Plant Ecology **166:** 275–293, 2003.
© 2003 *Kluwer Academic Publishers. Printed in the Netherlands.*

Germination in Baltic coastal wetland meadows: similarities and differences between vegetation and seed bank

Heli M. Jutila
Äijälänkatu 4B 12, Hämeenlinna, SF-13210, Finland (e-mail: heli.jutila@ymos.htk.fi; phone: (358) 3–625 1492)

Received 17 April 2001; accepted in revised form 21 March 2002

Key words: Coastal wet meadow, Grazing, Mature vegetation, Seedling, Species richness, Wetland diversity

Abstract

The abundance and variety of seedlings in Baltic coastal grasslands was studied in cattle grazed and ungrazed areas in seashore and delta on the western coast of Finland. The vegetation, seed bank and environmental conditions of the same sites were also studied. Altogether 4609 seedlings were observed in 79 field plots (20 cm × 20 cm) making an average of 1458.54 seedlings/m^2. The majority of the seedlings were dicots (67.5%) and perennials (96.8%). Altogether 44 species and an average of 4.14 species per plot were identified as seedlings. The most abundant taxon, *Carex* formed 23.2% of all the seedlings observed in the field. In the delta the seedling density was two times that found at the seashore. Also, the numbers of species of seedlings per plot were significantly higher in the delta than in the seashore, but in total, more species germinated from the seashore than from the delta even though the number of plots was higher in the delta (n = 51) than in the seashore (n = 28). The numbers of species and seedlings per plot were smaller in grazed sites than in ungrazed ones similar to the pattern earlier reported concerning the mature vegetation and seed bank. The mean numbers of seedlings were the highest at lower geolittoral plots (about 20 cm elevation), where the seed bank was also densest. About 60.0% of the mature species in the plots were also detected as seedlings and 91.4% of the seedling species were found in the mature vegetation of the plots. The number of seedlings was positively correlated with the cover of mature vegetation giving support to the nurse effect theory. Seedling numbers were negatively correlated with the abundance of litter indicating that litter restricts germination because it is a mechanical barrier but also decreases the amount of light. The number of seedlings and species, both in total and per unit area, were greater in the seed bank than in the field seedling population. The seedling population was more similar to the mature vegetation than to the seed bank.

Nomenclature: Nomenclature = Hämet-Ahti et al. (1998)

Introduction

Seedling establishment is a crucial phase in a plant's life history (e.g. Grubb (1977) and Harper (1977), Grime (1979), Fenner (1985)) and an important factor controlling the abundances of adult plants. Ecologists have mainly studied seedling establishment by using germination experiments in artificial settings. However, germination studies are frequently performed in ways that make it difficult to extrapolate results to the field. Furthermore, we still lack basic information about seedling germination in the field. Experimental studies are certainly needed, but they can be more useful when there is some basic information about the germination patterns and conditions in the field. Only a few studies have analysed relationships between seedling flora and mature vegetation in herbaceous communities (Freedman et al. 1982; McGraw and Shaver 1982; Bakker et al. 1985; Rusch 1988; Welling and Laine 2000) and even fewer have also used the seed bank in the same comparisons (Parker and Leck 1985; Leck and Simpson

(1993, 1994, 1995); Milberg 1993; Chambers 1995). Some studies have also looked at the relationships between seed rain and seedling flora at a community level (e.g. Peart (1989) and Milberg (1993), Debussche and Isenmann (1994), Leck and Simpson (1994), Chambers (1995), Houle (1995)). Schupp (1995) has recently elaborated on the topic of seed-seedling conflicts in habitat choice and the pattern of plant reproduction. Such conflicts are examples of parent – offspring conflicts, in which what is beneficial to the parent is not necessarily so for the offspring; thus, what is good for a seed, for a seedling or for an adult can differ. This is one good explanation for the apparent differences that have been detected or anticipated among the seed bank, the seedling flora and the mature vegetation. In his paper, Schupp (1995) mainly focused on the influence of herbivory and growth rate on the parent-offspring conflicts.

In many studies (Gough et al. 1994; Sanchez et al. 1996; Grace and Jutila 1999; Jutila 1999a) it has been shown that duration and depth of flooding are the most important factors shaping shore vegetation. Shore plants, which are affected by disturbances such as flooding, salinity, waves and ice, may survive the stressful conditions by using avoidance strategies, such as a persistent seed bank, or tolerance strategies, such as metabolic adaptations (Crawley 1986). Most shore plants use both strategies but with varying intensities and different methods at various life stages.

The seed bank forms a reserve that plants can use when disturbances create gaps for recruitment. Moore and Keddy (1988) showed that germination requirements are important in controlling recruitment of wetland species in response to disturbance. In my earlier seed bank studies (Jutila (1998a, 1998b)) I found that the seed banks of Baltic coastal grasslands are abundant (Jutila 1998a). However, a large seed bank does not necessarily mean abundant field germination. For example, although the seed bank was biggest in the geolittoral zone germination in the field was not necessarily also highest there because disturbances, like flooding, could inhibit germination or restrict it to only short drawn-down periods.

In this study I wanted to find out what portion of the abundant seed bank germinates in the field as to estimate better its importance in structuring the shore community. Two study sites were located in the delta area and the rest along the sea; half of them were grazed by cattle and the other half was ungrazed. I compared seedling populations, to both the mature vegetation and the seed bank, in Baltic coastal grasslands. I anticipated differences between the seedling densities and flora and between the delta and the seashore areas based on my previous work (Jutila (1998a, 1998b)). I also expected that cattle grazing would decrease the numbers and species of germinating seedlings. One question to be considered was if the seedling flora resembles more closely the seed bank or the adult vegetation, and what the reasons might be. I hypothetised that seedling germination in these environments is most related to the light availability and so increasing cover of vegetation and increasing amount of litter would mean less seedlings. I also expected that I would find some differences in germination within life form groups of plants as their response to different environmental factors.

Materials and methods

Study area

The study area is situated on the western coast of Finland, along the Baltic Sea, near the town of Pori (lat. 61°30′–61°33′, long. 21°28′–21°41′). Nine transects were established (running from the mean water line to the woods) in different shore meadows in order to study the vegetation, seedlings and seed bank. Elevations along the transects were measured using an altimeter at horizontal intervals of five meters. The ungrazed reference transects were selected to be as similar as possible to the grazed ones, forming transect pairs. A detailed description of the study sites is found elsewhere (Jutila et al. 1996; Jutila 1997a). Seedling plots were located along five transects, two were in the delta of the Kokemäenjoki River (Fleiviiki, delta grazed, abbreviated as DG and Teemuluoto, delta ungrazed, abbreviated as DUG) and the rest by sea (Kuuminainen, seashore grazed abbreviated as SG1, Hevoskari, seashore ungrazed abbreviated as SUG1 and Eteläranta, seashore grazed abbreviated as SG3). Three of these transects were grazed by cattle (SG1, SG3, DG; G referring to grazed) and two had been ungrazed for several decades (SUG1, DUG; UG referring to ungrazed). SG1 was about 1 km from SUG1 and SG3 about 5 km from these. The delta transects were about 1 km from each other and about 4 km from SG3.

The annual mean temperature of the study area is +4.3 °C (−6.5 °C in January, +16.0 °C in July), the annual mean precipitation 536 mm (22 mm February, 75 mm August) and the average duration of snow cover 94 days (Finnish Meteorological Station Service, the time period 1961–1990). The sea is frozen for an average of 95 days (Seinä and Peltola 1991) and the salinity of the Baltic water is about 0.5% at Pori. The Baltic Sea does not have regular tides, but seasonal and daily fluctuations in the water level are important factors shaping the shore vegetation. Usually the water level increases towards the end of the growing season. The land uplift rate at Pori is 7 mm per year. The study area belongs to the southern boreal zone and the bedrock is predominantly Jotnian sandstone, with occasional olivine diabase intrusions.

Methods

Seedling plots (20 × 20 cm^2, n = 79) were located randomly along the transects by first picking the number indicating the distance from the water line, then choosing the side of the transect and finally picking a number indicating the distance (less than 10 m) from the transect. Seedlings were counted in the field plots in June 1993 and July 1994 (SG1: 20 plots, on 7 June and 22 June 1994, SUG1: seven plots on 13 June 1994, SG3: one plot on 13 June 1994, DG: 31 plots, on 9 June, 14 June and 21 June 1993, DUG: 20 plots, on 15 June and 16 June 1993). The cover of the adult vegetation (also divided to monocots vs. dicots and annuals vs. perennials), cover of litter and mosses, cover of bare ground, were estimated in these small seedling plots (20 × 20 cm^2, n = 79) on a percent scale. In addition, vegetation data that were collected for other studies were used to interpret the results (Jutila 1997a; Jutila b. Erkkilä 1999b; Jutila 2001a). Elevation from the mean water level was measured for each plot. Also the seed bank of the study sites was studied using the germination method. Part of the seed bank data has been published (see Jutila (1998a, 1998b)). For this study I used the seed bank sample data (samples 4.8 cm in diameter, 10 cm in depth) collected along the same transects where the seedling counts were made and only the seed bank samples (n = 79) which were located exactly at the same sites or very close to the seedling plots were included. The treatment, growing and identification of the seed bank samples mainly follows the procedures represented in Jutila (1998b) for the immediately germinated samples.

Seedlings were divided according to taxonomy into monocotyledons, dicotyledons and gymnosperms, and according to life-history types into annuals, biennials and perennials. In the statistical tests, annuals and biennials were combined as annuals. The life history type, taxonomy and nomenclature were according to Hämet-Ahti et al. (1998).

Statistics

Statistical analyses were performed using the Statistical Analysis System (SAS Institute Inc. (1989–1996)). Location (in delta or seashore) and grazing were fixed variables in MANOVA and numbers of species and seedlings (also of taxonomic groups and life history types) were response variables. Mantel test in the PC-ORD (McCune and Mefford 1995) and Spearman's rank correlation coefficient were used to test the relationships between seedling population (density and composition) and mature vegetation. Several ordinations were run for the seedling, seed bank and mature vegetation data in the PC-ORD and DCA (Detrended Correspondence Analysis) was selected to present their patterns. The effect of grazing on individual species was tested with the Mann-Whitney U-test. Regression analysis was used to study the relationship between elevation vs. seedling and species numbers. The abundance of seedlings in different elevation classes (1: < 20 cm; 2: 20–50 cm; 3: 50–70 cm; 4: > 70 cm) were compared with ANOVA and in the case of individual species with non-parametric Kruskal-Wallis test. Ln(x+1) transformation was used when needed.

Results

Seedling germination in the field

Altogether 4609 seedlings were observed in the 79 field plots (20 cm × 20 cm) making an average of 1458.54 ± 1470.13 seedlings/m^2. The two highest numbers of seedlings in a plot were 418 (10450 seedlings/m^2) and 304, both which were detected in a grazed delta transect (DG). The variation in the seedling populations was large and the distribution was patchy. A majority of the seedlings were dicots (67.5%) and most of the identified species were perennials (96.84%), while 16.84% of the dicots could not be determined to species or genus level. Six short-lived species (the only annuals and biennials), *Atriplex longipes*, *Myosotis stricta*, *Odontites litoralis*, *Pedicularis palustris*, *Rhinanthus serotinus* and *Viola* *tricolor*, contributed a total of 122 seedlings, which is only 3.26% of the seedlings that were identified to species or genus level (so that the life-cycle could be defined).

Numbers of seedlings differed significantly between seashore and delta and within transects. The number of seedlings per delta plots were double compared to the seashore ones (Figure 1a). Significantly more both monocot and dicot seedlings were found in the delta than in the seashore. On average, the seedling densest transect was DUG if SG3, which only had one seedling plot, is not considered. DUG also had the highest numbers of monocots and dicots, but proportionally, SUG1 had the richest dicot and annual seedling population: all observed seedlings were dicots and 28% were annuals. The smallest number of seedlings germinated from the marine grazed transect, SG1.

On average 4.14 species were identified per seedling plot. Most of the species were dicots (2.59 species/plot) and perennials (3.99 sp./plot). The number of species per plot was significantly higher in the delta than in the seashore (Figure 1c). However, the MANOVA indicated a significant interaction between location and the grazing effect. In the delta no seedlings of annual species were identified. The species richest seedling plots were found in SUG1 (6.29 sp./plot) and DUG (5.00 sp./plot); the species poorest transect was SG1 (1.75 sp./plot). The number of species in the seedling population was significantly positively correlated with the number of seedlings ($r = 0.755$, $p = 0.0001$, $n = 79$) and this was true also for both monocots and dicot species vs. seedlings ($r = 0.448$, $p = 0.0001$, $n = 79$; $r = 0.723$, $p = 0.0001$, $n = 79$, respectively).

Altogether 44 species (three identified only to genus level) were observed as seedlings in the field plots (which covered up to 3.16 m^2). The total numbers of germinating seedlings/m^2 are presented by species in the Appendix. Among the 12 most common (identified) species were ten dicots and two monocots, which is opposite to the result of the seed bank study which indicated monocot dominated seed bank. The most abundant taxon, *Carex*, formed 23.21% of all the seedlings observed in the field. In total more species germinated from the seashore seedling plots (29 identified to species or genus) than from the delta ones (13 identified to species or genus), even though the number of seedling plots was clearly higher in the delta (n = 51) than in the seashore (n = 28).

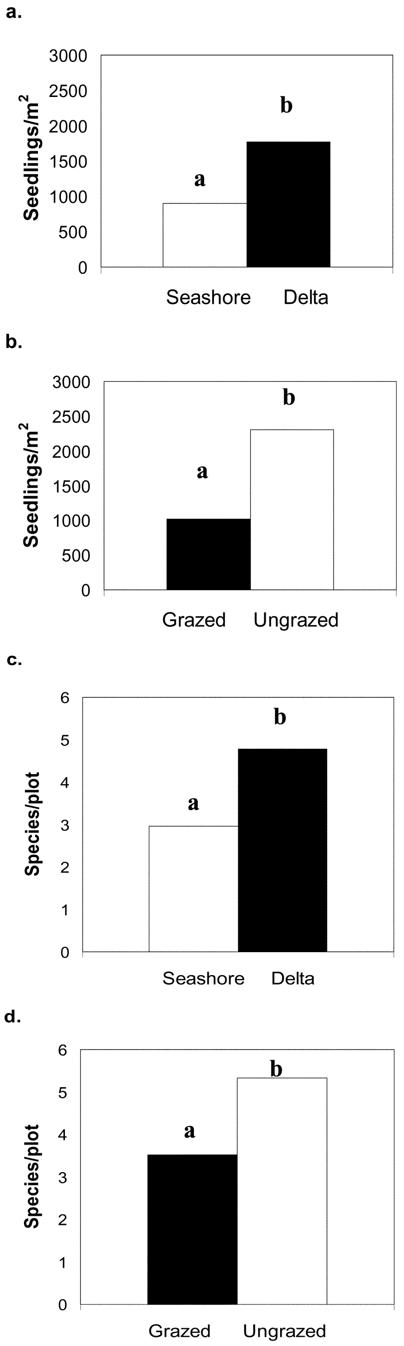

Figure 1. Number of germinating seedlings/m^2 a) in the seashore (SG1, SUG1, SG3) and delta (DG, DUG), and b) in the grazed (SG1, SG3, DG) and ungrazed samples (SUG1, DUG). c) Number of species of germinating seedlings in field plots in the seashore and delta, and d) in the grazed and ungrazed field plots.

Carex (most abundant in DG) and *Potentilla palustris* (most abundant in DUG) were the most abundant seedling taxa in the delta and they were not found at all in the seashore (Appendix). Other species that were significantly more common in delta than in the seashore plots were *Viola palustris* (restricted to the delta), *Galium palustre, Leontodon autumnalis* and the group of unidentified dicots. 301 seedlings of *Veronica chamaedrys* were only found in one DG plot (Appendix).

Likewise, on the seashore, each transect had its own most abundant species: in SG1 it was *Festuca rubra*, in SUG1 *Filipendula ulmaria* and *Rhinanthus serotinus* and in SG3 *Trifolium repens*. The first three of these and *Agrostis stolonifera, Anthoxanthum odoratum, Glaux maritima, Parnassia palustris* and *Plantago maritima* were significantly more common on the seashore than on the delta, and did not actually occur as seedlings on the delta at all (Appendix). In SUG1 the second most abundant seedling species was the annual *Rhinanthus serotinus* that formed 28% of the seedlings counted there.

Effect of grazing

Both on the delta and seashore, fewer seedlings were observed in the grazed than in ungrazed plots (Figure 1b). On the delta lower numbers of both monocots and dicots were associated with grazing, but on the seashore the number of monocot seedlings was actually higher in grazed plots.

The number of species per plot was smaller in the grazed than in ungrazed plots in the whole dataset (Figure 1d) and in the seashore. Fewer annual species and seedlings were found in the grazed than in the ungrazed seashore plots. In total, the grazed plots (n = 52) had 31 species (including one taxon defined on genus level) versus 22 species (including two taxa defined to genus level) in the ungrazed plots (n = 27).

Seven species (+ the group of unidentified dicots) had significantly fewer seedlings in grazed plots than in ungrazed ones (Mann-Whitney U-test): *Anthoxanthum odoratum*, *Carex spp.*, *Filipendula ulmaria*, *Galium palustre*, *Potentilla palustris*, *Rhinanthus serotinus* and *Rumex acetosa* (Appendix). However, three species, *Leontodon autumnalis*, *Trifolium repens* and *Viola palustris*, were more common in grazed than in ungrazed plots (Appendix).

Elevation

The numbers of seedlings were on average the highest at the lowest geolittoral (about 20 cm elevation; Figure 2a). In SUG1 the number of seedlings significantly decreased with elevation, while in DUG it significantly increased with elevation. Thus, it seems that the plots in DUG are in the increasing part of a bell-shaped curve and in SUG1 they are in the decreasing part. In the case of species richness the relationship to elevation was somewhat unclear (Figure 2b). In SUG1 the species richness decreased significantly with elevation.

Some species were more likely to be found as seedlings in lower elevation plots and others in upper ones. *Carex* species (C. *nigra* and *C. aquatilis*) germinated in the two lowest elevation classes (e.g. < 50 cm) and *Galium palustre* in the three lowest ones. Seedlings of *Potentilla palustris* were found in all elevation classes, but there were significant differences in the number of germinating seedlings, the greatest being in the two lowest elevation classes. *Filipendula ulmaria*, *Leontodon autumnalis* and *Trifolium repens* germinated in all elevation classes except the lowest one, however *F. ulmaria* demonstrated less germination at higher elevations, while *L. autumnalis* and *T. repens* showed increasing germination at higher elevations. Seedlings of *Agrostis stolonifera*, *Festuca rubra* and *Glaux maritima* were found only in elevation classes 2 and 3. *Veronica chamaedrys* was only found in the two upper most classes and *Rumex acetosa* and *R. acetosella* only in class 3. The numbers of all the above mentioned species differed significantly between elevation classes.

Comparisons between seedlings and mature vegetation

According to Mantel's test the species composition of seedling population differed significantly from the one in the mature vegetation. In the small seedling plots I found in total 47 species as seedlings and 69 species as adult plants. About 60.0% of the mature species (making 40 species) in these small plots were also detected as seedlings. There were twenty species that were always found in the mature vegetation when they were detected as seedlings in the same plot. There were some other species which were almost always both in the mature vegetation and in the seedling population. Altogether there were only four species, which appeared as seedlings but not as adults in seedling plots. However, all these species, *Betula* spp., *Lathyrus palustris, Lythrum salicaria* and *Pinus sylvestris* were found in the flora of the study sites. Furthermore, seedlings of certain species, like *Leontodon autumnalis*, which has wind dispersed

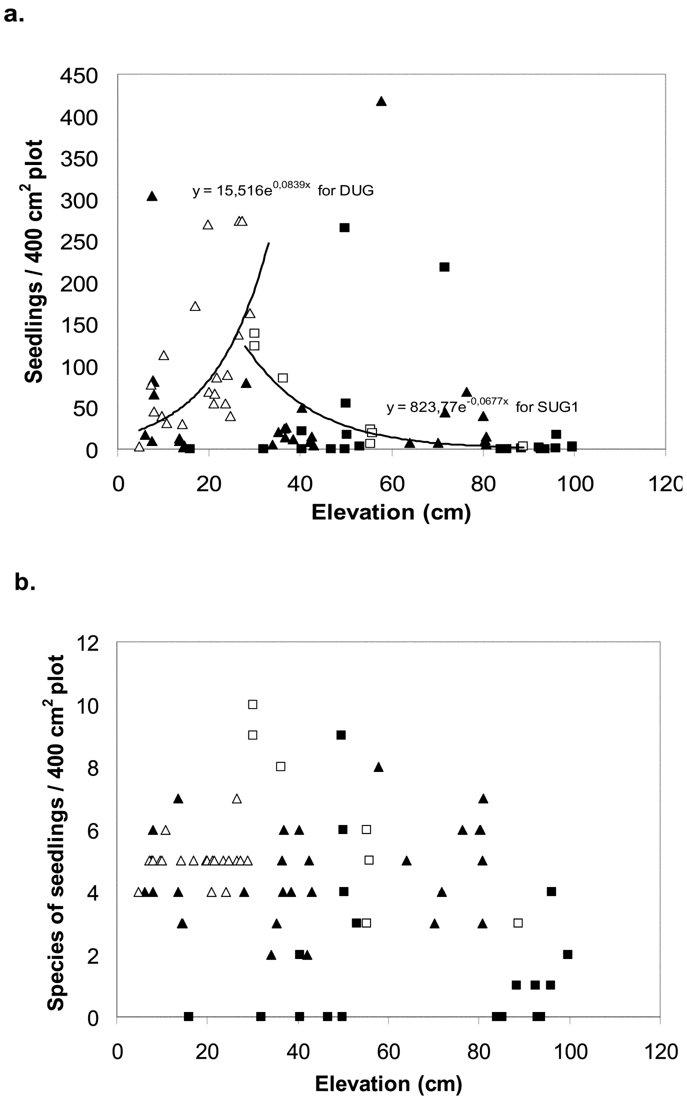

Figure 2. Numbers of a) seedlings and b) species in different elevations in grazed and ungrazed seashore and delta plots. Filled squares indicate SG1 and SG3 plots, empty squares SUG1 plots, filled triangles DG plots and empty triangles DUG plots. The curves in a) represent exponential trend of increase in the numbers of seedlings with elevation in DUG, decreasing trend in SUG1. Elevation 0 cm is the mean water level.

propagules, were often found in plots where this species was not growing in the mature vegetation. There were 21 species, which were found simultaneously as seedlings of mature plants and also in the seed bank of the site.

The species richness of the mature vegetation explained neither the numbers of all species nor seedlings in the plots, but the number of species of seedlings was correlated with the dicot species richness in the mature vegetation (r = 0.26, p = 0.023). Also the numbers of annual seedlings and annual species of seedlings and numbers of dicot species of seedlings were positively correlated with the number of species in the mature vegetation (r = 0.52, p = 0.0001; r = 0.52, p = 0.0001; r = 0.23, p = 0.045; respectively, Table 1). These same variables were also correlated with the numbers of dicot species in the mature vegetation with somewhat higher coefficients. Surprisingly the number of all seedlings found in the field was positively correlated with the cover of mature vegetation (r = 0.230, p = 0.0443) and negatively correlated with the amount of bare soil (r = –0.270, p

Table 1. Correlations between variables of seedling population and the mature vegetation. First row for each variable is Spearman correlation coefficient and the second row is prob > |R|. Significant results are in bold.

	MATURE VEGETATION											
SEEDLINGS	Cover	Cover-(mosses + litter)	Mono-cot cover	Dicot cover	Annual cover	Perennial cover	Litter	Mosses	Bare	Species	Mono-cot species	Dicot species
Total seedlings	0.2299	0.2264	−0.2339	0.3796	0.176	0.153	−0.2197	−0.2313	−0.2703	−0.0781	−0.2305	0.117
	0.0443	**0.0477**	**0.0407**	**0.0007**	0.1207	0.1841	0.0517	**0.0403**	**0.016**	0.4998	**0.0438**	0.3109
Monocot seedlings	0.1045	0.1278	−0.17	0.2037	0.1623	0.0248	0.0043	−0.2415	−0.115	−0.1492	−0.2102	−0.0192
	0.3658	0.268	0.1394	0.0756	0.153	0.8302	0.9699	**0.032**	0.3131	0.1955	0.0665	0.8682
Dicot seedlings	0.2996	0.2234	−0.2719	0.4797	0.1255	0.1809	−0.3216	−0.156	−0.2515	−0.0252	−0.242	0.1943
	0.0081	0.0508	**0.0167**	**0.0001**	0.2703	0.1154	0.0039	0.1699	**0.0253**	0.8281	**0.034**	0.0905
Annual seedlings	−0.0083	0.0035	0.0046	0.0304	**0.7867**	−0.1687	−0.0707	−0.0556	−0.0399	**0.5241**	0.181	**0.5439**
	0.9427	0.9762	0.9683	0.7933	**0.0001**	0.1424	0.5361	0.6265	0.7273	**0.0001**	0.1152	**0.0001**
Perennial seedlings	0.2353	0.2283	−0.2275	0.3763	0.1335	0.1581	−0.216	−0.2386	−0.2792	−0.1061	−0.2338	0.0864
	0.0394	**0.0458**	**0.0466**	**0.0007**	0.2409	0.1696	0.0559	**0.0342**	**0.0127**	0.3584	**0.0407**	0.4548
Total species	0.2333	0.1776	−0.1502	0.3316	0.2426	0.0949	−0.2985	−0.1359	−0.1743	0.1243	−0.1193	0.2586
	0.0411	0.1223	0.1924	**0.0032**	**0.0313**	0.4116	**0.0075**	0.2325	0.1245	0.2814	0.3014	**0.0232**
Monocot species	0.1796	0.1241	−0.013	0.1232	0.2615	0.0363	−0.0594	−0.2091	−0.1236	0.1184	−0.067	0.1916
	0.118	0.2824	0.9109	0.2856	**0.0199**	0.7539	0.6034	0.0644	0.2777	0.3052	0.5625	0.0951
Dicot species	0.2133	0.2018	−0.183	0.3737	0.3071	0.1034	−0.3652	−0.0879	−0.2131	0.2288	−0.0779	0.3688
	0.0625	0.0784	0.1111	**0.0008**	**0.0059**	0.3707	0.0009	0.4411	0.0594	**0.0454**	0.5006	0.001
Annual species	−0.017	−0.0066	−0.0012	0.0348	**0.7713**	−0.1742	−0.0638	−0.0522	−0.0401	**0.5216**	0.1729	**0.5442**
	0.8835	0.9548	0.9916	0.7639	**0.0001**	0.1297	0.5764	0.6479	0.7258	**0.0001**	0.1327	**0.0001**
Perennial species	0.2389	0.1635	−0.1391	0.3159	0.1757	0.1101	−0.3034	−0.1226	−0.1628	0.066	−0.1414	0.1988
	0.0364	0.1554	0.2276	**0.0051**	0.1213	0.3406	**0.0066**	0.2818	0.1518	0.5688	0.2199	0.083

= 0.016). While this result was also significant for dicot and perennial seedlings it did not seem to apply for the monocot seedlings. However, the increasing amount of litter seemed to reduce the number of dicot seedlings and species (Table 1). The numbers of both annual species and seedlings were in a strong correlation with the cover of the annuals in the mature vegetation ($r = 0.79$, $p = 0.0001$; $r = 0.77$, $p = 0.0001$, respectively).

In DCA ordinations the delta transects are located close to each other based on seedling, mature vegetation and seed bank data (Figure 3). SG1 and SUG1 are separated from the delta samples but also from each other in both seedling and mature vegetation ordinations. In Figure 3a x-axis relates to the number of seedlings and y-axis to the number of species so that the highest numbers are close to the origo. A number of species were located close to the same transect in both seedling and vegetation data indicating clear similarities.

Comparisons between seed bank and seedling plots

Many fewer seedlings germinated in the field than were observed germinating from the seed bank samples in the greenhouse. When considering the sample surface areas of seedling plots (20 × 20 cm^2) and seed bank samples (18.1 cm^2) ($n = 79$), the number of seeds germinating per unit area was about 43 times bigger in the seed bank samples (63789.32 seeds/m^2) than in the seedling plots (1458.54 seeds/m^2). However, if the surface area of the pot (17.5 cm × 13 cm pot) where the 10 cm deep seed bank samples were spread as a thin layer to germinate is used in com-

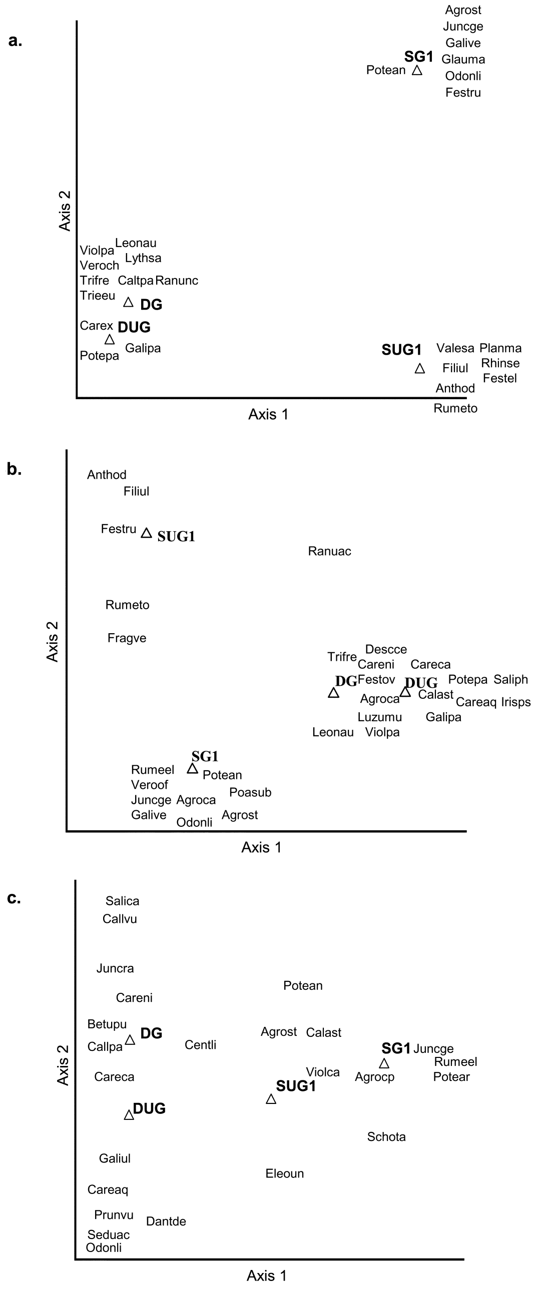

Figure 3. DCA ordinations for a) the seedling data (400 cm^2 plots), b) mature vegetation data in the seedling plots (400 cm^2) and for c) seed bank data (same study areas). Triangles indicate the averages of separate transects (SG1, SUG1, DG, DUG). The locations of species are approximate, because several species were clumped in the same place. The species are indicated with abbreviations using the four first letters of the genus name and two first letters of species name, except that Agrocn= *Agrostis canina*, Agrocp = *Agrostis capillaris*, Rumeell = *Rumex acetosella* and Rumeto = *Rumex acetosa.* Ordinations are run with all the species in the dataset for a) and b) and for 33 species in c) (due to inability to run the DCA with more species). 25 species are shown in a), 30 in b) and 24 in c).

parisons, the seed bank was only about three (3.48) times bigger. If we divide the number of seedlings per m^2 in the field by the number of seeds per m^2 in the seed bank and multiply it by 100, we get an estimate of the effectiveness of the seed bank in germination (E_g). However, this is only valid in the case where there is no seed dispersal. It seems that the germination from the seed bank was somewhat more effective in the delta than in the seashore (E_g = 2.47% and E_g = 2.19%, respectively). In seashore plots more such species were found in the seedling flora that must have arrived to the site by seed rain. In ungrazed plots the germination from the seed bank was clearly greater than in the grazed sites (E_g = 3.53% and E_g = 1.82%, respectively). E_g was 36.52% in SG3, 7.32% in SUG1, 3.19% in DUG, 1.91% in DG and 0.79% in SG1.

The germinable seed bank was mainly composed of monocots (84.27%), but in field plots most of the seedlings were dicots (67.5%). In both cases perennials dominated. The seed bank was significantly greater in the delta than in the seashore (71498.39 ± 3614.35 seeds/m^2 vs. 40893.99 ± 4745.31 seeds/m^2, respectively) and also significantly greater in the ungrazed than in grazed samples (65280.29 ± 4638.946 seeds/m^2 vs. 56062.9 ± 3881.838 seeds/m^2, respectively) following the pattern also observed in the seedling plots. On average, the densest seed bank was found in DUG (82036.66 ± 7592.157 seeds/m^2), which also had the greatest seedling population in the field. The fewest seedlings germinated from seed bank samples of transect SUG1 (19525.96 ± 5102.239 seeds/m^2).

The numbers of seedling species per a seedling plot were about 56.48% of the number of species found per a seed bank sample. This comparison is an artificial one due to different size of the samples, but it shows that, in general, more species per unit were found in the seed bank than in seedling plots. SUG1 had the most even distribution of species between seed bank and field plots, but none of the seven most common species in the seed bank of SUG1 were found to germinate in the field seedling plots.

About 50.0% of the total number of species identified in the seedling plots (44 species) were also found in the seed bank samples taken at the same sites (altogether 68 seed bank species) and 32.35% of the species found in the seed bank samples were also found as seedlings.

The most abundant taxon both in the seedling plots (23.21% of seedlings) and also in the seed bank samples was *Carex* (47.36% of the seed bank). Even thought *Juncus gerardii* formed 19.03% of the seed bank and was the second most common species and the most common one in the seashore seed bank, it was not found among the 12 most abundant species in the seedling plots. *Potentilla palustris*, the third most common species in the seed bank of the ungrazed delta transect (DUG), only contributed 0.34% of all the seed bank, but was found to be second most abundant species in all the seedling plots. It seems that the seed bank and the field seedling population were more similar in the delta than in the seashore. In general the list of most common species of seedlings observed in the field was dominated by dicots, while the most common seed bank species were monocots.

Discussion

The observed average seedling densities (1 458.54 seedlings/m^2) were in the range of those observed in tidal freshwater wetlands by Leck and colleges (Leck et al. 1989; Leck and Simpson 1993), which is one of the few studies which has focused on the seedling density in the field. The distribution of seedlings was very patchy. The majority of the seedlings were dicots, even though both in the vegetation and seed bank monocots were more common.

In the delta, the seedling density was twice that in the seashore. Also the seed bank of the delta was more abundant than the seashore, as previously reported (Jutila 2000). There may be several reasons for the larger seedling populations in the delta than in the seashore: 1) More propagules are available in the delta due to a bigger seed bank assuming that the direct seed rain is somewhat similar in both places. In the delta, however, the seed bank might be bigger due to sediments carrying seeds that are transported by the river. However, this does not necessarily lead to bigger seedling population. 2) In the seashore salinity may at least occasionally restrict germination (see the results of Shumway and Bertness (1992)). 3) A coarser grained soil may be restricting the germination in the seashore (see more about the effect of soil particle size in Chambers (1995)). 4) The moisture conditions might be less extreme in the delta than in the seashore, and so the risk of desiccation and drowning of the seedlings is smaller in the delta (also linked to the grain size). 5) Physical hazards like flooding, waves and ice disrupt seedling establishment more often in the seashore than in the delta.

Seedling counts were made at the beginning and middle of the growing season, when the sea water levels are typically low and the seedling plots had not experienced flooding during the same season. Flooding has in many studies shown to decrease germination (van der Valk and Davis 1978; Smith and Kadlec 1983; Leck and Simpson 1987), but flooding and draw-down conditions have also been reported to increase germination (Leck and Graveline 1979; Kadlec and Smith 1984). In my previous study flooding and subsequent draw-down increased germination of several species from seed bank (Jutila 2001b). Thus, it would be interesting to study seedling germination and survival in flooded-draw-down areas in the field for a longer period of time so that the assumptions concerning the stimulating effects of flooding for germination (see also Jutila (1998b)) could be ascertained or rejected. The method of counting the seedlings in each plot only at once may prevent detection of some species which appear in the seedling populations of either earlier or later in the season. This may be the case for *Juncus gerardii*, which is probably germinating in the field in the end of growing season (Jutila 1998b). Seedlings germinating in autumn may avoid interference from other species as well as summer drought, but may suffer high winter mortality. However, Parker and Leck (1985) have reported no or little germination after spring.

Effect of grazing

Grazing was associated with a reduced number of monocot and dicot seedlings in the delta and a reduced number of dicot seedlings in the seashore, where the numbers of monocot seedlings were increased by grazing; a pattern which also was evident in the monocot component of the mature vegetation (Jutila 1999a). Grazing decreased the density and species richness of seed bank and the cover of vegetation of all other species groups except monocots in these grasslands (Jutila 1999a). Tyler (1969) also found that most seashore species are negatively affected by grazing, although the most frequent species seem rather indifferent. Species suffer directly from grazing and trampling, but they may also suffer indirectly from the altered salinity and compression of the soil. Grazing has also been seen as creating safe sites for seeds. In a world-wide review Milchunas and Lauenroth (1993) showed that in half of the studies the species richness of a community was increased and in the other half decreased by grazing with large herbivores.

Grazing reduced the number of seedlings of seven individual species. Of them *Filipendula ulmaria*, *Galium palustre* and *Rhinanthus serotinus* have previously been shown to suffer from grazing both in vegetation (Kauppi 1967; Tyler 1969; Jutila 1999a) and in the seed bank (Jutila (1998a, 1998b)) and *Anthoxanthum odoratum* only in the vegetation (Jutila 1999a; Jutila b. Erkkilä 1999b). Furthermore, of the three dicot species which had more seedlings in grazed plots than in ungrazed ones, *Leontodon autumnalis* and *Trifolium repens* were reported to increase in cover in the grazed mature vegetation (Jutila 1999a; Jutila b. Erkkilä 1999b). The seedling germination in field in relation to the size of the seed bank was more effective in the ungrazed than in the grazed sites. Maybe the grazed sites are harsh for the seedlings which die very quickly and would not be detected in this kind of study. Maybe denser sward in the grazed plots actually leads to less light to the soil surface even though the cover of vegetation appears less than in the ungrazed plots.

The total number of seedling species found in the grazed seedling plots (31) was higher than in the ungrazed ones (22 species) and this was evident both in the seashore and delta. In contrast, the seed bank flora of the grazed sites was clearly smaller in the seashore (Jutila 1998a). However, the total number of species in the seed bank of the delta was somewhat higher in the grazed than in the ungrazed site. Results seem to indicate that in grazed plots the seedling flora was more diverse than in ungrazed ones, but it should be noted that the number of grazed plots was greater than ungrazed plots. It might be expected that the grazing would have increased the number of ruderal species in the seedling population, but actually only one clear ruderal could be detected and it was represented only by one seedling. The mosaic structure of the vegetation in grazed sites may provide suitable germination requirements for more species than the ungrazed sites, even though the numbers of seedlings remain small.

Elevation

The species richness of vegetation of these coastal meadows in closely linked to the elevation (Jutila 1997a). The relationships between elevation and the number of seedlings in both seed bank and in the field are less obvious. The biggest seedling populations were found in the lowest geolittoral (about 20 cm elevation), at about the same level where the highest density of the seed bank occurred in the delta (10–30 cm elevation: Jutila b. Erkkilä (1999b)). However, in the ungrazed seashore the peak of the germination was clearly at a lower level than where the maximum density of the seed bank had been reported (20–50 cm, Jutila (1998b)). Maybe there was more light and moisture and less shade from the trees and shrubs in the lower geolittoral than in the upper part of it. Individual transects which were located at somewhat different elevations showed different elevational patterns, and due to huge variations in the numbers of seedlings, the patterns were not clear. Species growing in the geolittoral vegetation seemed to have seedlings in all elevation zones, while species growing in the epilittoral vegetation were somewhat more confined to the upper zones, but individual species could also show disparities from this pattern.

Comparisons between seedlings and mature vegetation

Even though Mantel's test indicated a significant difference between the seedling population and the mature vegetation, there was clearly a very close relationship between these for many species (Figure 3). About 60% of the adult species found in the seedling plots produced a new seedling generation in the same plots. The seeds of several species were found germinating close to the adult plants indicating a short dispersal distance.

The fact that total cover of vegetation was positively correlated with the seedling density and negatively with bare ground does not support the idea that germination would happen only in gaps. Bare soil and most open gaps were available in SG1, where the seedling populations were the smallest. This is in agreement with Ryser (1993) who did not find any evidence for a gap-dependence of seedling establishment. Maybe the gabs are too harsh environment for seedlings and in the coastal grasslands physical hazards such as flooding, waves and ice, control seedling survival to a larger extent than competition from vegetation. It is probable that the moisture conditions in the delta were more suitable for germination than in the seashore, where the vegetation usually covered less and was also shorter. Some species might even be unable to establish without shelter of vegetation (see also Ryser (1993)). Thus, a kind of a nurse effect of the vegetation to the seedlings (see Ryser (1993) and Wied and Galen (1998)) was more apparent in the delta than in the seashore, though it was observed also in some places in seashore. The nurse effect implies that there is no apparent parent – offspring conflict. In conclusion, it seems that gaps are of minor importance for recruitment in these coastal grasslands.

The cover of monocot species, however, seemed to be negatively correlated with the number of seedlings, particularly of dicots (Table 1). The graminous species might have a more dense structure and so less light would reach ground than under dicots. The amount of litter seemed to be in negative correlation with the number of dicot seedlings and species and an almost significant correlation was observed with the number of seedlings, while no significant correlations were apparent in monocots. These results might indicate that the germination of dicots is more restricted by the mechanical barrier of litter and light availability than that of monocots. Maybe temperature fluctuations play more important role as a germination cue for dicots than for monocots.

In the epilittoral, desiccation may be a restricting factor for seedling germination, establishment and survival (personal observations and Jutila's unpublished data). However, in the moist geolittoral, seedlings germinate abundantly, but they are likely to die because of disturbances like flooding, waves and ice or possibly competition for light by other species and individuals. It is generally believed that competition in the geolittoral is less extreme than in the epilittoral (Jutila b. Erkkilä 1999b; Lenssen et al. 1999), but this may apply mainly to the adult phase.

Comparisons between seed bank and seedling plots

Many fewer seedlings germinated in the field than were observed germinating from the seed bank samples in the greenhouse following the pattern observed also by Parker and Leck (1985) and by Milberg (1993). There may be several reasons for this. Firstly, conditions in the greenhouse are maybe close to optimal for many species, while in the field germination is restricted by many factors like drought, particle size, flooding and depth of burial. Secondly, the duration of the seed bank germination was several months so there was much more time and effort used to identify the species in the greenhouse than in the field where the counting was conducted only once per plot (see Parker and Leck (1985) for the usefulness of single time count of seedlings). However, it seems quite possible that the seed bank is more species diverse than the seedling population at a particular time (see Leck and Simpson (1995)). It is estimated that for about 50–70% of the seedling species a likely source of germinable seeds was the seed bank.

It seems that monocots were much less effective in germinating from the seed bank than the dicots. Their strategy is probably to produce abundant seeds, for which fairly small amount of resources are used, and to wait for the window of opportunity in which they have an advantage to germinate. For example, even though *Juncus gerardii* was the second most common species in the seed bank, it was not found among the 12 most abundant species in the seedling plots. Dicots instead invest more on each seed, which will have a better chance to germinate. Maybe their germination is more continuous and steady and not as restricted to particular windows of opportunity.

It is likely that in the DUG where both the seed bank and seedling population were the biggest, the seedlings germinate mainly from the seed bank, while in SUG1 seed rain seems to play a more important role than in other transects. In general it would be expected that in the seashore the dispersal of seeds by winds and water (see Leck and Simpson (1994)) would distort the pattern between the mature vegetation, seed bank and seedling population.

In conclusion, it can be judged that the more common the species is in the above-ground vegetation, the greater the chances that it also has a persistent seed bank. This seems to apply at least for these coastal grasslands.

Dynamics of various life history stages

In Figure 4 the interaction between mature vegetation, seed bank and seedling populations is presented based on the results of this study. The patterns of turnover are certainly more complicated than what can be judged based on one study. However, I have tried to divide the species into turnover groups (see Appendix).

Group 1 is composed of species found in all life history stages, in the seed bank, seedling population and mature vegetation. They are likely to represent species which have a transient (or short-term persistent) seed bank and which seem to germinate and establish well. There are also some species like *Juncus gerardii* which have a large seed bank including both transient and persistent seeds. Actually, many of the species in this group are the dominants of the vegetation and often have several successful strategies. For

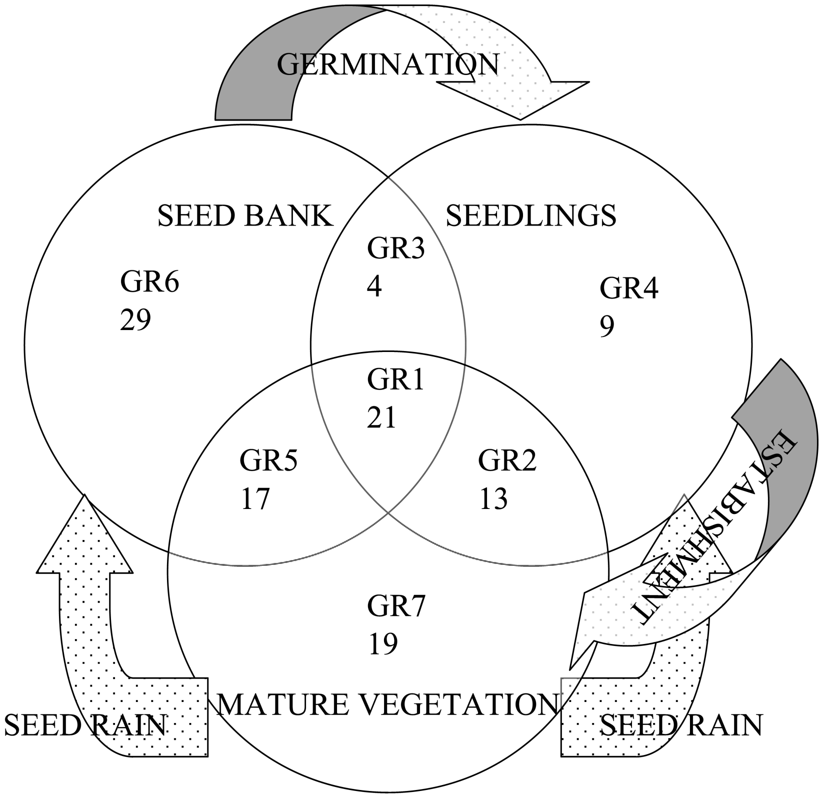

Figure 4. A schematic presentation of the dynamic interaction between mature vegetation (20×20 cm^2 seedling plots, n = 79), seed bank (values given in seeds/m^2, n = 79; partly the same data used in Jutila (1998a)) and seedling population (20×20 cm^2 seedling plots, n = 79). Numbers of species are given by groups (gr), which are the same as indicated for each species in Appendix. See more explanation in the text.

example, dominants of grazed sites like *Festuca rubra*, *Trifolium repens* and *Leontodon autumnalis* base their strategy on seed dispersal, transient seed banks and vegetative spread. *Filipendula ulmaria*, which is found in ungrazed sites, is a competitor or stress-tolerant competitor (Grime et al. 1988), and therefore counts both on vegetative dispersal by rhizomes and on abundant production of seeds and seedlings. *Potentilla anserina* and *Glaux maritima* are interstitial dicots known to have some seed dormancy and evidently the seed bank really provides an opportunity for germination.

Both groups 2 (in mature vegetation and as seedlings) and 4 (found only as seedlings) are composed of species which do not have a seed bank, are restricted in their establishment to special conditions and rely on seed rain and/or long life expectancy. Of the annuals, *Atriplex longipes*, *Myosotis stricta* and *Rhinanthus serotinus*, belong to this group. In principal the group 3 (species both in seed bank and in seedling population, but not in mature vegetation) would seem to be restricted by establishment. In this study group 3 is small and artificial (see Appendix).

Group 5 is fairly large group and it is composed of several graminous species which are difficult to identify as seedlings (thus, some of these species could actually belong to group 1). Some species in this group may be adapted to geminate later in the season. Group 6 is composed of species which have a persistent seed bank and are restricted to suitable germination conditions. They may be relicts of earlier vegetation or species which have an abundant production of seeds and good dispersability. Anyway, the seeds have some form of dormancy. For example mud-flat annuals, such as *Limosella aquatica* and *Juncus bufonius*, were not found in the field because there was not a suitable habitat for them. *S. tabernaemontani* is an example of seed bank species which is a dominant in the mature vegetation, but in the hydrolittoral which was not sampled for this study.

The species in group 7 are only found in the mature vegetation and may rely on vegetative dispersal.

They may also have a poor seed production, short longevity of seeds or poor germinability.

In general it seems that germination works as a stronger environmental sieve than the establishment of seedlings. This is evident when comparing for example the numbers of species in seed bank, seedling population and mature vegetation. Seed availability does not seem to be a problem for most species in these environments based on the high number of species found in the seed bank.

When I tried to relate the effect of grazing on seed bank, seedlings and mature vegetation and the groups presented in Figure 4, I could not detect any clear trends. In the group 1 the number of seedlings in the field in four species was decreased by grazing and in two species it was increased. In the case of seed bank grazing increased the abundance of one species, but decreased that of five species. In this same group 1, the cover of mature vegetation was decreased in six species and increased in 11 species.

Conclusions

The seedling densities observed in the Baltic coastal grasslands were moderate indicating that generative reproduction has a role in these stressed and disturbed communities. Smaller seedling densities in the seashore than in the delta can be explained by smaller seed banks and germination restrictions related to greater salinity and larger soil particle size. Highest seedling densities were found in the geolittoral where the most seeds in the seed bank have been detected. Mainly the seedlings were the same species which were found in the vegetation.

Cattle grazing seemed to cause a decrease, in particular, of the number of dicot seedlings, which is also related to the reported negative effects of grazing to the mature vegetation and seed bank (Jutila 1999a). Interestingly increasing number of dicot seedlings was related to increasing cover of mature vegetation. This gives support to the nurse effect theory (Wied and Galen 1998). However, abundance of litter was negatively correlated with the seedling numbers indicating that litter restricts germination, being a mechanical barrier but also decreasing the amount of light. Furthermore, it is quite possible that a denser sward in the grazed plots actually leads to less light to the soil surface even though the cover of vegetation appears less than in the ungrazed plots. Quite often it is supposed that grazing creates safe sites for germination. Maybe these coastal grasslands or wet meadows differ from other kinds of grasslands and the main effect of grazing appears to be negative. Flooding may work as an effective environmental sieve, which influences which species become established. It is possible that when increasing monocot component in the vegetation grazing leads to less abundant generative reproduction for dicots, but at the same time grazing may modify the pattern of vegetation to a more mosaic one where more dicot species have a chance to germinate.

Clearly, a knowledge of the interactions of various life history stages is necessary to fully understand the vegetation dynamics of these coastal wetland meadows. Based on this study it seems that germination works as a stronger environmental sieve than establishment. Our knowledge on germination in wetlands and grasslands is still restricted in many cases and in future more field studies with big sample sizes are needed to understand the strategies and critical life stages for different species.

Acknowledgements

I thank Prof. James Grace, Dr. Philippe Hensel, Karri Jutila, Tracey McDonnell and Larry Allain for their comments on the manuscript. Thanks also for Dr S. Galatowisch and two anonymous referees for their corrections. I'm grateful for the staff at Satakunta Environmental Research Centre for helping in the seed bank germinations and NWRC, USGS for providing research facilities during the writing of this paper. This research was supported by the Academy of Finland.

Appendix

Table A1. Comparison between seedlings (20 × 20 cm^2 seedling plots, n = 79), seed bank (partly the same data used in Jutila (1998a); values given in seeds/m^2, n = 79) and mature vegetation by species (20 × 20 cm^2 seedling plots, n = 79). Species groups indicated with superscript in front of the name are explained in the Figure 4 and text. The number of seedlings in plots in the delta (DG and DUG), seashore (SG1, SUG1, SG3), grazed (SG1, SG3, DG) and ungrazed sites (SUG1, DUG) are given and comparisons are indicated by the level of significance.

Species	Seedlings in field								Seed bank		Mature vegetation	
	Delta	Sea-shore	Sign.	Grazed	Ungrazed	Sign.	All /m^2	Std err /m^2	Seeds/m^2	Stderr seeds/m^2	Cover %	Freq.
Species as seedlings in the field												
^{1}*Agrostis stolonifera*	0	16	**	16	0	ns.	5.33	9.61	2595.22	412.82	5.20	20
^{1}*Anthoxanthum odoratum*	0	22	**	0	22	**	7.33	13.22	13.99	13.99	1.24	7
^{2}*Atriplex longipes*	0	1	ns.	1	0	ns.	0.33	0.63			0.00	1
^{4}*Betula spp.*	0	1	ns.	0	1	ns.	0.33	0.63				
^{2}*Caltha palustris*	8	0	ns.	8	0	ns.	2.67	5.00			0.09	2
^{2}*Cardamine pratensis*	1	0	ns.	0	1	ns.	0.33	0.63			0.00	1
^{4}*Carex spp.*	1070	0	***	505	565	***	356.67	486.55				
^{2}*Deschampsia flexuosa*	0	1	ns.	0	1	ns.	0.33	0.63			0.20	4
^{3}Dicot	761	15	***	106	670	***	258.67	321.53	1951.66	1112.15		
^{4}*Eleocharis acicularis*	0	1	ns.	0	1	ns.	0.33	0.63				
^{2}*Festuca elatior*	0	3	ns.	0	3	ns.	1.00	1.88			0.08	2
^{1}*Festuca rubra*	0	283	***	262	21	ns.	94.33	168.15	27.98	27.98	5.18	25
^{1}*Filipendula ulmaria*	0	140	***	0	140	***	46.67	82.22	27.98	22.04	1.43	10
^{1}*Galium palustre*	130	3	***	17	116	***	44.33	58.47	237.84	111.17	2.78	36
^{1}*Galium uliginosum*	0	1	ns.	1	0	ns.	0.33	0.63	825.43	183.81	0.01	2
^{2}*Galium verum*	0	4	ns.	4	0	ns.	1.33	2.47			1.68	10
^{1}*Glaux maritima*	0	30	**	30	0	ns.	10.00	18.03	111.92	111.92	0.22	4
^{3}Grass	21	16	ns.	32	5	ns.	12.33	23.70	7.00	7.00		
^{2}*Iris pseudacorus*	1	0	ns.	0	1	ns.	0.33	0.63			0.42	4
^{1}*Juncus gerardii*	0	5	ns.	5	0	ns.	1.67	3.12	12136.69	4656.13	4.98	13
^{4}*Lathyrus palustris*	0	1	ns.	1	0	ns.	0.33	0.63				
^{1}*Leontodon autumnalis*	205	1	**	206	0	**	68.67	108.32	13.99	13.99	1.74	19
^{3}*Lythrum salicaria*	5	0	ns.	5	0	ns.	1.67	3.12	48.97	28.49		
^{3}Monocot	52	9	ns.	51	10	ns.	20.33	30.30	573.61	319.90		

Table A1. Continued.

Species	Seedlings in field								Seed bank		Mature vegetation	
	Delta	Sea-shore	Sign.	Grazed	Ungrazed	Sign.	All /m^2	Std err /m^2	Seeds/m^2	Stderr seeds/m^2	Cover %	Freq.
[4]*Myosotis stricta*	0	1	ns.	1	0	ns.	0.33	0.63				
[1]*Odontites litoralis*	0	5	ns.	5	0	ns.	1.67	3.08	629.57	240.13	0.38	2
[1]*Parnassia palustris*	0	33	**	5	28	ns.	11.00	19.83	13.99	13.99	0.09	3
[4]*Pedicularis palustris*	0	1	ns.	0	1	ns.	0.33	0.63				
[4]*Pinus sylvestris*	2	0	ns.	0	2	ns.	0.67	1.25				
[1]*Plantago maritima*	0	27	**	2	25	ns.	9.00	16.22	13.99	13.99	0.30	11
[1]*Potentilla anserina*	23	31	ns.	54	0	ns.	18.00	31.58	1035.29	348.36	1.94	19
[1]*Potentilla palustris*	747	0	***	17	730	***	249.00	370.93	216.85	90.93	14.46	31
[4]*Ranunculus spp.*	61	0	ns.	61	0	ns.	20.33	37.14				
[2]*Rhinanthus serotinus*	0	112	***	1	111	**	37.33	65.77			0.09	4
[4]*Ribes alpinum*	0	1	ns.	1	0	ns.	0.33	0.63				
[2]*Rumex acetosa*	0	13	ns.	0	13	*	4.33	8.02			0.13	5
[1]*Rumex acetosella*	0	3	ns.	0	3	ns.	1.00	1.88	202.86	97.13	0.87	8
[1]*Sagina procumbens*	0	1	ns.	1	0	ns.	0.33	0.63	41.97	31.12	0.03	1
[1]*Sedum acre*	0	1	ns.	1	0	ns.	0.33	0.63	188.87	119.84	0.15	5
[1]*Stellaria palustris*	18	0	ns.	3	15	ns.	6.00	10.82	7.00	7.00	0.08	4
[2]*Trientalis europaea*	4	0	ns.	4	0	ns.	1.33	2.50			0.25	2
[1]*Trifolium repens*	93	215	ns.	308	0	*	102.67	175.70	13.99	13.99	3.49	12
[2]*Valeriana sambucifolia*	0	6	**	1	5	ns.	2.00	3.61			0.23	3
[1]*Veronica chamaedrys*	313	0	ns.	313	0	ns.	104.33	191.19	48.97	30.18	0.13	2
[1]*Viola canina*	0	1	ns.	0	1	ns.	0.33	0.63	83.94	71.16	0.38	3
[2]*Viola palustris*	88	0	**	88	0	*	29.33	48.23			0.72	9
[2]*Viola tricolor*	0	2	ns.	2	0	ns.	0.67	1.25			0.05	1
In total	**3603**	**1006**	*******	**2118**	**2491**	*******	**32.69**	**49.65**	**842.78**	**323.97**	**1.44**	**8.38**
Species in seed bank, but not as seedlings in the field												
[5]*Agrostis canina*									41.97	21.75	0.38	2
[5]*Agrostis capillaris*									328.77	153.43	3.32	12
[6]*Alnus incana*									7.00	7.00		
[6]*Betula pendula*									13.99	13.99		

Table A1. Continued.

Species	Seedlings in field							Seed bank		Mature vegetation	
	Delta	Sea-shore	Sign.	Grazed	Ungrazed	Sign.	All /m^2	Std err /m^2	Seeds/m^2	Stderr seeds/m^2	Cover %	Freq.
[6]*Betula pubescens*									209.86	54.81		
[6]*Bidens tripartita*									41.97	41.97		
[5]*Calamagrostis stricta*									377.74	127.32	0.94	7
[6]*Calla palustris*									496.66	115.93		
[6]*Calluna vulgaris*									1035.29	424.42		
[5]*Carex aquatilis*									3770.42	1825.52	5.14	19
[5]*Carex canescens*									18439.37	3994.53	2.94	13
[6]*Carex glareosa*									76.95	76.95		
[5]*Carex nigra*									3301.74	1555.72	7.78	27
[6]*Centaurium littorale*									2819.07	845.75		
[5]*Cerastium fontanum*									13.99	13.99	0.01	1
[6]*Chenopodium album*									69.95	69.95		
[6]*Cicuta virosa*									7.00	7.00		
[6]*Danthonia decumbens*									118.92	55.14		
[6]*Eleocharis palustris*									13.99	9.83		
[5]*Eleocharis uniglumis*									5008.57	1236.70	0.03	2
[5]*Elymus repens*									27.98	19.66	0.20	5
[6]*Epilobium palustre*									69.95	46.02		
[5]*Equisetum fluviatile (spore bank)*									69.95	51.12	0.15	4
[6]*Festuca pratensis*									7.00	7.00		
[5]*Fragaria vesca*									69.95	57.51	0.09	2
[6]*Gnaphalium uliginosum*									7.00	7.00		
[6]*Juncus bufonius*									174.88	127.71		
[6]*Juncus bufonius ssp. Ranarius*									1657.86	514.92		
[5]*Juncus filiformis*									62.96	35.88	0.00	1

Table A1. Continued.

Species	Seedlings in field								Seed bank		Mature vegetation	
	Delta	Sea-shore	Sign.	Grazed	Ungrazed	Sign.	All /m^2	Std err /m^2	Seeds/m^2	Stderr seeds/m^2	Cover %	Freq.
[6]*Limosella aquatica*									7.00	7.00		
[5]*Linaria vulgaris*									7.00	7.00	0.01	1
[6]*Poa palustris*									13.99	9.83		
[5]*Potentilla argentea*									244.83	110.75	0.06	1
[6]*Prunella vulgaris*									1154.21	309.14		
[6]*Ranunculus cymbalaria*									7.00	7.00		
[6]*Rubus idaeus*									13.99	13.99		
[6]*Salix caprea*									1049.28	737.17		
[6]*Schoenoplectus lacustris*									62.96	39.81		
[6]*Schoenoplectus tabernaemontani*									167.89	124.09		
[6]*Spergularia rubra*									7.00	7.00		
[6]*Stellaria graminea*									160.89	82.79		
[5]*Taraxacum officinale*									118.92	61.11	0.10	1
[5]*Triglochin maritima*									7.00	7.00	0.02	2
[6]*Typha latifolia*									27.98	13.72		
[6]*Urtica dioica*									55.96	29.19		
[5]*Veronica officinalis*									13.99	13.99	0.51	1
In total	**0**	**0**		**0**	**0**		**0.00**	**0.00**	**901.32**	**284.76**	**1.27**	**5.94**
Species only in vegetation												
[7]*Achillea millefolium*											3.67	3
[7]*Angelica sylvestris*											0.32	3
[7]*Carex disticha*											0.19	2
[7]*Carex rostrata*											0.13	1
[7]*Deschampsia cespitosa*											1.20	4
[7]*Festuca ovina*											0.61	1
[7]*Hierochloe odorata*											0.04	1
[7]*Juniperus communis*											0.03	1

Table A1. Continued.

Species	Seedlings in field								Seed bank		Mature vegetation	
	Delta	Sea-shore	Sign.	Grazed	Ungrazed	Sign.	All /m^2	Std err /m^2	Seeds/m^2	Stderr seeds/m^2	Cover %	Freq.
[7]*Luzula multiflora*											0.65	5
[7]*Lysimachia vulgaris*											0.15	5
[7]*Nardus stricta*											0.19	2
[7]*Peucedanum palustre*											0.13	1
[7]*Phragmites australis*											0.19	3
[7]*Poa subcaerulea*											1.58	16
[7]*Ranunculus acris*											0.63	3
[7]*Salix phylicifolia*											0.71	4
[7]*Sedum telephium*											0.13	2
[7]*Triglochin palustris*											0.05	4
[7]*Vicia cracca*											0.23	4
In total	**0**	**0**		**0**	**0**		**0.00**	**0.00**	**0.00**	**0.00**	**0.57**	**3.42**
In total in all groups	**3603**	**1006**		**2118**	**2491**		**32.69**	**49.65**	**880.71**	**298.57**	**1.13**	**6.493**

Sign.: ns.= not significant
* = p < 0.05
** = p < 0.01
*** = p < 0.001).

References

Bakker J.P., Dijkstra M. and Russchen P.T. 1985. Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt marsh gradient. New Phytologist 101: 291–308.

Chambers J.C. 1995. Relationships between seed fates and seedling establishment in an alpine ecosystem. Ecology 76: 2124–2133.

Crawley M.J. 1986. Plant Ecology. Blackwell Scientific Publications, Oxford.

Debussche M. and Isenmann P. 1994. Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. Oikos 69: 414–426.

Fenner M. 1985. Seed Ecology. Chapman and Hall, London.

Freedman B., Hill N., Svoboda J. and Henry G. 1982. Seed banks and seedling occurrence in a high Arctic oasis at Alexandra Fjord, Ellesmere Island, Canada. Canadian Journal of Botany 60: 2112–2118.

Gough L., Grace J.B. and Taylor K.L. 1994. The relationship between species richness and community biomass: The importance of environmental variables. Oikos 70: 271–279.

Grace J.B. and Jutila H. 1999. The Relationship between Species Density and Community Biomass in Grazed and Ungrazed Coastal Meadows. Oikos 85: 398–408.

Grime J.P. 1979. Plant Strategies and Vegetation Processes. John Wiley & Sons, Chichester.

Grime J.P., Hodgson J.P. and Hunt R. 1988. Comparative Plant Ecology: A Functional Approach to Common British Species. Unwin Hyman, London.

Grubb P.J. 1977. The maintenance of species-richness in plant communities: the importance of regeneration niche. Biological Reviews 52: 107–145.

Hämet-Ahti L., Suominen J., Ulvinen T. and Uotila P. 1998. Retkeilykasvio (Field Flora of Finland). Finnish Museum of Natural History. 4th edn. Botanical Museum, Helsinki.

Harper J.L. 1977. Population Biology of Plants. Academic Press Inc, London.

Houle G. 1995. Seed dispersal and seedling recruitment: The missing link(s). Ecoscience 2: 238–244.

Jutila H. 1997a. Vascular plant species richness in grazed and ungrazed coastal meadows, SW Finland. Annales Botanici Fennici 34: 245–263.

Jutila H. 1998a. Seed bank of grazed and ungrazed Baltic seashore meadows. Journal of Vegetation Science 9: 395–408.

Jutila H. 1998b. Effect of different treatments on the seed bank of grazed and ungrazed Baltic seashore meadows. Canadian Journal of Botany 76: 1188–1197.

Jutila H. 1999a. Effect of grazing on the vegetation of shore meadows along the Bothnian Sea, Finland. Plant Ecology 140: 77–88.

Jutila b. Erkkilä H. 1999b. Vegetation and Seed Bank of Grazed and Ungrazed Baltic Coastal Meadows, in SW Finland. Annales Universitatis Turkuensis Series AII Tom.

Jutila H. 2000. On the seed banks of grazed and ungrazed Baltic coastal grasslands. In: Proceedings IAVS Symposium. IAVS, Opulus Press, Uppsala, Sweden, pp. 272–277.

Jutila H. 2001a. How does grazing by cattle modify the vegetation of coastal grasslands along the Baltic Sea? Ann. Bot. Fennici 38: 181–200.

Jutila H.M. 2001b. Effect of flooding and draw-down disturbance on the germination from coastal a grassland seed bank. J. Veg. Sci 12: 729–738.

Jutila H., Pykälä J. and Lehtomaa L. 1996. Satakunnan Perinnemaisemat. Alueelliset ympäristöjulkaisut 14. Suomen ympäristökeskus, Helsinki, Finland.

Kadlec J.A. and Smith L.M. 1984. Marsh plants establishment on newly flooded salt flats. Wildlife Soc. Bull. 12: 388–394.

Kauppi M. 1967. Uber den Einfluss der Beweidung auf die Vegetation der Uferwiesen an der Bucht Liminganlahti im Nordteil des Bottnischen Meerbusens. Aquilo Series Botanica 6: 347–369.

Leck M.A. and Graveline K.J. 1979. The seed bank of a freshwater tidal marsh. Am. J. Bot. 66: 1006–1015.

Leck M.A. and Simpson R.L. 1987. Seed bank of a freshwater tidal wetland: turnover and relationship to vegetation change. Am. J. Bot. 74: 360–370.

Leck M.A. and Simpson R.L. 1993. Seeds and seedlings of the Hamilton Marshes, a Delaware River Tidal freshwater wetland. Proceedings of the Academy of Natural Sciences of Philadelphia 144: 267–281.

Leck M.A. and Simpson R.L. 1994. Tidal freshwater wetland zonation: Seed and seedling dynamics. Aquatic Botany 47: 61–75.

Leck M.A. and Simpson R.L. 1995. Ten-year seed bank and vegetation dynamics of a tidal freshwater marsh. American Journal of Botany 11: 1547–1557.

Leck M.A., Simpson R.L. and Parker V.T. 1989. The Seed Bank of a Freshwater Tidal Wetland and Its Relationship to Vegetation Dynamics. In: Sharitz and Gibbons (eds), Freshwater Wetlands and Wildlife. DOE Symposium Series. Vol. 61., pp. 189–205.

Lenssen J., Menting F., Van Der Putten W. and Blom K. 1999. Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. Oikos 86: 523–534.

McCune B. and Mefford M.J. 1995. PC-ORD. Multivariate Analysis of Ecological Data, Version 2.0. MjM Software Design, Gleneden Beach, Oregon, USA.

McGraw J.B. and Shaver G.R. 1982. Seedling density and seedling survival in Alaskan cotton grass tussock tundra. Holarctic Ecology 5: 212–217.

Milberg P. 1993. Seed bank and seedlings emerging after soil disturbance in a wet semi-natural grassland in Sweden. Annales Botanici Fennici 30: 9–13.

Milchunas D.G. and Lauenroth W.K. 1993. Quantitative Effects of Grazing on Vegetation and Soils over a Global Range of Environments. Ecological Monographs 63: 327–366.

Moore D.R. and Keddy P.A. 1988. Effects of a water-depth gradient on the germination of lakeshore plants. Canadian Journal of Botany 66: 548–552.

Parker V.T. and Leck M.A. 1985. Relationship of seed banks to plant distribution patterns in a freshwater tidal wetland. American Journal of Botany 72: 161–174.

Peart D.R. 1989. Species interactions in a successional grassland. I. Seed rain and seedling recruitment. Journal of Ecology 77: 236–251.

Rusch G. 1988. Reproductive regeneration in grazed and ungrazed limestone grassland communities on Öland. Preliminary Results. Acta Phytogeographica Suecica 76: 113–124.

Ryser P. 1993. Influences of neighbouring plants on seedling establishment in limestone grassland. Journal of Vegetation Science 4: 195–202.

Sanchez J.M., Izco J. and Medrano M. 1996. Relationships between vegetation zonation and altitude in a salt-marsh system in northwest Spain. Journal of Vegetation Science 7: 695–702.

SAS Institute Inc. 1989–1996. The Statistical Analysis System. Ver. Release, 6.12.

Schupp E.W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 82: 399–409.

Seinä A. and Peltola J. 1991. Jäätalven kestoaika- ja kiintojään paksuustilastoja Suomen merialueilla 1961–1990. (Duration of the ice season and statistics of fast ice thickness along the Finnish coast 1961–1990). Finnish Marine Research 258: 1–46.

Shumway S.W. and Bertness M.D. 1992. Salt stress limitation of seedling recruitment in a salt marsh plant community. Oecologia, Berlin 92: 490–497.

Smith L.M. and Kadlec J.A. 1983. Seed banks and their role during drawdown of a North American marsh. J. Appl. Ecol. 20: 673–684.

Tyler G. 1969. Studies in the ecology of Baltic sea-shore meadows. II Flora and vegetation. Opera Botanica 25: 1–101.

van der Valk A.G. and Davis C.B. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59: 322–335.

Welling P. and Laine K. 2000. Characteristics of the seedling flora in alpine vegetation, subarctic Finland, I. Seedling densities in 15 plant communities. Annales Botanici Fennici 37: 69–76.

Wied A. and Galen C. 1998. Plant parental care: Conspecific nurse effects in *Frasera speciosa* and *Cirsium scopulorum*. Ecology 79: 1657–1668.