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The effect of successional stage and salinity on the vertical distribution of seeds in salt marsh soils

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ABSTRACT

Seed bank density and similarity between above-ground vegetation and seed bank with depth were compared between two adjacent salt marshes that differ in age. In addition, the effect of salinity on the variation in seed bank density and similarity between above-ground vegetation and seed bank with depth was compared between euhaline against mesohaline conditions in three salt marshes.

Ten plots of 2 m × 2 m were situated in a new salt marsh (existing since 2002) and 80 plots in three old salt marshes. Soil samples were collected at three different depths (0–5, 5–10, 10–15 cm) in spring 2006. Soil seed bank was investigated in germination experiments under greenhouse conditions. Germination experiments lasted 6 months and all seedlings were identified and removed after identification. Above-ground vegetation composition was determined during the growing season in all plots.

Viable seed density was calculated for each plot and for the three different depths; the similarity between seed bank and floristic composition of the above-ground vegetation was calculated. A general linear model was used to investigate the effect of soil depth, salinity and age of the salt marsh on density and similarity between seed bank and above-ground vegetation.

The results showed that seed density decreased with depth in all salt marshes, irrespective of their age and soil salinity. Seed density and similarity between seed bank and above-ground vegetation were higher in the new salt marsh than in the old one in the same study area. This is because in young as well as in old successional stages, the seed bank was mostly composed of new colonizers, while most perennial species were absent from the soil seed bank, although they were dominant in the standing vegetation of the old salt marsh.

The characteristics of the seed bank of a mesohaline salt marsh were found not to be fundamentally different from that of both euhaline salt marshes.

Introduction

The persistence of seeds is a fundamental aspect of plant biology. It plays a key role in the conservation and restoration of plant communities and is important for the potential response of plant species to changing land use and climate (Thompson et al., 1997). Seed banks are crucial for the restoration of plant communities (Bakker et al., 2002; Bossuyt et al., 2005; Klug-Pümpel and Scharfetter-Lehrl, 2008), the recovery of endangered plant species and the conservation of genetic diversity (Wolters and Bakker, 2002).

Additionally, knowledge of the vertical distribution of seeds in soil and the ability to predict the vertical distribution and emergence of viable seeds can be vital for vegetation restoration (Espinar et al., 2005). The density of soil seed banks is normally highest at the soil surface and declines monotonically with depth. This pattern is assumed to reflect regular seed input at the surface and a more-or-less gradual decline in viability through aging or during downward seed transport. However, sometimes peak densities occur in lower soil layers or density of soil seed bank remains constant along the soil depth gradient. For instance, Espinar et al. (2005) found that the total seed density of certain

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plant species at a depth of 15 cm is higher than at more shallow soil depths in the non-tidal part of the Doñana salt marsh (southwest Spain), due to seasonal disturbance processes (soil cracking during the dry season).

Adam (1990) states that in salt marsh habitats salinity is a determining factor for seed germination. Increasing soil salinity decreases the proportion of germinating seeds and slows down or delays seed germination and many seeds remain dormant due to low water potentials at high salinity levels (Chapman, 1974; Noe and Zedler, 2000; Qu et al., 2008; Rubio-Casal et al., 2003; Tobe et al., 2000; Ungar, 1962, 2001; Wei et al., 2008). Merely for the sake of the general deceleration of seed germination and the prolonged dormancy of the seeds in a saline environment, we hypothesize that they have a longer period to penetrate deeper into the soil (whether actively or through sediment accretion) and additionally to remain viable longer. Consequently, in high salinity habitat the decrease of seed density with soil depth is expected to be lower than in a less saline habitat.

It can also be expected that the similarity between seed bank and vegetation (hereafter called similarity) in higher salinity condition remains constant with depth, while in less saline conditions, it decreases with depth. The similarity between seed bank and above-ground vegetation and seed density has frequently been investigated in salt marsh habitats in the past. Grazing for example has been proven to be an important factor influencing these characteristics, although conclusions are often contradictory (Chang et al., 2001; Erkkilä and Heli, 1998; Ungar and Woodell, 1993, 1996). Study on the variation of seed density and similarity was not investigated yet in relation to different degrees of salinity. Hereafter we compare euhaline and mesohaline salt marshes in that respect.

The stage of succession (age) is also an important factor, which may significantly affect seed bank characteristics. The seed bank richness and density declined from initial to terminal successional stages in fallow land in which the number of species in the seed bank decreased significantly during the course of succession (Falinska, 1999). Succession in semi-natural grassy or meadow communities tends to show other types of change (Donelan and Thompson, 1980; Milberg, 1995; Patridge, 1989). Species number and seed bank size increased in the course of primary succession in an Alpine glacier foreland, with higher similarity between seed bank and standing vegetation of the early stages (Marcante et al., 2009). Chambers (1995) found in an alpine herb field that for late successional stages the seed bank was dominated by species producing less persistent seeds. In sandy dune slack habitat, Bossuyt and Hermy (2004) found that similarity between vegetation and the 0–5 cm layer in the seed bank increased with increasing slack age. Similarity between vegetation and the deeper soil layer was much lower and showed no significant correlation with age. In addition, they stated that during the course of succession there is a sharp increase in seed density with time and that the seed longevity index decreases during succession. Seed bank composition followed above-ground vegetation in time. As far as we know, the seed bank characteristics of young versus old salt marshes have not yet been compared in detail.

We tested the following two hypotheses: i) the seed bank in both old and new salt marsh is composed of early successional species, since early successional species tend to form persistent seed banks and late successional species tend to show a more transient seed bank (e.g. Bossuyt and Hermy, 2004); ii)in mesohaline salt marsh, seed density and similarity with above-ground vegetation decrease strongly with depth as compared with euhaline salt marsh, where a more constant seed bank density and composition is expected, due to better preservation circumstances, combined with the worse germination conditions in the latter environment.

Material and methods

Study areas

Our study areas consist of three salt marshes with different environmental conditions. Soil cores were sampled at three salt marsh sites, the mesohaline salt marsh 'Verdronken Land van Saeftinghe' in the Netherlands (further on called: Saeftinghe) with a west–east salt gradient of 5.5–8 psu of the river water along the Scheldt estuary, and the euhaline salt marshes IJzermonding and Zwin (salinity >15 psu) in Belgium. All sites are protected as nature reserves. The intertidal area of the IJzermonding has recently (2002) been increased during a large-scale restoration project by creation of a new 14 ha large area with a full 0.01–100% inundation frequency gradient. Large amounts of sand and slurry were removed in the period 2000–2002 (hereafter called 'new' salt marsh). In other parts of the IJzermonding, two smaller salt marsh relicts remained intact for centuries (hereafter called 'old salt marsh').

Data collection

Data were collected in 90 2 m × 2 m plots, 50 of which were established in Saeftinghe, 26 in the IJzermonding (10 in the new and 16 in the old salt marsh) and 14 in the Zwin. Seed bank composition was assessed by seedling germination under greenhouse conditions. Soil samples were collected in March 2006 when natural stratification had already taken place in the field. With an auger with a diameter of 3 cm, 25 soil cores were collected at random up to a depth of 15 cm in each plot. These samples were divided in three subsamples (0–5, 5–10 and 10–15 cm) and the subsamples were then pooled per soil layer for each plot. This resulted in an average of 0.88 liter soil sample in each plot for each layer, which exceeds the recommended 0.8 liter soil necessary to determine the species composition of the seed bank (Hutchings, 1986). The methodology of Ter Heerdt et al. (1996) was used to concentrate the soil seed bank samples, which were washed through a coarse (2 mm mesh width) and a fine (0.18 mm mesh width) sieve. The first sieve removes most roots and coarse vegetative parts. High water pressure together with finger pressure was used to make sure that all seeds were able to cross through the first sieve. The second sieve withholds all of the seeds while the majority of silty soil material is washed out. The concentrated samples were then spread in a thin layer (maximum 0.4 cm thick) in 40 cm × 40 cm trays filled with sterilized potting soil. In March 2006, the trays were randomly placed on shelves with a natural light regime and were kept moist by regular rain water spraying. Air temperature varied between 14 and 25 °C. 24 control trays, filled with the same sterilized potting soil were also placed randomly on the shelves to test for possible greenhouse and potting soil contamination.

Seedlings were identified as soon as possible after germination, counted and removed or, if they could not be identified immediately, transplanted to pots to allow further growth and identification.

After 6 months, when no further seedlings germinated, the trays were left to dry for two weeks. This allowed the samples to be crumbled to expose deeper buried seeds to the light. After watering the samples for another 3 weeks and changing the light into a light regime of 8 h dark/16 h light, no new seedlings emerged. Nevertheless, the residual soil was checked for remaining seeds by viewing small random samples taken from the trays under a microscope and probing seeds with a needle in order to distinguish between firm and empty seeds. Since the number of seeds that remained in the investigated soil samples was very low, we did not need to correct germination data for remaining viable seeds.

Above-ground vegetation composition was determined during the growing season of 2006 by visually estimating the cover of all vascular plant species with a decimal scale (Londo, 1976) in the 90 2×2 m^2 plot, used earlier for the soil seed bank sampling.

Plant species nomenclature follows Lambinon et al. (1998).

Data analysis

Seedling counts were recalculated to germinable seed density expressed per m^2 for each 5 cm soil depth layer and for each species separately. Similarity between the species composition of the standing vegetation and the soil seed bank was assessed with the quantitative Czekanowski similarity index (Kent and Coker, 1995) for each depth separately.

Seed density was transformed to $\log_{10}$ to meet normal distribution requirements for parametric analysis. General linear modeling and post-hoc tests were used to compare the seed density and similarity between new and old salt marsh for the IJzermonding data. Seed density and similarity were introduced as dependent variables while depth categories (0–5, 5–10 and 10–15) and age categories (old and new) were introduced as fixed factors. An interaction between depth and age was also considered in the model. Furthermore, the data were divided into two groups: Zwin and IJzermonding as euhaline plots and Saeftinghe as mesohaline plots. Seed density and similarity were introduced as dependent variables and depth and salinity (euhaline and mesohaline) as fixed factors. Interactions between fixed factors were also entered in the model.

Additionally, an analysis was performed to compare the seed density and similarity among three salt marshes. In this analysis, the data collected in Zwin, Saefinghe and the old salt marsh in IJzermonding were used separately. Again seed density and similarity were introduced as dependent variables and depth and different salt marshes as fixed factors. Interaction between fixed factors was also entered into the model. In all analyses, the impact of depth is assumed to be put into evidence by a significant interaction between depth and salt marsh factors (old and new; euhaline and mesohaline).

Results

Seed bank properties and succession stage

Densities of viable seeds in old and new salt marshes at the IJzermonding were significantly different, respectively, 3656 and 6604 seeds/m^2 (df=1, F=2.84 and $p < 0.05$). In both old and new salt marshes, the seed density was highest in the upper layer. The interaction between depth and age was not significant (df=2, F=2.11 and p=0.13) (Fig. 1).

Similarity between seed bank and standing vegetation in the new salt marsh was higher than in the old salt marsh (df=1, f=13.74 and $p < 0.01$). Highest similarity was observed in the upper 0-5cm soil layer, although this was not significant as indicated by a non significant interaction between depth and age (df=2, F=1.47 and $p < 0.05$; df=2, F=2.01 and p=0.14, respectively).

Plant species in the above-ground vegetation and seed bank of old and new salt marsh at the IJzermonding are compared in Table 1 (only typical salt marsh species with Ellenberg salinity index higher than 3 and *Juncus bufonius* were shown). Species not found in the vegetation relevés of the plots and only sparsely present in the whole area are *Artemisia maritima, Atriplex littoralis, Chenopodium rubrum, Juncus bufonius, Juncus gerardii* and *Plantago maritima*. The dominant species of the above-ground vegetation of the old salt marsh are the perennial species *Elymus athericus, Spartina townsendi* and *Limonium vulgare*. They are absent or nearly absent in the seed banks of new and old salt marsh. Dominant in the vegetation of the new salt marsh are the annuals *Salicornia* spp., *Suaeda maritima* and *Spergularia* spp. All are well represented in all local seed banks.

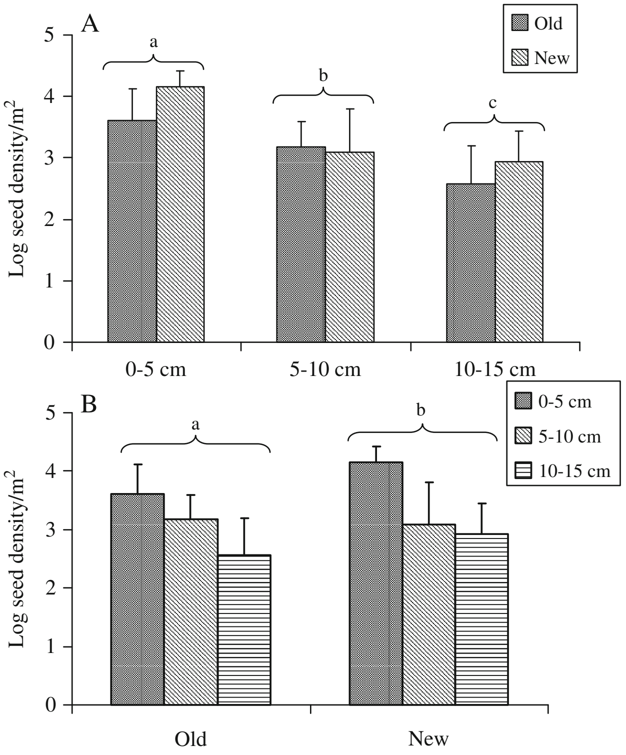

Fig. 1. The variation of seed density according to depth (A) and succession stage (B) at IJzermonding. a, b and c indicate significant differences.

Seed bank properties and salinity

Seed density was significantly different in two euhaline and mesohaline salt marshes (df=1, F=32.19 and $p < 0.001$) with highest in mesohaline. Although the effect of depth was significant (df=2, F=32.76 and $p < 0.001$), there was no significant interaction between depth and salinity (df=2, F=0.54 and p=0.58) (Fig. 2).

Species composition of seed bank and standing vegetation was significantly different in two euhaline and mesohaline salt marshes (df=1, F=4.94 and $p < 0.05$) with highest difference in euhaline area. Lowest similarity was observed between seed bank composition in the deepest layer and floristic composition of the standing vegetation while the interaction of depth and salinity had no significant effect on similarity (df=2, F=4.26 and $p < 0.05$; df=2, F=0.049 and p=0.95 respectively).

Seed bank properties in three old salt marshes

Seed density was significantly different in the three old salt marshes (df=2, F=23.92 and $p < 0.05$). The effect of depth was also significant (df=2, F=23.92 and $p < 0.01$) while the

Table 1
Relative abundance (%) of every salt marsh species in relation to the total number of seeds of all species in the seed bank and in the referred layer versus mean cover percentage of every species in the above-ground vegetation in new and old salt marshes in IJzermonding. S_{Ell} is the Ellenberg salinity index. Only species which are expected to appear in salt marshes (i.e. Ellenberg index > 3, Ellenberg et al., 1991) and *Juncus bufonius* are shown.

Species		Seed bank New				Old				Above-ground vegetation	
	S_{Ell}	0–5 cm	5–10 cm	10–15 cm	Total	0–5 cm	5–10 cm	10–15 cm	Total	New	Old
Aster tripolium	8	0.3	0.0	0.0	0.1	1.6	0.9	0.0	0.8	0.0	0.3
Atriplex littoralis	7	2.2	0.8	0.0	1.0	3.7	3.3	6.3	4.4	0.0	0.0
Elymus athericus	6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.6	41.8
Glaux maritima	7	0.0	0.5	0.0	0.2	1.5	0.1	0.0	0.5	0.0	0.1
Halimione portulacoides	8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2
Juncus bufonius agg.	0	0.4	0.5	1.3	0.7	2.4	5.2	8.3	5.4	0.0	0.0
Juncus gerardii	7	0.0	3.1	1.4	1.5	0.0	1.4	0.6	0.7	0.0	0.0
Limonium vulgare	8	0.0	0.0	0.0	0.0	0.2	0.3	0.0	0.1	2.3	10.6
Parapholis strigosa	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.4	0.8
Puccinellia maritima	8	0.0	0.0	0.0	0.0	1.2	0.3	0.0	0.5	1.7	4.8
Sagina maritima	4	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.0	0.0
Salicornia spp.	9	43.3	20.6	29.6	31.2	26.6	23.2	11.8	20.4	23.6	4.8
Spartina townsendi	8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21.2
Spergularia spp.	8	16.7	5.4	8.1	10.1	18.4	25.4	20.6	21.6	11.3	3.6
Suaeda maritima	8	4.5	6.2	1.2	4.1	8.3	4.4	2.4	5	32.6	0.8
Triglochin maritimum	8	0.0	0.0	0.5	0.1	14	13.3	12.5	13.2	0.0	0.1

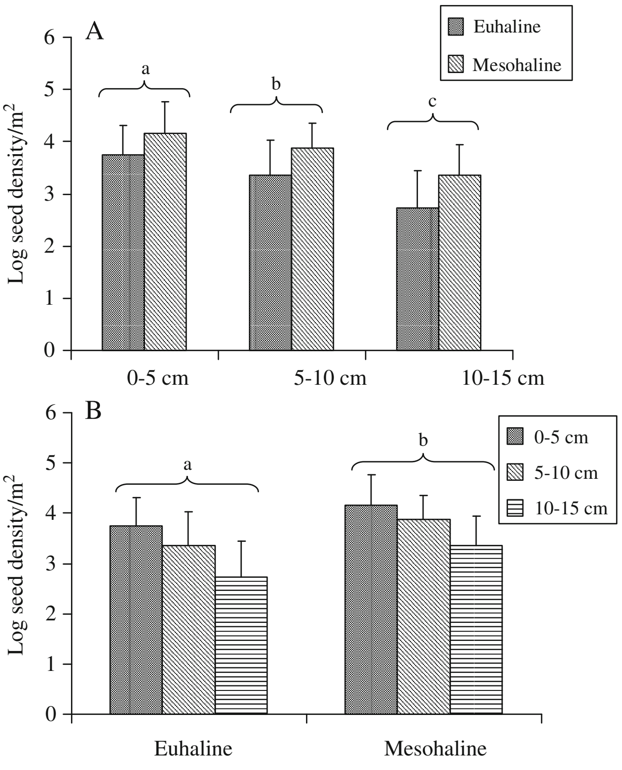

Fig. 2. The variation of seed density at different depths (A) in euhaline and mesohaline salt marshes (B). a, b and c indicate significant differences.

interaction between depth and different salt marshes was not significant (df=4, F=0.45 and p=0.79). Highest seed densities were found in Saeftinghe and the Zwin, with an average of 20,318 and 16,048 seeds per m^2, respectively, while the lowest seed density was found in IJzermonding with an average of only 3656 seeds per m^2.

As shown in Table 2, Saeftinghe and Zwin have as common difference with IJzermonding (Table 1) due to the massive presence of *Juncus* spp. in their seed banks. Also occurring with high numbers in the seed bank of Saeftinghe is *Scirpus maritimus*. The dominant perennials for Saeftinghe (*Elymus athericus, Puccinellia maritima* and *Spartina townsendi*) and for Zwin (*Elymus athericus, Halimione portulacoides* and *Limonium vulgare*) are absent or nearly absent in the respective seed banks. The annuals *Chenopodium rubrum, Glaux maritima, Salicornia* spp. and *Spergularia* spp. occur in high numbers in the seed banks, and are not present or relatively sparse in the above-ground vegetation.

Discussion

There was a pronounced difference between the seed density in the new and the old salt marsh of the IJzermonding nature reserve. Since seed bank density is the result of the balance between seed rain and seed disappearance (Fenner, 1985), the high seed density in the early successional stages can be attributed to a high seed input by pioneer species (e.g. *Salicornia* spp., *Suaeda maritima* and *Spergularia* spp.) and to a low seed loss by seed decay i.e. a high longevity of these species. Pioneer species are known to produce high amounts of seeds (Davy et al., 2001; Wolters and Bakker, 2002) that remain viable for a long period (Thompson et al., 1997). Similar patterns were found in grass and heathland communities, where there was a decrease in total seed density with increasing age (Bossuyt and Hermy, 2003). Remarkably, seed density was higher in the early successional stages in all three consecutive soil layers. If the seeds are persistent enough, they also become incorporated in the deeper soil layer (Grandin, 2001; Thompson et al., 1997).

Despite the dominance of *Suaeda maritima* in the vegetation of the recently created salt marsh, seeds of this species were not dominant in the soil. Since seed production per individual plant of *Suaeda* is higher than that of *Salicornia* plants (pers. observations of the first author) and most probably also of individual *Spergularia* plants (not counted though), we can indirectly conclude that *Suaeda* seeds are most probably less persistent than *Salicornia* and *Spergularia* seeds. Immediate germination is a probable cause for its low abundance in the soil (Tessier et al., 2000).

Three distinct relationships between vegetation and soil seed bank can be considered to exist along vegetation succession in relation to underlying ecological processes in the community assembly (Chang et al., 2005): 1) the seed bank composition

Table 2
Relative abundance (%) of every salt marsh species in relation to the total number of seeds of all species in the seed bank in the referred layer versus mean cover percentage of every species in the above-ground vegetation in old salt marshes (Saeftinghe and Zwin). S_{Ell} is the Ellenberg salinity index. Only species which are expected to appear in salt marshes (i.e. Ellenberg index > 3, Ellenberg et al., 1991) and *Juncus bufonius* are shown.

Species		Seed bank Saeftinghe				Zwin				Above-ground vegetation	
	S_{Ell}	0–5 cm	5–10 cm	10–15 cm	Total	0–5 cm	5–10 cm	10–15 cm	Total	Saeftinghe	Zwin
Aster tripolium	8	0.00	1.73	0.02	0.62	1.50	1.23	0.00	0.95	2.88	5.22
Atriplex littoralis	7	0.00	0.04	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.00
Chenopodium glaucum	3	0.02	0.40	0.00	0.15	0.08	0.00	1.20	0.35	0.00	0.00
Elymus athericus	6	0.09	0.00	0.00	0.03	0.00	0.00	0.00	0.00	12.03	10.22
Glaux maritima	7	0.78	2.56	2.17	1.84	4.41	2.87	7.85	4.60	2.59	0.94
Halimione portulacoides	8	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.03	0.00	34.11
Juncus bufonius agg.	0	35.14	23.59	26.21	28.31	38.83	53.58	48.84	48.99	0.00	0.00
Juncus gerardii	7	6.71	7.41	6.38	6.86	14.48	9.42	6.23	9.66	6.17	0.17
Limonium vulgare	8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.72
Parapholis strigosa	5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.38	0.00
Puccinellia maritima	8	0.05	0.12	0.08	0.08	0.17	0.00	0.00	0.04	8.98	4.22
Salicornia spp.	9	16.68	13.85	12.73	14.46	6.81	6.97	0.59	5.16	4.36	1.39
Scirpus maritimus	–	5.54	7.29	9.49	7.38	0.00	0.07	0.00	0.03	4.06	0.00
Spartina townsendi	8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.31	0.50
Spergularia spp.	8	17.21	25.22	26.88	23.02	17.43	0.98	3.57	5.35	1.20	1.50
Suaeda maritima	8	0.00	0.01	0.00	0.00	0.77	2.82	0.20	1.64	0.29	4.11
Triglochin maritimum	8	1.90	1.99	2.17	2.02	0.00	1.23	0.00	0.62	0.43	0.00

varies with the established vegetation along vegetation succession seres; 2) the seed bank composition remains rather constant and is composed mainly of early successional species that produce many seeds that persist along the succession sere, and 3) the seed bank composition remains constant but contains a matrix of species found in the different stages. Results of this study mainly coincide with the second relationship, in which colonizing species of the early successional stage i.e. *Salicornia* spp., *Suaeda maritima* and *Spergularia* spp. produced many persistent seeds. In late successional stages the seed bank mostly consisted of the same species as in the early succession stages, despite of perennial dominance (e.g. *Elymus athericus*) in above-ground vegetation. A study on the seed bank of the old salt marsh in IJzermonding in 2001–02 (Stichelmans, 2002 cit. in Hoffmann and Stichelmans, 2006) also showed that *Salicornia* spp. *Spergularia* spp. *Chenopodium rubrum*, *Atriplex prostrata* and *Suaeda maritima* were dominant in this seed bank. They still were dominant after five years. Although frequently found in this former seed bank analysis of the old marsh at the same study site (Stichelmans, 2002 cit. in Hoffmann and Stichelmans, 2006), we did not detect any seedlings of *Sagina apetala* and few of *S. maritima* during the last seed bank analysis. Our results are in accordance with studies of primary succession along an uplifted seashore (Grandin, 2001) and of secondary succession in species-rich meadows (Kalamees and Zobel, 1998) and old fields (Lavorel et al. (1993)), in which the seed bank is mostly dominated by early successional species. In other lowland environments, some authors demonstrated that the seed bank of early successional stages disappeared as species disappeared in the vegetation (Bossuyt and Hermy, 2004 for fresh water dune slack conditions).

While in early successional stages new colonizers become incorporated to a large extent in the seed bank leading to a relatively high similarity between seed bank and above-ground vegetation, in the late successional stage most dominant species have a very transient seed bank or almost no seed input (e.g. *Elymus athericus* and *Spartina towsendii*). Immediate germination (Tessier et al., 2000), absence of seed production due to pathogen infection (Chang et al., 2005), pollen limitation (Bertness and Shumway, 1992), or infection by fungi might explain the absence of seeds of a particular species in the seed bank. Furthermore, seeds of some species (e.g. *Elymus athericus*) are relatively large and heavy and remain attached to bracts after detachment from the spike. Due to their relatively large size, seeds of these species are unlikely to percolate downwards through the soil; they readily germinate in the soil or become concentrated in the driftline (Chang et al., 2005; Peart, 1984; Thompson et al., 1994).

As a consequence of the above discussed differences in seed production and longevity, our results also show that similarity between seed bank composition and standing vegetation decreases during succession.

Although salinity can promote seed dormancy (Tobe et al., 2000) and give seeds a higher chance to penetrate into the soil deeper and deeper (or be buried deeper through sediment accretion) with time, two salt marshes (euhaline and mesohaline) showed the same pattern in vertical seed distribution, with highest densities in the top soil. This pattern indicates the general rules of seed distribution in which regular seed input at the surface by seed rain increases the number of seeds in the top soil. As the seeds penetrate in deeper soil layers, they probably lose part of their viability. Espinar et al. (2005) showed that seeds of some salt marsh species suffer a rapid loss of viability when buried.

Both the similarity relations between standing vegetation and seed bank composition and seed density of the plots show a similar pattern: both decrease with increasing soil depth. The decreasing similarity with increasing depth could be related to decreasing seed density with depth. This result is in accordance with the previous studies in terrestrial habitats (e.g., Bossuyt and Hermy, 2004; Marcante et al., 2009). However, the similarity between seed bank and above-ground vegetation in the three salt marshes was different. The low similarity in the Zwin and IJzermonding (old) was mainly caused by the dominance of *Halimione portulacoides* and *Elymus athericus* in the vegetation, species that were never found in the seed bank.

Seed density in Saeftinghe and the Zwin was significantly higher than in the IJzermonding. *Juncus bufonius* had the highest seed density recovered in the greenhouse and the highest densities of emerging seeds were found in samples from Saeftinghe and the Zwin, indicating that the high seed density is probably due to the high abundance of *Juncus bufonius*.

Juncus bufonius was the most abundant species in the seed bank. This species has been reported as the dominant representative in the seed bank of many, environmentally quite diverse terrestrial ecosystems in and outside Europe (e.g. forest: Devlaeminck et al., 2005; coastal subarctic ecosystems: Staniforth et al., 1998; dry acidic dune grasslands: Bossuyt et al., 2007; as a non-indigenous species in temperate rain forest: Sem and Enright, 1996; in alkaline marsh vegetation: Vyvey, 1983); it is one of the most abundant seed bank species in Baltic seashore meadows (Erkkilä and Heli, 1998). In a Mediterranean salt marsh *Juncus bufonius* produced a large number of seeds that persist in the soil seed bank with a mean density of 5083 seeds/m^2 at a depth of 0–10 cm (Marañón, 1998). This species ranks 17th in frequency appearance in NW European studies on seed banks (Thompson et al., 1997). *Juncus bufonius* is a weedy, widely distributed and low salt-tolerant annual species (the Ellenberg index for salinity is 0; the Ellenberg index for salinity for the closely related, hard to distinguish *J. ambiguus* is 4; this suggests that on the salt marshes we might be dealing with the latter species in most cases; seedlings of both cannot be distinguished though). Probably, salinity prevents the appearance of this species in the vegetation (Marañón, 1998). After washing the soil by fresh water in the laboratory and watering by fresh water in the greenhouse, this species appears abundantly. This is apparently also the case for the other species only sparsely present in the standing vegetation but abundant in the seed bank (*Atriplex littoralis, Chenopodium rubrum* and *Juncus gerardii*). When seeds of species of low to moderate salt tolerance are dispersed into a region of high salinity, the salt concentration of the soil will prevent the germination of the seeds and hence their establishment in the vegetation (Shumway and Bertness, 1992). Therefore, seeds of these species can remain viable in the soil and seed density may increase in time.

The three investigated seed banks of old salt marshes do not fundamentally differ from each other. The mesohaline has the same vertical profile as both euhaline seed banks. In all three, the dominant salt marsh plant seeds are of annuals; seeds of perennials are largely lacking.

Conclusion

We have provided evidence that the seed bank of young as well as of old salt marshes is primarily composed of seeds from early successional colonizers. This could explain the very low similarity between seed bank and above-ground vegetation in that habitat, particularly in its late successional stage. This implies that restoration is possible from a long-term persistent seed bank only if the target species would be pioneer colonizers. Late successional species largely need to colonize from often only sparsely present seed sources in surrounding salt marshes or by vegetative propagules, such as rhizome parts. The characteristics of the seed bank of the mesohaline salt marsh were found not to be fundamentally different from that of the investigated euhaline salt marshes.

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