.6	0.4	-	-	-	-	-	-	-	-	-
Ranunculus acris	0.15	0.9	-	0.8	-	-	-	-	-	-	-	-	-	-
Alopecurus pratensis	0.12	-	-	1.6	-	-	-	-	-	-	-	-	-	-
Sium latifolium	0.12	-	0.8	0.8	-	-	-	-	-	-	-	-	-	-
Phleum pratense	0.12	-	1.6	-	-	-	-	-	-	-	-	-	-	-
Carex elata	0.12	-	-	0.8	0.8	-	-	-	-	-	-	-	-	-
Carex glareosa	0.12	-	0.8	0.8	-	-	-	-	-	-	-	-	-	-
Galium uliginosum	0.12	-	0.8	0.8	-	-	-	-	-	-	-	-	-	-
Peucedanum palustre	0.10	-	-	1.4	-	-	-	-	-	-	-	-	-	-
Carex disticha	0.12	0.6	-	0.8	-	-	-	-	-	-	-	-	-	-
Sonchus oleraceus	0.09	-	-	1.2	-	-	-	-	-	-	-	-	-	-
Medicago lupulina	0.12	1.1	-	-	-	-	-	-	-	-	-	-	-	-
Succisa pratensis	0.12	1.1	-	-	-	-	-	-	-	-	-	-	-	-
Plantago major	0.09	0.4	0.6	-	-	-	-	-	-	-	-	-	-	-
Parnassia palustris	0.10	1.0	-	-	-	-	-	-	-	-	-	-	-	-
Dactylorhiza majalis	0.07	-	0.4	0.6	-	-	-	-	-	-	-	-	-	-
Cardamine pratensis	0.07	0.4	-	0.4	-	-	-	-	-	-	-	-	-	-
Poa trivialis	0.06	-	-	0.8	-	-	-	-	-	-	-	-	-	-
Eleocharis palustris	0.06	-	0.8	-	-	-	-	-	-	-	-	-	-	-
Eriophorum vaginatum	0.06	-	-	0.8	-	-	-	-	-	-	-	-	-	-
Lysimachia vulgaris	0.06	-	-	0.8	-	-	-	-	-	-	-	-	-	-
Filipendula vulgaris	0.04	-	-	0.6	-	-	-	-	-	-	-	-	-	-
Hypochaeris radicata	0.04	-	0.6	-	-	-	-	-	-	-	-	-	-	-
Scorzonera humilis	0.04	-	-	0.6	-	-	-	-	-	-	-	-	-	-
Briza media	0.06	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Equisetum pratense	0.06	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Stellaria alsine	0.06	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Deschampsia cespitosa	0.06	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Fraxinus excelsior (juv.)	0.04	0.4	-	-	-	-	-	-	-	-	-	-	-	-
Plantago lanceolata	0.04	0.4	-	-	-	-	-	-	-	-	-	-	-	-
Primula farinosa	0.04	0.4	-	-	-	-	-	-	-	-	-	-	-	-
Epilobium palustre	0.03	-	-	0.4	-	-	-	-	-	-	-	-	-	-
Cicuta virosa	0.01	-	-	0.2	-	-	-	-	-	-	-	-	-	-
Carex flacca x panicea	0.01	0.1	-	-	-	-	-	-	-	-	-	-	-	-
only EST - only in restored														
Poa annua	0.06	-	-	-	0.8	-	-	-	-	-	-	-	-	-
Lysimachia thyrsiflora	0.06	-	-	-	0.8	-	-	-	-	-	-	-	-	-
Linum catharticum	0.04	-	-	-	0.6	-	-	-	-	-	-	-	-	-
Lycopus europaeus	0.01	-	-	-	0.2	-	-	-	-	-	-	-	-	-
only in MV														
Inula britannica	0.12	-	-	-	-	-	-	1.6	-	-	-	-	-	-
Urtica dioica	0.10	-	-	-	-	-	-	1.4	-	-	-	-	-	-
Anthriscus sylvestris	0.04	-	-	-	-	-	-	0.6	-	-	-	-	-	-
Calystegia sepium	0.04	-	-	-	-	-	-	0.6	-	-	-	-	-	-
Potentilla erecta	0.04	-	-	-	-	-	0.6	-	-	-	-	-	-	-
only in SH														
Carex extensa	0.21	-	-	-	-	-	-	-	-	2.8	-	-	-	-
Cochlearia anglica	0.18	-	-	-	-	-	-	-	0.8	0.8	0.8	-	-	-
Lolium perenne	0.16	-	-	-	-	-	-	-	0.8	0.6	0.8	-	-	-
Cotula coronopifolia	0.16	-	-	-	-	-	-	-	2.2	-	-	-	-	-
Lepidium latifolium	0.13	-	-	-	-	-	-	-	-	1.0	0.8	-	-	-
Convolvulus arvensis	0.06	-	-	-	-	-	-	-	-	-	0.8	-	-	-
Chenopodium spec.	0.06	-	-	-	-	-	-	-	-	-	0.8	-	-	-
Althaea officinalis	0.06	-	-	-	-	-	-	-	-	0.8	-	-	-	-
Apium graveolens	0.06	-	-	-	-	-	-	-	-	-	0.8	-	-	-
Linaria vulgaris	0.04	-	-	-	-	-	-	-	-	0.6	-	-	-	-
Thalictrum flavum	0.04	-	-	-	-	-	-	-	-	-	0.6	-	-	-
only in DK														
Cochlearia officinalis	0.31	-	-	-	-	-	-	-	-	-	-	0.8	0.4	3.0
Cochlearia danica	0.24	-	-	-	-	-	-	-	-	-	-	0.8	1.6	0.8
Danthonia decumbens	0.12	-	-	-	-	-	-	-	-	-	-	-	0.8	0.8
Radiola linoides	0.10	-	-	-	-	-	-	-	-	-	-	-	0.6	0.8
Stellaria graminea	0.10	-	-	-	-	-	-	-	-	-	-	-	0.6	0.8
Empetrum nigrum	0.09	-	-	-	-	-	-	-	-	-	-	-	0.6	0.6
Anthoxanthum odoratum	0.06	-	-	-	-	-	-	-	-	-	-	-	-	0.8
Atriplex pedunculata	0.04	-	-	-	-	-	-	-	-	-	-	0.6	-	-
Bupleurum tenuissimum	0.04	-	-	-	-	-	-	-	-	-	-	0.6	-	-
Ranunculus sceleratus	0.03	-	-	-	-	-	-	-	-	-	-	-	-	0.4
Angelica archangelica ssp. *litoralis*	0.01	-	-	-	-	-	-	-	-	-	-	-	-	0.2
Heracleum mantegazzianum	0.01	-	-	-	-	-	-	-	-	-	-	-	-	0.2
Galeopsis spec.	0.13	-	-	0.6	-	-	0.6	0.6	-	-	-	-	-	-
Dactylorhiza spec.	0.07	0.4	-	-	0.4	-	-	-	-	-	-	-	-	-
Lathyrus spec.	0.04	-	0.6	-	-	-	-	-	-	-	-	-	-	-
Epilobium spec. (juv.)	0.06	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Betula spec. (juv.)	0.03	0.3	-	-	-	-	-	-	-	-	-	-	-	-
Rumex spec. (juv.)	0.03	-	-	-	-	0.4	-	-	-	-	-	-	-	-
Sonchus spec. (juv.)	0.15	-	-	-	-	-	-	-	-	-	2.0	-	-	-
Carex spec.	0.09	-	-	-	-	-	-	-	0.6	0.6	-	-	-	-
Cerastium spec.	0.09	-	-	-	-	-	-	-	-	-	-	-	0.6	0.6
Poaceae	0.10	-	-	-	-	-	-	-	0.6	0.8	-	-	-	-
unknown	0.09	-	-	0.2	0.2	-	-	-	0.8	-	-	-	-	-
number of species (without taxa on genus level)	153	77	60	73	64	25	35	46	38	41	34	42	44	57

Annex 3

Mean cover (%) of individual species (on 1 m²) in the vegetation of grazed, early and late successional sites; in Estonia (EST), Mecklenburg-Vorpommern (MV), Schleswig-Holstein, (SH) and Northern Denmark (DK). Species are grouped by the impact of management or by their distribution in the regions. Results of statistical tests in table 4-18.

Region	Management			Region			
Management	G	ES	LS	EST	MV	SH	NDK
max in grazed							
Juncus gerardii	27.1	15.0	8.9	21.5	16.1	16.7	14.5
Agrostis stolonifera	23.6	11.5	6.8	12.0	27.8	12.4	5.3
Puccinellia maritima	12.2	4.7	0.0	0.0	2.0	10.2	11.8
Glaux maritima	9.7	6.1	5.8	8.7	5.0	8.7	6.5
Plantago maritima	16.1	13.4	6.4	9.1	5.4	18.3	16.0
Triglochin maritimum	5.7	6.0	3.0	6.1	4.3	4.7	4.4
max in early succ.							
Bolboschoenus maritimus	1.5	7.5	2.8	1.4	7.8	2.6	3.9
Festuca rubra	15.4	42.3	25.4	25.1	28.7	28.3	27.4
Artemisia maritima	1.7	6.2	1.0	0.0	0.3	5.6	6.1
Limonium vulgare	1.5	2.9	0.4	0.0	0.0	3.2	3.2
Festuca arundinacea	0.4	2.1	1.8	2.6	2.5	0.3	0.1
Elymus repens	1.3	8.2	12.0	7.2	11.5	2.0	7.2
max in late succ.							
Phragmites australis	1.4	1.4	68.3	18.7	26.3	25.8	21.6
Galium palustre	0.8	1.0	2.5	3.6	1.2	0.0	0.5
Eleocharis uniglumis	1.1	3.2	4.7	9.1	1.2	0.3	0.4
max (or only) in EST							
Carex panicea	1.5	1.0	0.4	3.6	0.0	0.0	0.0
Leontodon autumnalis	1.8	1.3	1.4	3.4	1.0	0.5	1.0
Carex nigra	1.1	0.7	0.3	2.5	0.0	0.0	0.0
Angelica palustris	0.5	0.6	0.1	1.5	0.0	0.0	0.0
Carex distans	1.4	1.9	1.3	3.2	0.0	1.2	1.3
Vicia cracca	0.4	1.4	3.5	1.5	0.3	0.2	4.8
max in DK							
Aster tripolium	2.0	4.3	1.9	1.1	4.1	2.8	3.1
Potentilla anserina	4.1	6.3	4.1	6.6	3.2	5.1	4.0

Annex 4

Mean frequency of individual species (%-frequency in five 1-m²-subplots per site) in the vegetation of grazed, early and late successional sites; in Estonia (EST), Mecklenburg-Vorpommern (MV), Schleswig-Holstein, (SH) and Northern Denmark (DK). Species are grouped by the impact of management or by their distribution in the regions. Results of statistical tests in table 4-19.

	grazed	early succ.	late succ.	EST	MV	SH	DK
max in grazed							
Spergularia salina	34.5	1.0	1.0	0.0	17.3	20.0	16.0
Puccinellia maritima	36.4	11.0	0.0	0.0	14.7	26.7	26.7
Juncus gerardii	98.2	92.0	73.0	95.3	86.7	85.3	84.0
Trifolium fragiferum	12.7	4.0	0.0	16.5	1.3	4.0	0.0
Agrostis stolonifera	91.8	89.0	71.0	98.8	85.3	80.0	70.7
Centaurium littorale	18.2	7.0	2.0	24.7	0.0	0.0	10.7
Spergularia media	36.4	13.0	4.0	0.0	13.3	28.0	34.7
Triglochin maritimum	90.0	88.0	50.0	92.9	68.0	54.7	88.0
Plantago maritima	97.3	82.0	36.0	80.0	65.3	60.0	84.0
Glaux maritima	86.4	86.0	61.0	85.9	74.7	77.3	73.3
Odontites litoralis	31.8	28.0	10.0	52.9	2.7	0.0	34.7
Leontodon autumnalis	30.9	32.0	16.0	69.4	12.0	2.7	16.0
Salicornia europaea	20.9	4.0	1.0	0.0	0.0	16.0	21.3
Suaeda maritima	16.4	1.0	0.0	0.0	0.0	8.0	17.3
max in early succ.							
Festuca rubra agg.	84.5	99.0	75.0	87.1	89.3	78.7	89.3
Artemisia maritima	9.1	31.0	15.0	0.0	1.3	28.0	45.3
Festuca arundinacea	5.5	19.0	16.0	32.9	14.7	1.3	1.3
Elymus repens	11.8	41.0	53.0	40.0	45.3	20.0	32.0
max in late succ.							
Phragmites australis	14.5	13.0	100.0	43.5	49.3	38.7	34.7
Sonchus asper	0.0	6.0	16.0	0.0	16.0	9.3	4.0
Oenanthe lachenalii	0.0	8.0	19.0	0.0	25.3	8.0	2.7
Bolboschoenus maritimus	12.7	28.0	31.0	16.5	34.7	17.3	26.7
Galium palustre	11.8	19.0	39.0	63.5	14.7	0.0	8.0
Eleocharis uniglumis	14.5	29.0	24.0	68.2	9.3	1.3	4.0
max (or only) in Estonia							
Carex panicea	18.2	5.0	6.0	36.5	0.0	0.0	0.0
Molinia caerulea	11.8	6.0	3.0	25.9	0.0	0.0	0.0
Rhinanthus angustifolius	7.3	13.0	1.0	25.9	0.0	0.0	0.0
Blysmus rufus	10.9	5.0	3.0	23.5	0.0	0.0	0.0
Carex nigra	11.8	2.0	4.0	22.4	0.0	0.0	0.0
Angelica palustris	11.8	9.0	3.0	29.4	0.0	0.0	0.0
Selinum carvifolia	1.8	2.0	3.0	8.2	0.0	0.0	0.0
Trifolium pratense	13.6	15.0	12.0	37.6	4.0	0.0	9.3
Potentilla anserina	38.2	41.0	38.0	71.8	26.7	22.7	30.7
Carex distans	20.0	25.0	15.0	42.4	0.0	9.3	25.3
Juncus articulatus	10.0	4.0	6.0	17.6	0.0	0.0	8.0
Taraxacum officinale	2.7	4.0	2.0	9.4	0.0	0.0	1.3
Trifolium repens	15.5	12.0	3.0	23.5	4.0	6.7	5.3
Schoenoplectus tabernaemontani	8.2	4.0	17.0	29.4	6.7	0.0	0.0
Centaurea jacea	6.4	3.0	0.0	10.6	1.3	0.0	0.0
Lotus corniculatus/tenuis	17.3	12.0	5.0	20.0	12.0	5.3	8.0
max in SH and/or MV							
Cirsium arvense	1.8	7.0	9.0	1.2	8.0	14.7	0.0
Atriplex prostrata	30.9	45.0	61.0	17.6	56.0	62.7	48.0
max (or only) in DK							
Limonium vulgare	20.9	29.0	6.0	0.0	0.0	20.0	57.3
Armeria maritima	19.1	20.0	9.0	0.0	5.3	13.3	48.0
Aster tripolium	46.4	48.0	45.0	21.2	49.3	50.7	68.0
Cochlearia officinalis	3.6	1.0	12.0	0.0	0.0	0.0	22.7
max in DK and EST							
Centaurium pulchellum	25.5	12.0	5.0	18.8	1.3	6.7	30.7

Annex 5

Mean seed density (seeds/m²) and mean cover (%, on 25 m²) of all taxa found in the vegetation and/or seed bank of the matched data set (Estonia), in grazed, early and late successional sites. Species traits: life cycle: a: annual, b: biennial, p: perennial; BBCM: 'characteristic species' of Boreal Baltic Coastal Meadows according the the EU-Habitats Directive (EC 2007, see methods, 3.3.2); species group: socio-ecological species groups (see methods, 3.3.2). Species are grouped by their occurrence in the seed bank (SB) and/or aboveground vegetation (AV), and ranked by abundances.

	grazed		early succ.		late succ.					
	seeds/ m²	% cover	seeds/ m²	% cover	seeds/ m²	% cover	in SB/AV	life cycle	x	species group
in seed bank and vegetation										
Juncus gerardii	33852	23	24852	7	28692	15	SB+AV	p	x	salt marsh
Juncus articulatus	14662	4	801	3	1677	-	SB+AV	p		fen/small sedge
Eleocharis uniglumis	4130	3	2191	6	10019	10	SB+AV	p	x	reed bed
Glaux maritima	1408	3	5057	10	3207	2	SB+AV	p		salt marsh
Agrostis stolonifera	1911	5	1165	5	796	7	SB+AV	p	x	flood meadow
Centaurium littorale	915	3	893	3	21	-	SB+AV	a	x	salt marsh
Carex flacca	1192	4	185	3	105	-	SB+AV	p		indifferent
Centaurium pulchellum	840	4	119	4	629	-	SB+AV	a	x	ruderal
Schoenoplectus tabernaemontani	146	4	715	3	650	4	SB+AV	p		reed bed
Plantago maritima	594	4	278	5	42	4	SB+AV	p	x	salt marsh
Carex nigra	739	3	66	4	21	-	SB+AV	p	x	fen/small sedge
Carex distans	292	3	569	3	42	3	SB+AV	p		indifferent
Triglochin maritimum	262	3	291	3	314	3	SB+AV	p	x	salt marsh
Potentilla anserina	503	3	66	8	21	2	SB+AV	p		flood meadow
Galium palustre	106	4	86	4	1551	13	SB+AV	p		reed bed
Atriplex prostrata	211	-	258	3	0	4	SB+AV	a		ruderal
Trifolium fragiferum	241	3	199	3	21	-	SB+AV	p		flood meadow
Festuca rubra agg.	231	16	159	27	0	3	SB+AV	p	x	salt marsh
Leontodon autumnalis	121	4	252	4	21	4	SB+AV	p		grassland
Cardamine pratensis	30	2	33	-	608	2	SB+AV	p		indifferent
Carex viridula var. viridula	171	3	0	3	0	-	SB+AV	p		indifferent
Molinia caerulea	15	3	192	3	0	-	SB+AV	p		indifferent
Odontites litoralis	60	4	106	3	0	-	SB+AV	a	x	salt marsh
Trifolium repens	101	4	0	4	0	-	SB+AV	p		grassland
Taraxacum officinale agg.	86	2	13	-	0	1	SB+AV	p		not classified
Lotus corniculatus	86	4	7	4	0	2	SB+AV	p		grassland
Aster tripolium	25	2	26	4	84	3	SB+AV	b		salt marsh
Carex panicea	60	3	7	2	0	-	SB+AV	p		fen/small sedge
Bolboschoenus maritimus	35	-	13	3	21	1	SB+AV	p	x	reed bed
Ranunculus repens	45	4	0	-	0	-	SB+AV	p		indifferent
Trifolium pratense	40	4	0	3	0	1	SB+AV	p		grassland
Festuca arundinacea	25	3	0	3	0	-	SB+AV	p		flood meadow
Mentha aquatica	10	-	0	-	42	2	SB+AV	p		reed bed
Achillea millefolium	15	3	0	3	0	-	SB+AV	p		grassland
Pedicularis palustris	0	-	0	2	42	1	SB+AV	b		fen/small sedge
Elymus repens	0	-	13	3	0	3	SB+AV	p		ruderal
Phragmites australis	5	3	7	2	0	37	SB+AV	p		reed bed
Sesleria caerulea	5	3	0	-	0	-	SB+AV	p		fen/small sedge
Rhinanthus angustifolius	5	3	0	3	0	-	SB+AV	a		indifferent
Ranunculus acris	5	4	0	-	0	-	SB+AV	p		grassland
Juncus bufonius agg.	*583*	-	*490*	-	*21*	-	SB(+plots)	a		ruderal
only in seed bank										
Poa annua	55	-	0	-	42	-	SB	a		indifferent
Poa pratensis	50	-	13	-	0	-	SB	p		grassland
Carex spec.	50	-	7	-	0	-	SB	p		
Rorippa palustris	10	-	26	-	84	-	SB	b		ruderal
Linaria vulgaris	0	-	66	-	0	-	SB	p		ruderal
Sagina procumbens	30	-	20	-	0	-	SB	p		ruderal
Plantago major ssp. winteri	15	-	33	-	21	-	SB	p		not classified
Sonchus oleraceus	35	-	0	-	21	-	SB	a		ruderal
Agrostis gigantea	15	-	33	-	0	-	SB	p		grassland

		grazed		early succ.		late succ.			life		
	m²	cover	m²	cover	m²	cover	in SB/AV		life cycle	x	species group
Poa spec.	0	-	53	-	0	-	SB				
Hypericum tetrapterum	0	-	0	-	0	-	SB		p		grassland
Linum catharticum	15	-	7	-	0	-	SB(+plots)		a		grassland
Filago vulgaris	20	-	0	-	0	-	SB		a		grassland
Ranunculus sceleratus	20	-	0	-	0	-	SB		a		ruderal
Lycopus europaeus	15	-	0	-	0	-	SB		p		reed bed
Lolium perenne	10	-	7	-	0	-	SB		p		grassland
Poa trivialis	15	-	0	-	0	-	SB		p		grassland
Juncus spec.	0	-	0	-	63	-	SB				
Sagina maritima	10	-	0	-	0	-	SB		a		salt marsh
Spergularia media	10	-	0	-	0	-	SB		p		salt marsh
Cirsium oleraceum	5	-	0	-	21	-	SB		p		grassland
Poa compressa	10	-	0	-	0	-	SB		p		ruderal
Ranunculus spec.	10	-	0	-	0	-	SB				
Suaeda maritima	5	-	0	-	0	-	SB(+plots)		a		salt marsh
Typha angustifolia	0	-	7	-	0	-	SB		p		reed bed
Gnaphalium uliginosum	0	-	7	-	0	-	SB		a		ruderal
Persicaria lapathifolia	0	-	7	-	0	-	SB		a		ruderal
Plantago major	5	-	0	-	0	-	SB		p		ruderal
Alopecurus geniculatus	5	-	0	-	0	-	SB		p		flood meadow
Myosurus minimus	0	-	0	-	21	-	SB		a		flood meadow
Potentilla reptans	5	-	0	-	0	-	SB		p		flood meadow
Veronica arvensis	5	-	0	-	0	-	SB		a		grassland
Silene flos-cuculi	0	-	7	-	0	-	SB		p		grassland
Juncus tenuis	0	-	7	-	0	-	SB		p		ruderal
Rumex acetosella	5	-	0	-	0	-	SB		p		indifferent
Fragaria spec.	5	-	0	-	0	-	SB		p		
Rhinanthus spec.	5	-	0	-	0	-	SB				
only in aboveground vegetation											
Angelica palustris	0	4	0	3	0	-	AV		p		grassland
Blysmus rufus	0	2	0	4	0	4	AV		p	x	salt marsh
Vicia cracca	0	3	0	3	0	-	AV		p		grassland
Centaurea jacea	0	3	0	3	0	-	AV		p		grassland
Frangula alnus (juv.)	0	2	0	-	0	-	AV		p		forest (edge)
Sonchus arvensis	0	-	0	3	0	-	AV		p		ruderal
Valeriana officinalis	0	-	0	2	0	-	AV		p		grassland
Juniperus communis	0	2	0	-	0	-	AV		p		indifferent
Equisetum pratense	0	4	0	-	0	-	AV		p		forest (edge)
Ophioglossum vulgatum	0	3	0	3	0	-	AV		p	x	grassland
Parnassia palustris	0	4	0	-	0	-	AV		p		fen/small sedge
Galium boreale	0	4	0	-	0	-	AV		p		grassland
Sium latifolium	0	-	0	-	0	3	AV		p		reed bed
Briza media	0	4	0	-	0	-	AV		p		grassland
Epilobium spec. (juv.)	0	3	0	-	0	-	AV		p		
Succisa pratensis	0	3	0	-	0	-	AV		p		grassland
Phleum pratense	0	-	0	4	0	-	AV		p		grassland
Medicago lupulina	0	3	0	-	0	-	AV		a		grassland
Inula salicina	0	3	0	4	0	-	AV		p		grassland
Carex disticha	0	4	0	3	0	-	AV		p		reed bed
Triglochin palustre	0	3	0	-	0	-	AV		p		fen/small sedge
Galium verum	0	3	0	-	0	-	AV		p		grassland
Blysmus compressus	0	3	0	4	0	-	AV		p		indifferent
Melilotus altissimus	0	3	0	-	0	-	AV		b		ruderal
Rumex crispus	0	-	0	2	0	-	AV		p		flood meadow
Eleocharis palustris	0	-	0	4	0	-	AV		p		reed bed
Primula farinosa	0	3	0	-	0	-	AV		p		fen/small sedge
Fraxinus excelsior (juv.)	0	3	0	-	0	-	AV		p		forest (edge)
Hierochloe odorata	0	2	0	-	0	-	AV		p		grassland
Lathyrus palustris	0	-	0	-	0	3	AV		p		grassland
Filipendula ulmaria	0	-	0	2	0	-	AV		p		grassland
Selinum carvifolia	0	4	0	-	0	-	AV		p		grassland
Stellaria alsine	0	3	0	-	0	-	AV		p		reed bed
Plantago major ssp. Intermedia	0	3	0	-	0	-	AV		p		flood meadow
Sagina nodosa	0	3	0	-	0	-	AV		p		flood meadow

	grazed		early succ.		late succ.			life		
	m²	cover	m²	cover	m²	cover	in SB/AV	cycle	x	species group
Plantago lanceolata	0	3	0	-	0	-	AV	p		grassland
Hypochoeris radicata	25	-	0	3	0	-	AV	p		grassland
Epilobium palustre	0	-	0	-	0	3	AV	p		fen/small sedge
Cicuta virosa (juv.)	0	-	0	-	0	1	AV	p		reed bed
Peucedanum palustre	0	-	0	-	0	1	AV	p		reed bed
Atriplex littoralis	0	-	0	1	0	-	AV	a		salt marsh
Galium aparine	0	-	0	1	0	-	AV	a		ruderal
Carex flacca x panicea	0	1	0	-	0	-	AV	p		
Lathyrus spec.	0	-	0	2	0	-	AV	p		
Rumex spec. (juv.)	0	-	0	-	0	2	AV			
unknown	15	-	26	-	63	-	SB			

Summary

Introduction

Along the Baltic Sea coasts, salt grasslands are affected by pronounced ecological gradients. Salinity decreases towards the Northeast, climate becomes colder towards the North and more continental towards the East. Land rise at the northern Baltic coasts causes vegetation zones to move seaward resulting in the occurrence of salt grasslands on young shallow soils. In contrast, land subsidence in the Southwest enhances the formation of coastal peatlands.

Salt grasslands of the Baltic Sea coast have developed from brackish reed beds due to centuries of human use for grazing and mowing. Consequently, traditional use is also essential for their maintenance. Baltic salt grasslands have been severely reduced by diking, drainage, and intensification of agriculture. Today, salt grasslands in the whole Baltic Sea region are threatened by cessation of traditional use.

As a conservation measure, grazing is financially supported in the Baltic Sea region. Beyond that, restorative grazing is currently re-introduced in many formerly abandoned sites with the aim to restore salt grasslands. The restoration potential of degraded sites depends *inter alia* on dispersal and persistence of seeds of characteristic species in the soil seed bank.

Salt grasslands are not only important as habitats, but do also support a number of ecosystem functions. Particulate matter and nutrients can be deposited in salt grasslands by sedimentation and peat formation, and various transformation processes take place in these ecosystems. Thus, salt grasslands can play an important role in the nitrogen, phosphorous and silica balance of coastal waters. Due to the functional interactions between salt grasslands and coastal waters, salt grasslands can be interpreted as a part of the coastal and transitional waters according to the Water Framework Directive. Consequently, they should be included in the classification of the ‘ecological status’ of coastal waters.

Aims of the thesis

This thesis aims to analyse patterns of succession and phytodiversity of grazed and abandoned salt grasslands along the complex ecological gradient along the Baltic Sea coast. The potential of grazing as a conservation and restoration measure in salt grasslands shall be estimated.

Furthermore, the restoration potential from the soil seed banks of abandoned Estonian salt grasslands shall be assessed.

Finally, the relevance of coastal marshes of the German Baltic Sea for the ecological status of coastal waters shall be highlighted, and a method for classifying these marshes for the European Water Framework Directive will be proposed.

Methods

Four regions along the salinity gradient were selected: Northern Denmark with a salinity of 22-28 psu, Schleswig-Holstein (Western Germany, salinity of 10-18 psu), Mecklenburg-Vorpommern (east of the Darß sill, Eastern Germany, salinity of 7-9 psu) and Western Estonia (6-7 psu). In all four study regions, continuously grazed salt grasslands were compared with early and late successional stages of abandoned salt grasslands. 'Late successional stage' was determined by the invasion of *Phragmites australis* with a cover of > 25%. For each region and management class, 5-7 replicate sites were selected. In addition, five 'restored' sites were investigated in Estonia: formerly 'late successional' sites where grazing has been reintroduced 2-4 years ago.

Vegetation was examined between July and September in the years 2004 to 2007 on a representative plot of 25 m x 25 m in the lower salt marsh zone. Species composition of vascular plants was recorded on the whole 625 m²-plot, on 5 subplots of 25 m² and 5 subplots of 1 m² (in a nested design). Species composition and vegetation structure were recorded. In addition, site conditions were characterised by measuring or estimating parameters such as elevation, flooding frequency, management history and soil parameters. Furthermore, mean Ellenberg indicator values were calculated.

The seed bank was sampled on five grazed, four 'early successional' and two 'late successional' sites in Estonia in November 2004. A pooled sample of approx. 800 ml was taken per 25 m²-subplot and divided into two horizons (0-5 cm, 5-10 cm). The number and species composition of seeds was determined using the seedling emergence method.

Plant species were categorised by various traits (life-cycle, CSR-strategy type, socio-ecological species groups, Red List species and 'characteristic species' according to the EU-Habitats Directive). For species with a sufficient number of seeds and detections in the seed bank, a longevity index (LI) was calculated. The LI was calculated both based on the own data and in combination with data derived from the data base of Thompson et al. (1997).

Impact of management on Baltic salt grassland vegetation along a complex ecological gradient

The most pronounced changes between the regions occurred in Estonia, be it in abiotic parameters or in vegetation characteristics. Soil salinity was significantly lower in Estonia, as well as the salt indicator value. The stress gradient connected with salinity was also indicated by a higher stress component (after the CSR-strategy types of Grime 1979) in Denmark. An increase in soil phosphate content and nitrogen indicator values towards the Western end of the Baltic Sea (Denmark) indicated a nutrient gradient, which was correlated to anthropogenic nutrient loads. Species numbers were higher in Estonia, primarily on a larger scale (625 m²), which was also reflected in the steeper slope and the higher intercept of the species-area-curves. Also the evenness of the vegetation was higher in Estonia.

A number of abiotic parameters did not reflect differences between the four regions, but revealed that two different salt grassland soil types with different development histories exist. A 'shallow soil type' with a low organic layer, lower nutrient values and mostly high pH values dominates the land rise areas (Estonia, Danish island of Læsø) and occurs also in some beach ridge systems at the Southern Baltic coast (Schleswig-Holstein, Mecklenburg-Vorpommern). The shallow soil type has a species-rich vegetation with a high evenness, probably due to lower competition, higher small-scale variability of site conditions and more natural transitions towards non-saline habitats. In sites of the shallow soil type, species numbers slightly increased from early to late successional sites.

In contrast, the ‘deep salt grassland soil type’ has a deep organic layer with higher nutrient values and a lower pH. It dominates in the Southern Baltic regions representing coastal peatlands. It occurs also at the Danish mainland, where land rise is only marginal and sites are located at Fjord entrances or along the outer shore and are more strongly influenced by nutrient run-off from agricultural fields (compared to the island of Læsø). In sites of the deep soil type, species numbers and evenness decreased from early to late successional sites.

In the course of succession, the vegetation structure changed already in early successional sites: Here, vegetation cover and canopy were higher and the litter layer was thicker. Major shifts in species groups and species composition occurred primarily towards late successional sites. Evenness decreased in late successional sites. Species numbers in general varied strongly between sites and were not significantly affected by management. Species numbers decreased only in late successional sites in Schleswig-Holstein, where time since abandonment was longer than in the other three regions. The decrease in species richness was only significant on small scales of 1 and 25 m², but not on 625 m². In late successional sites of all regions, species numbers per m² decreased with increasing cover of *Phragmites australis*. The species-area-curves were steeper in late successional sites. With respect to the CSR-strategy types, the competitive component increased in early and late successional sites, whereas the ruderal and stress components decreased.

‘Characteristic species’ according to the Habitats Directive declined in late successional sites. The decline was more pronounced on small scales (1 and 25 m²). The percentage of Red List species showed a peak in early successional sites in Schleswig-Holstein, followed by a steep decline in late successional sites. In contrast, it steadily decreased in Mecklenburg-Vorpommern, where it was in general lower than in Schleswig-Holstein.

It is concluded that salinity as well as geomorphology and soil development affect Baltic salt grassland vegetation and determine their species richness at different spatial scales. Abandonment does not necessarily lead to a loss of species or species richness. Only if succession to dense reed beds takes place, this development can be expected in the long run. Furthermore, the effect of abandonment on species richness occurs primarily on small spatial scales. Even if all salt grasslands were abandoned, it is unlikely that any salt grassland plant species would become extinct on a larger scale.

The regions along the Baltic Sea gradient differ with respect to speed and direction of succession: In the western regions, Denmark and Schleswig-Holstein, succession towards brackish reed beds is slower and in general less likely. The studied ‘early successional stage’ of salt grasslands dominated by e.g. *Festuca rubra, Artemisia maritima* etc. can persist for at least several decades. It is even likely to represent the terminal stage of succession in the majority of Northern Danish salt grasslands, and possibly also in some sites in Schleswig-Holstein, where factors such as exposure, disturbances, low nutrient availability or herbivores prevent the spread of *Phragmites australis*. Thus, succession towards brackish reed beds is not necessarily expected for all sites here.

In contrast, the succession towards brackish reed beds is much quicker in the eastern, less saline regions Mecklenburg-Vorpommern and Estonia. In Mecklenburg-Vorpommern, it is accelerated by high nutrient availability of the prevailing coastal peatlands. Only in exceptional cases, with a low nutrient availability (‘shallow soil type’), additional disturbing factors (such as exposure, ice scouring, ‘natural’ grazing etc.) may retard (or prevent) the succession towards brackish reed beds.

The peak of Red List species in early successional sites in Schleswig-Holstein representing an intermediate ‘charming phase of succession’ indicates that some rare and endangered species profit from the cessation of grazing, while others decline. The same management regime may therefore not favour all rare and endangered plant species. Thus, the nature conservation target ‘protection of rare and endangered plant species’ can only be fulfilled if a variety of management regimes or at least grazing intensities is applied on regional scale.

Impact of grazing, abandonment and restoration on vegetation and seed banks of salt grasslands in Estonia

A significant change of vegetation species numbers occurred neither in the course of progressive nor of retrogressive succession. No major loss of species occurred during abandonment (so far). Plant species composition of ‘restored’ Estonian salt grasslands was ‘halfway’ between that of late successional and grazed salt grasslands. Most species which declined after abandonment increased again after restorative grazing. Likewise, most species which increased after abandonment decreased again after restorative grazing, except for *Phragmites australis* and *Elymus repens* which still persisted in the vegetation of restored sites with a high frequency, but lower cover.

The seed bank contained seeds of 78 taxa, nearly as many as in the vegetation of the matched data set (85). Seed density was generally high (more than 50,000 seeds/m²). Neither seed density nor species number did change in the course of progressive succession. The species composition changed relatively little compared to the changes in the vegetation. Salt marsh species declined in the vegetation after abandonment, but not in the seed bank. The seed bank was dominated by ‘characteristic species’ (according to the EU-Habitats Directive), which were overrepresented in the seed bank of early and late successional sites compared to the vegetation. This pattern was mainly caused by the strong dominance of primarily *Juncus gerardii*, accompanied in late successional sites by *Eleocharis uniglumis*. *Centaurium littorale* and *C. pulchellum* decreased in the vegetation during abandonment, but were overrepresented in the seed bank of early successional sites. They increased in the vegetation after restoration, indicating a re-establishment from a (at least short-term) persistent seed bank. ‘Characteristic species’ and salt marsh species showed comparatively high seed persistence.

It is concluded that restoration of salt grasslands from reed-dominated ‘late’ successional stages (after 10-25 years of abandonment) by restorative cattle grazing is promising. However, although vegetation changes are reversed, more time than 2-4 years is needed to restore the vegetation of salt grasslands. A sufficient grazing pressure, especially in spring and early summer, has to be maintained to further suppress late successional species such as *Phragmites australis* and *Elymus repens*.

The seed banks of the studied Estonian salt grasslands have a high potential for the restoration of characteristic vegetation, but will not necessarily enhance species richness. In contrast to other habitats, there is no ‘risk’ in activating the seed bank, since there are no ‘weed’ or ‘problem’ species in the seed bank that could out-compete target species. Restorative grazing may activate the seed bank and contribute to the re-establishment of characteristic plant species.

A method for classifying coastal marshes of the German Baltic Sea for the European Water Framework Directive

Angiosperms are identified in the European Water Framework Directive (WFD) as one of the biological quality elements used to classify the ecological status of coastal waters. This comprises not only sea grasses, but also salt marshes of the intertidal zone. It is suggested including also coastal marshes at the non-tidal Baltic Sea in the WFD-classification, since they are relevant to the quality of coastal waters particularly regarding eutrophication.

A classification method for Baltic coastal marshes which is based on vegetation and hydromorphological parameters was developed. Vegetation parameters include ‘quantity’ indicated by the areal extent of coastal marshes as well as coastal marsh ‘quality’ indicated by zonation of the vegetation and species composition. Hydromorphological indicators such as creeks, ditches and dikes are used to support the vegetation parameters because they indicate anthropogenic alterations more directly than other quality elements and without any time lag. Since no negative impact of grazing on water quality is known, reference conditions include grazed marshes as well as ungrazed reed beds. While vegetation parameters such as zonation and species composition should be assessed in the field, areal extent and hydromorphological parameters are primarily based on existing GIS-based information, which must be complemented and verified in the field.

Finally, recommendations are given for a field trial to validate the classification method. Monitoring after a 6-year interval should be carried out further to comply with the requirements of the WFD and the Habitats Directive.

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Antonia Wanner

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