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Seed banks of river delta meadows on the west coast of Finland

Heli M. Jutila

Äijälänkatu 4B 12, FIN-13210 Hämeenlinna, Finland (e-mail: heli.jutila@ymos.htk.fi)

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The seed banks of two delta meadows were studied on the west coast of Finland (61°33´N, 21°39´–21°41´E) to evaluate the possibilities of using seed bank in the restoration of coastal wetland meadows. The objective of the study was to determine the size, composition and species richness of germinable seed bank, estimate the effect of flooding on the seed bank, and describe the similarities and differences between seed bank and the aboveground vegetation. The study areas are conservationally important. A total of 125 samples were taken with a corer of 4.8 cm in diameter to the depth of 10 cm. Altogether 4977 seedlings were observed, yielding an average of 22 005 ± 1880 seedlings/m^2. Most seedlings and species in the seed bank were monocotyledons, perennials and hemicryptophytes, similar to the aboveground vegetation. Although 36 species were found in both the seed bank and vegetation, there was a significant lack of similarity overall (Mantel test). The seed bank flora included 24 dicot vs. 25 monocot species and 41 perennial vs. 8 annual species. Many of the species found only in the seed bank were annuals or biennials (13 species, 46% of total) and those growing only in the aboveground vegetation were mainly perennials (52 species, 92% of total). The most abundant species found in the seed bank were *Carex nigra*, *C. aquatilis*, *Juncus gerardii*, *Calla palustris*, and *Potentilla palustris*, which together made up 74% of the seed bank. The numbers of species differed significantly between different elevation classes and were highest at middle elevations. Seed bank is an important part of these delta grassland communities and can be utilised in restoration.

Key words: coastal grassland, delta meadows, ecology, germination, grazing, seed bank, vegetation

Introduction

Understanding the relationships among seed banks, vegetation, and environmental conditions may be vital in conservation, management and restoration of plant communities. Coastal and delta grasslands and wetlands are key biotopes, which have important biodiversity values, related to both animal and plant life. Constant succession of new land due to land uplift characterises most Baltic coastal grasslands. Kokemäenjoki is one of the biggest rivers in northern Europe and its delta expands seaward due to accumulation of sediments. This provides an excellent area to study the vegetation, seed bank and environmental factors and their influence on the prospects of restoration.

Density and composition of seed banks of freshwater wetlands can vary widely. Many studies have reported large multispecies seed banks (Chippindale & Milton 1934, van der Valk & Davis 1978, Keddy & Reznicek 1982, Nicholson & Keddy 1983, Skoglund 1990), while some have reported small seed reserves (van der Valk & Verhoeven 1988, Hytteborn *et al.* 1991). Variation in seed bank can be expected to result from a number of factors, such as established vegetation, flooding, soil properties, physical scouring, and animal influences. Many of them are directly or indirectly related to complex shoreline elevation gradients (Leck & Simpson 1994, Baldwin & Mendelssohn 1998, Jutila 1998b, Seabloom *et al*. 1998, Abernethy & Willby 1999). However, relatively few studies have characterised how seed banks vary along shoreline gradients (e.g. Jerling 1983, Keddy 1985, Jutila 1998b).

The aims of this study were: (1) to determine the abundance and species richness of germinable soil seed bank of grasslands of a river delta on the west coast of Finland; (2) to compare the seed bank at different elevations and flooding regimes; (3) to describe the similarities and differences between the seed bank and the aboveground vegetation; and (4) to estimate the possibilities of using seed banks in the restoration of delta grasslands. I made the following predictions at the beginning of the study: (1) because delta grasslands are productive and (for the most part of the year) undisturbed habitats, perennial competitors tend to dominate them, and because competitors generally have a persistent seed bank (Grime *et al*. 1986), the delta seed bank is expected to be persistent and fairly abundant; (2) based on my earlier studies the biggest seed bank should be found at intermediate levels of elevation; and (3) the seed bank is composed of species that are also found in the aboveground vegetation, but substantial differences in relative abundances are expected.

Material and methods

Study area and sites

The study area is situated on the west coast of Finland near the town of Pori (61°33´N, 21°39´–21°41´E) (Jutila 1997a). The seed banks of two shore meadows in the delta of the Kokemäenjoki were investigated in 1993 and 1994. In order to better represent the range of shore meadows in the region, one of the meadows selected for the study is grazed while the other represents ungrazed conditions.

The annual mean temperature of the study area is +4.3 °C (monthly average is –6.5 °C in January and +16.0 °C in July), the annual mean precipitation is 536 mm (22 mm in February, 75 mm in August), and the average duration of the snow cover in the area is 94 days (Finnish Meteorological Station Service). The sea at the Mäntyluoto station is frozen for an average of 95 days (Seinä & Peltola 1991). The water in the delta is mainly fresh, but there are occasional bursts of brackish water when the water level in the sea rises. The Baltic Sea does not have regular tides, but there are seasonal and daily water level fluctuations, which also affect the water levels in the delta. During the growing season, the water level usually fluctuates approximately within a 20 cm range, but changes of up to one metre can occur. In spring and fall the changes are the highest. The river carries sediment into the bay of Pihlavanlahti extending the delta seaward. The land upheaval rate in Pori is 7 mm per year. When the effect of sedimentation (about 7 mm per year) is added to that, it can be judged that the studied transects were under water still at the beginning of this century.

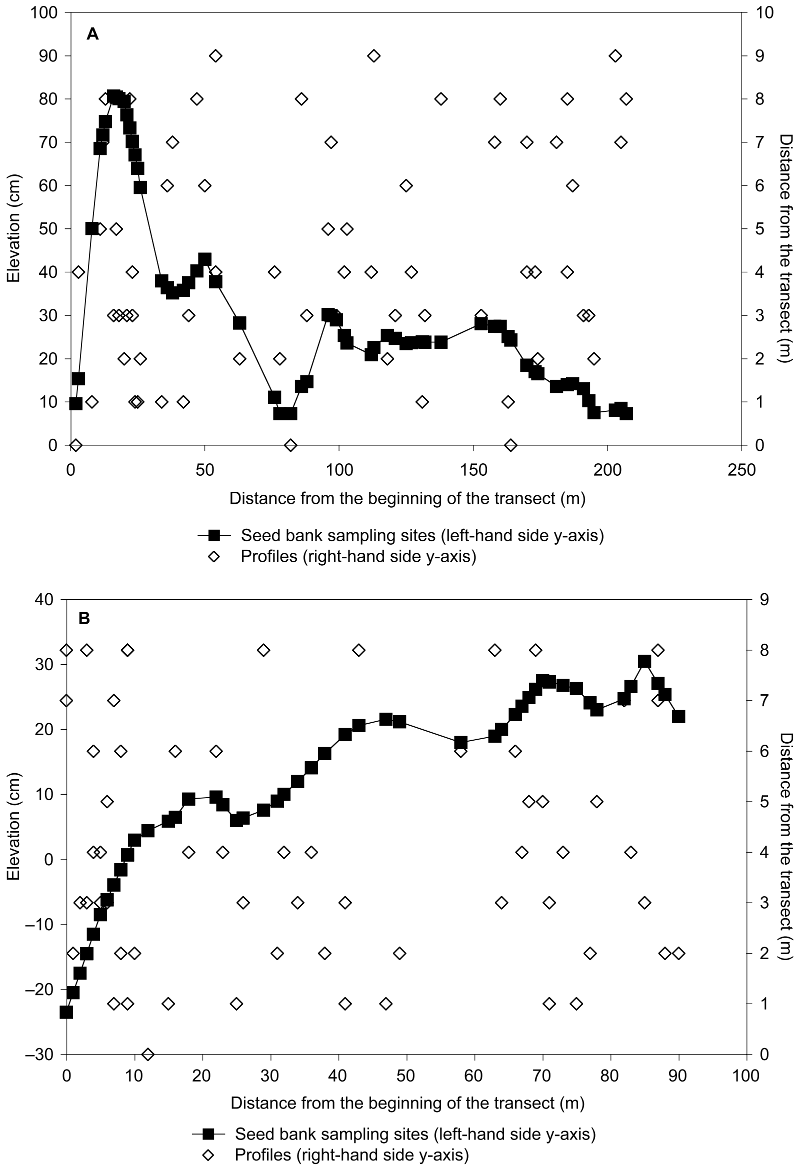

Fig. 1. Seed bank sampling sites and profiles of the study transects. — **A**: Profile of Fleiviiki. — **B**: Profile of Teemuluoto. Profiles and diamonds indicating transects should be read against the first *y*-axis (elevation; zero level is the mean water level) and squares indicating seed bank sampling sites against the second *y*-axis, distance from the transect, in metres to west (+) or to east (–).

The study area belongs to the southern boreal zone and the bedrock is predominantly sandstone.

In the spring of 1993, one study transect (Fig. 1) was established perpendicular to the shoreline both in a pasture grazed by cattle at Fleiviiki and in an ungrazed meadow at Teemuluoto, located about 1.5 km downstream. The meadow of Fleiviiki has been grazed by cattle and horses since the beginning of this century. The vegetation of Fleiviiki consists of wet (*Potentilla palustris–Carex aquatilis*), moist (*Calamagrostis stricta–Festuca rubra–Potentilla palustris–Carex nigra*), mesophilous (*Carex nigra–Potentilla anserina–Trifolium repens*), and even dry meadows (*Nardus stricta–Festuca ovina*; Jutila 1999a, 1999b). At the ungrazed meadow, Teemuluoto, there was a zone of *Schoenoplectus lacustris–Eleocharis palustris* at low elevation, then wet (*Potentilla palustris–Carex aquatilis*) and moist (*Calamagrostis stricta–Carex aquatilis–Potentilla palustris*) meadows.

At higher elevations *Salix phylicifolia* was abundant. Both transects were on river sediments: in the grazed transect clay was mixed with sand and in the ungrazed transect peat was mixed with clay. More information of the study sites can be found in Jutila (1994, 1997b, 1998c) and Jutila *et al.* (1996).

Methods

The beginnings of both transects were established where the emergent vegetation began, i.e. approximately at the average summer water level. The transects ran perpendicularly from the shore to the woods, through 3–4 vegetation zones. Sampling points were identified by the distance from the beginning of the transect and by the right-angled distance from the transect (always less than ten metres).

In 1994 the elevation of the points along the transects were determined with an altimeter at distance intervals of five metres. The water level was referenced to the station data from Mäntyluoto, Pori and the profiles of the transects were drawn (Fig. 1). The elevation of each metre in the transect was linearly interpolated from the values measured. For certain analyses, the data were divided into three or four elevation classes (< 10 cm, 10–20 cm, 20–31 cm, > 31). Because only after measuring the elevations I realised that the transects were at somewhat different levels, I had to shift my focus from studying the effects of grazing. However, because 64 samples (30 + 34) were taken in both transects in the elevation classes 2 and 3, I was still able to test the effect of grazing using this subset of data.

A total of 125 seed bank samples were collected, 65 from Fleiviiki and 60 from Teemuluoto. Samples were taken randomly inside vegetation zones in June 1993 with a corer 4.8 cm in diameter and to a depth of 10 cm. The transient seeds of the seed bank were presumed to have germinated and new seeds had not yet fallen (there were no spring annuals in the aboveground vegetation), and thus the samples expressed the persistent seed bank.

The percentage cover of different species in vegetation along the transects was studied within 1-m^2 plots located so that the seed bank sampling point was in the corner of the plot (there were vegetation plots only for every second seed bank sampling point along the transects). This data was used for statistical tests comparing the seed bank and aboveground vegetation.

Nomenclature of plants follows Hämet-Ahti *et al.* (1998).

Treatment of seed bank samples

In this study, the seed bank was examined by germinating seeds from soil samples. This method is commonly used and provides an accurate measure of wetland seed bank composition (Poiani & Johnson 1988; different methods *see* e.g. Major & Pyott 1966, Gross 1990, Brown 1992).

To mimic the natural conditions all samples were preserved in a cold room (temperature 5 °C) for about five months, then frozen two weeks (–1 °C) and again kept in a cold room for two weeks until germinated in November of 1993. These treatments ensured that the seeds entered another winter dormancy and the seedlings germinating from the samples after the treatment indicated a persistent seed bank.

The topmost part of the sample was rinsed with water through a sieve (to exclude vegetative parts and regrowth; 1 mm holes) and the bigger seeds were picked back to the sample. The part of the sample without many vegetative parts was directly spread out in a 0.5 cm layer (Wesson & Wareing 1967) to germinate on a mixture of fertilised peat and sand (1:1). Twenty control trays filled with pure substrate were used to monitor any airborne seed contamination (which was not detected).

The samples were germinated in the greenhouse of the Satakunta Environmental Research Centre. Samples were given a photoperiod of 16 hours of light and 8 hours of dark. The temperature was programmed for 20 °C by day and 15 °C by night, because seeds of many plants have been shown to have fluctuating temperature requirements for germination (Dietert & Shontz 1978, van Tooren & Pons 1988). A mesh was used to prevent seeds from entering the greenhouse. Samples were watered once or twice a day depending on the temperature. On very hot days, water was automatically sprayed to air to lower the temperature.

All samples were exposed to germination conditions for three months, after which all the plants were removed and the soil with the substrate was mixed and exposed again for three more months. The germination had clearly slowed down after this point. The seedlings that could not be identified to species were planted and grown until they flowered or died, or for two and a half years. The first seedlings emerged in less than a week. I observed the sample pots every week and made an inventory four times during the growth period (the final in the end of the experiment). In this paper the total germination data are used. The data were divided into systematic groups (monocotyledons, dicotyledons and gymnosperms), life-history types (annuals + biennials vs. perennials; modified according to Hämet-Ahti *et al.* 1998) and Raunkiaer's life forms (phanerophytes, chamaephytes, hemicryptophytes, geophytes, helophytes, hydrophytes and therophytes; according to Grime *et al.* 1988). All these groupings have ecological significance and can help to understand the studied system.

Statistics

Statistical analyses were performed using Statistical Analysis System (SAS 1989–1996). I used non-parametric statistics (mainly Mann-Whitney *U* and Kruskal-Wallis tests) to compare seed banks in different elevation classes. The only species with normally distributed data was *Carex nigra*, for which I ran ANOVA to determine the effect of elevation class. I used covariance analyses with elevation as covariate and ln-transformed data to study the differences between transects. I compared the number of seeds of different life-history groups (annuals + biennials vs. perennials) by a pairwise *t*-test. Mantel tests were run using mean difference (in PATN, Belbin 1993) to check the similarity between the seed bank and the aboveground vegetation, and only those samples and plots that were adjacent to each other were used (n = 50). Sorensen's similarity indices were calculated to compare the whole flora of seed bank (n = 125) and of aboveground vegetation (plots and other vegetation studies in the area).

Results

Seed bank density

Altogether 4977 seedlings, and on average 39.8 ± 3.40 per sample (Fig. 2), germinated from the 125 cold-treated samples. This translates to an average of 22 005 ± 1880 seeds/m^2 (19 494 ± 2411 seeds/m^2 in Fleiviiki and 24 721 ± 2898 seeds/m^2 in Teemuluoto). Pairwise *t*-tests showed that there were significantly more monocot (79.5%) than dicot (20.5%) seedlings and perennial (96.0%) than annual + biennial (2.2%; the rest were unidentified) seedlings in the whole data and in different transects. Most of the seedlings were hemicryptophytes (78.6%).

Seed bank flora

In the germinating seed bank, I identified in total 49 species and 20 families and a mean of 6.2 species per sample. The plant family represented most frequently was Cyperaceae, and other common families in the seed bank were Juncaceae, Araceae, Rosaceae and Betulaceae. Sixty-four percent of the species per sample were hemicryptophytes and 14% helophytes. Pairwise *t*-tests showed that there were significantly more monocot (57.8%) than dicot (42.1%) and perennial (93.6%) than annual + biennial (6.4%) species in the whole data and in the transects separately. The predominance of perennial species was higher in Fleiviiki than in Teemuluoto.

The total seed bank flora (49 species) of these delta meadows was comprised of 24 dicot species vs. 25 monocot species and 41 perennial species vs. 8 annuals. There were 30 hemicryptophyte, eight therophyte, six helophyte, three hydrophyte and two phanerophyte species (Table 1). The total number of species in the seed bank was somewhat higher in Fleiviiki (37 species) than in Teemuluoto (33 species), but so was the number of samples (Fleiviiki, n = 65; Teemuluoto, n = 60) and the number of species in the aboveground vegetation (76 vs. 43, respectively).

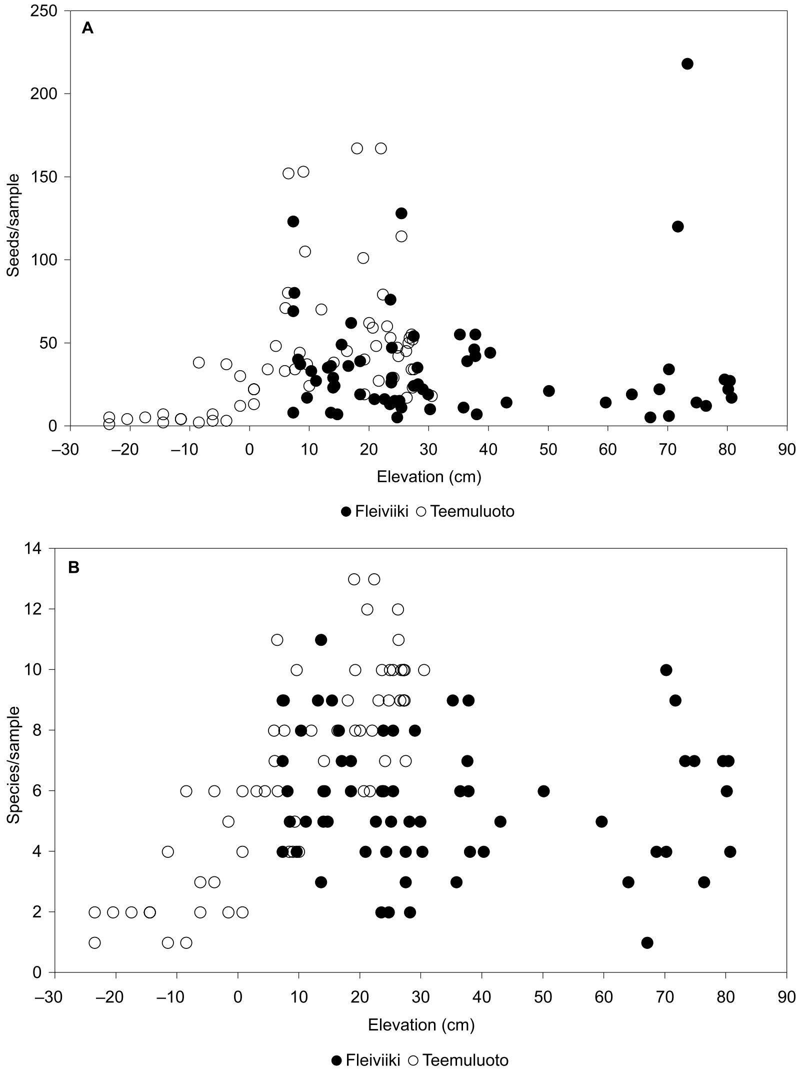

Fig. 2. Effect of elevation on the seed bank of grazed and ungrazed samples. — **A**: Number of seeds per sample. — **B**: Number of species per sample. Filled squares indicate grazed samples and open squares indicate ungrazed samples.

The most abundant species in the seed bank (Table 2) were *Carex nigra*, *C. aquatilis*, *Juncus gerardii*, *Calla palustris* and *Potentilla palustris*, each represented by more than 200 seedlings and making up 74.1% of the seed bank. *Carex nigra*, *Cicuta virosa*, *Eleocharis palustris*, *Galium palustre*, *Juncus alpinoarticulatus*, *Lythrum salicaria*, *Polygonum lapathifolium*, *Potentilla palustris*, *Sparganium minimum* and *Stellaria palustris* were more abundant in Teemuluoto than in Fleiviiki, whereas *Agrostis canina*, *Calla palustris*, *Carex panicea*, *Elymus repens*, *Juncus bufonius*, *J. gerardii* and *Potentilla anserina* were more abundant in Fleiviiki than in Teemuluoto. Half of the seed bank species were common to both sites.

Seed bank in different elevation classes

The number of species ($\chi^2 = 0.002$, df = 3) differed significantly in the four elevation classes. On average the lowest species richness were found in the samples from elevations < 10 cm and > 31 cm and the highest abundance and richness were found in the middle elevations (10–20 cm and 20–31 cm; Fig. 2). Most hydrophyte seeds and species were found below

20 cm, most helophyte seeds and species between 10 and 31 cm and most hemicryptophyte species above 31 cm.

Carex nigra was the most abundant species in all elevation classes. Significant differences among four elevation classes were evident in e.g. *Agrostis canina*, *A. stolonifera*, *Calamagrostis stricta*, *Calla palustris*, *Eleocharis palustris*, *Festuca rubra*, *Galium palustre*, *Gnaphalium uliginosum*, *Juncus bufonius*, *Juncus gerardii*, *Polygonum lapathifolium*, *Potentilla anserina*, *Potentilla palustris*, and *Trifolium repens*.

When I used the subset of data taken at 10–31 cm elevation, I was able to test the effect of grazing. The species richness and number of seedlings in the seed bank were higher in ungrazed than in grazed samples (9.07 ± 0.37 vs. 5.76 ± 0.37 species/sample and 30 797.51 ± 3796.50 vs. 18 346.98 ± 2238.11 seeds/sample, respectively) and this was true for monocots, dicots (not for the number of species), annuals, perennials, etc. Only hydrophytes were found more often in grazed than in ungrazed samples.

Seed bank and aboveground vegetation

Mantel test indicated a significant lack of similarity ($p = 0.0001$; correlation 23%) between the seed bank and the aboveground vegetation in both transects, but the difference was significant only in one elevation class (Table 3). Fifty-two species found in the vegetation did not germinate from the seed bank. Thirty-six species, most of them (94.4%) perennials, were found both in the seed bank and in the aboveground vegetation. Thirteen species (*Bidens tripartita*, *Carex panicea*, *Chenopodium album*, *Eleocharis acicularis*, *Elymus repens*, *Gnaphalium uliginosum*, *Juncus alpinoarticulatus*, *J. bufonius*, *Limosella aquatica*, *Poa trivialis*, *Sagina procumbens*, *Stellaria graminea* and *S. media)* germinated from the seed bank but were not present in the aboveground vegetation of the transects. Six of these species were annuals or biennials. Only *Carex nigra*, *Betula pubescens* and *Cicuta virosa* made up a higher percentage of the seed bank than of the cover of aboveground vegetation.

Similarity indices (Table 4) were calculated for the whole data set and for the separate transects as well for different species groupings to show the similarity between the aboveground vegetation and seed bank. Teemuluoto had higher similarity between seed bank and aboveground vegetation than Fleiviiki. This was especially clear in monocots (the highest similarity value 0.84). In Fleiviiki the similarities were fairly low, but still in the total number of species Fleiviiki (29) had more

Table 1. The number of species in seed bank (SB) and in aboveground vegetation (AV). SB/AV = species both in seed bank and in aboveground vegetation.

	Fleiviiki			Teemuluoto			all samples		
Variable	SB	SB/AV	AV	SB	SB/AV	AV	SB	SB/AV	AV
All species	37	29	76	33	27	43	49	36	88
Monocots	19	15	38	18	16	17	25	19	42
Dicots	18	14	37	15	11	26	24	17	45
Gymnosperms	0	0	1	0	0	0	0	0	1
Annuals + biennials	6	2	5	3	1	2	8	2	6
Perennials	31	27	71	30	26	41	41	34	82
Phanerophytes	2	2	4	2	1	1	2	2	4
Chamaephytes	0	0	5	0	0	0	0	0	5
Hemicryptophytes	24	20	40	20	17	25	30	24	45
Helophytes	5	4	14	5	5	11	6	5	16
Hydrophytes	1	1	9	3	3	5	3	3	13
Therophytes	6	2	4	3	1	1	8	2	5

Table 2. The abundance of individual species in the seed bank. Abund. is a mean number of seedlings/m^2, S.E. is a standard error of the mean in numbers of seeds/m^2, Freq. is a number of samples in which species was encountered, and Sum is the total number of seedlings found in all samples.

Species	Abund.	S.E.	Freq.	Sum
Agrostis canina	248.68	70.311	20	56
Agrostis capillaris	66.31	23.150	9	15
Agrostis stolonifera	392.36	68.136	39	89
Anthoxanthum odoratum	8.84	8.842	1	2
Betula pubescens	641.04	69.449	71	145
Bidens tripartita	4.42	–	1	1
Calamagrostis stricta	276.31	56.014	34	63
Calla palustris	1177.08	320.143	31	266
Carex aquatilis	2868.10	848.294	47	649
Carex nigra	10024.53	1147.238	123	2268
Carex panicea	66.31	26.335	7	15
Carex rostrata	4.42	–	1	1
Chenopodium album	4.42	–	1	1
Cicuta virosa	121.58	51.713	13	28
Deschampsia cespitosa	13.26	13.263	1	3
Eleocharis acicularis	4.42	–	1	1
Eleocharis palustris	674.20	179.799	30	153
Elymus repens	27.63	12.327	5	6
Festuca rubra	276.31	58.761	34	63
Filipendula ulmaria	4.42	–	1	1
Galium palustre	513.94	91.005	45	116
Glyceria fluitans	44.21	28.491	3	10
Gnaphalium uliginosum	8.84	6.227	1	2
Iris pseudacorus	4.42	4.421	1	1
Juncus alpinoarticulatus	342.62	179.403	10	77
Juncus bufonius	154.73	69.506	10	35
Juncus filiformis	276.31	265.259	4	63
Juncus gerardii	1337.34	488.875	57	302
Leontodon autumnalis	4.42	–	1	1
Limosella aquatica	4.42	–	1	1
Luzula pilosa	4.42	–	1	1
Lythrum salicaria	149.21	43.661	19	34
Persicaria lapathifolia	303.94	55.247	36	69
Poa trivialis	13.26	9.854	2	3
Potentilla anserina	127.10	62.816	10	29
Potentilla argentea	4.42	–	1	1
Potentilla palustris	900.77	162.429	55	204
Rumex acetosella	8.84	8.842	1	2
Sagina procumbens	55.26	40.597	5	13
Salix phylicifolia	55.26	36.508	3	13
Schoenoplectus lacustris	8.84	6.227	1	2
Senecio vulgaris	4.42	–	1	1
Sparganium natans	44.21	14.855	9	10
Stellaria graminea	4.42	–	1	1
Stellaria media	4.42	–	1	1
Stellaria palustris	154.73	45.527	20	35
Trifolium repens	13.26	7.595	1	3
Viola palustris	17.68	8.734	1	4
unidentified grass	99.47	35.167	11	23
unidentified monocot	215.52	85.817	12	49
unidentified dicot	198.94	36.278	30	45

common species to seed bank and vegetation than Teemuluoto (27).

Discussion

Seed bank density

The seed densities in the persistent seed bank were high (an average of 22 005 ± 1880 seedlings/m^2). They were higher than in the nearby seashore meadows (on average 13 669 seeds/m^2; Jutila 1998b). They were also higher than in the freshwater tidal wetlands in New Jersey (Leck & Graveline 1979, Parker & Leck 1985), the river swamps of Savannah in South Carolina (Schneider & Sharitz 1986), river wetlands of Florida (Leck *et al.* 1989), a shore of a river-lake in Sweden (Grelsson & Nilsson 1991), and the quaking fens of the Netherlands (van der Valk & Verhoeven 1988). However, they were clearly smaller than those found in intermittently flooded wetlands of South Carolina (Kirkman & Sharitz 1994). Leck and Simpson (1987) obtained similar results in a high marsh and a shrub forest, but found a larger seed bank at a cattail site. van der Valk and Davis (1978) reported higher but later lower (van der Valk and Davis 1979) seed numbers from non-tidal freshwater marshes of Iowa. One reason for the high seed density found in this study could be that the delta acts as a sink for seeds transported from the upstream of the river.

Many wetland plants produce huge amounts of seeds, which never have a chance to germinate. This is related to the water level fluctuation. In a constantly evolving system like the delta new land is continuously formed and in natural conditions the seeds have at least some chance to germinate. The benefit of having a seed bank is that the species is more likely to be able to retain its space in the vegetation succession.

The high dominance of perennials, which was detected both in the seed bank and in the aboveground vegetation, was evident also in studies by Kirkman and Sharitz (1994). In this study, most species only had a small seed bank or none at all, maybe indicating that vegetative propagation is for many species more important in maintaining populations than propagation from seeds. The number of seeds recruited and seedlings that survived to maturity in shore communities with dense perennial vegetation has been shown to be minimal compared to the density of the seed bank (Smith & Kadlec 1983, Shumway & Bertness 1992, Allison 1996). Milberg (1993) found a species-rich seed bank in a wet semi-natural meadow, but only few species and seedlings contributed to regeneration after disturbance.

With the subset of data (elevations 10–31 cm) I was able to show that in the ungrazed samples the seed density and the species richness were higher than in the grazed samples, which is consistent with my previous results on seashore meadows (Jutila 1998b).

Seed bank flora

It is more difficult to make appropriate comparisons with the seed bank literature concerning the

Table 3. The results of the Mantel tests. Significant results indicate that respective seed bank and vegetation are significantly different. *N* = number of samples and plots.

Data	*N*	Similarity	*P*
All	50	0.228	0.0001***
G4	31	0.230	0.0020**
UG4	19	0.268	0.0001***
< 10 cm	8	0.270	0.0521°
10–20 cm	10	0.293	0.2820^{ns}
20–31 cm	22	0.212	0.0001***
> 31 cm	10	0.286	0.9147^{ns}

*** = ≤ 0.001; ** = 0.001 < *P* ≤ 0.01; ° = 0.05 < *P* ≤ 0.10; ^{ns} = not significant (*P* > 0.10).

Table 4. Similarity indices. The number indicates the number of species common to the seed bank and vegetation divided by the number of all species.

Variable	Index		
	Fleiviiki	Teemuluoto	All
Species	0.345	0.551	0.356
Monocots	0.357	0.842	0.396
Dicots	0.341	0.367	0.327
Annuals + biennials	0.222	0.250	0.167
Perennials	0.415	0.448	0.382

species richness than with the seed density because the sampling effort (both the individual sample size and the total volume in study) varies in different studies. However, it seems that the species numbers are in the range that is usually detected in these environments (*see* e.g. Leck *et al.* 1989, Grelsson & Nilsson 1991). Three of the detected species (*Calamagrostis stricta*, *Limosella aquatica* and *Persicaria lapathifolia*) have not been found earlier in the seed bank according to Thompson *et al.* (1997; but *see* Jutila 1998a, 1998b).

It appears that the total number of species in the seed bank and in the vegetation were higher in the grazed than in the ungrazed site. However, the differences were small and could not be tested statistically.

Effect of elevation and vegetation zone

Water level fluctuation can be regarded as a stress restricting photosynthetic production and it can also be regarded as a disturbance leading to total or partial destruction of plant biomass. In this study the water level fluctuation increased at lower elevations. I was able to show that the species richness of the seed bank was highest at the middle elevations (like Keddy 1985, Wisheu & Keddy 1991, Navie *et al.* 1996) at intermediate level of disturbance (as the intermediate disturbance hypothesis predicts; Grime 1973, Connell 1978). These results are in accordance with the predictions of the model of species richness and the density of seed bank versus disturbance presented by Jutila (1998b).

The reasons for the relatively small seed bank near the waterline may be the following: (1) waves and floods clean the shore of detached plant material and move it to higher elevations; (2) at lowest elevations vegetation is composed of a narrow pool of species adapted to flooding; 3) some of the species do not have a persistent seed bank (e.g. common reed); and (4) during drawdown there is free space available for germination and thus the seed bank may be depleted. Probably flooding kills most of these seedlings early and there may be difficulties in observing them in the field.

I expected that species would have most of their seeds in the same elevations where they are adapted to grow (like in seashore; Jutila 1998b), but this was not the case for all species. For example *Eleocharis palustris* that grows in lower littoral had the densest seed bank in middle littoral (20–31 cm). Explanations of the phenomena are probably related to the action of waves and possible depletion of seed bank at lower levels. However, most of the hydrophytes had their seed bank at low elevation, while helophytes at a somewhat higher and hemicryptophytes at an even higher elevation, all reflecting where the mature plants of these groups are found. As Grelsson and Nilsson (1991) suggested, long-floating species, like *Carex aquatilis*, *C. canescens* and *Galium palustre*, had most likely a seed bank and the highest abundance of seeds in the lower part of the shore.

Similarity between seed bank and aboveground vegetation

The seed bank and aboveground vegetation had a fairly low similarity in this study in spite of the fact that the most abundant species in the aboveground vegetation had a persistent seed bank. Still, over half of the angiosperm species (52) were solely found in the aboveground vegetation indicating that they either have a very small seed bank, which was not detected in this study, or their seeds are not retained in the seed bank for several years. Half of the species found only in the seed bank (13) were mainly short-living colonists (six annuals + biennials). Overall, the seed bank contained fewer species than the aboveground vegetation, but this pattern may at least partly reflect the smaller sampling area in the seed bank survey.

Many papers on different environments report the dissimilarity between aboveground vegetation and seed bank. These include Champness and Morris (1948), Chippindale and Milton (1934), Gilfedder and Kirkpatrick (1993), Jerling (1983), Leck *et al.* (1989), Oosting and Humphreys (1940), Roberts (1981), and van der Valk and Davis (1976). Loonley and Gibson (1995) and also Thompson and Grime (1979) found a low similarity between the seed bank and the aboveground vegetation despite the vegetation type. I tested the similarity of seed bank by elevation classes (representing vegetation zones) and the dissimilarity was significant only in one elevation class (20–31 cm). Ungar and Woodell (1993) conclude that there are relatively high similarities between aboveground vegetation and seed banks in annual-dominated vegetation, but low similarities in most perennial-dominated communities (opposite results to Hopkins & Parker 1984). The dissimilarities between seed bank and established vegetation in these perennial riverine meadows are consistent with such a generalisation.

Implications for restoration

The results of this study indicate that the delta grasslands have a large seed bank, in which the main dominants are represented. Thus, the seed bank can be utilized in restoration. However, in order to be successful the exact methods of restoration should be studied. The first step in the restoration of an overgrown delta grassland is cutting or burning. Subsequent management should be able to keep the woody species in control and compensate for the excess of the nutrients being released from the roots of the cut trees and shrubs. Seed bank can be activated by creating small (1–2 m^2) open spots in the vegetation to facilitate germination.

Conclusions

- The persistent seed bank of delta grasslands was large and fairly diverse.
- The species composition and richness varied at different elevations, the richness being highest at middle elevations, probably due to the effect of fluctuating water.
- About half of the species and most dominants in the vegetation were represented in the persistent seed bank.
- Seed bank was bigger in the ungrazed site than in the grazed site.
- Activation of seed bank provides one method for restoring delta grasslands, but it should be used carefully and in combination with other methods.

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