

## Article (refereed)

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Abstract: We evaluated the process of salt-marsh colonization in early successional stages and investigated how the sequence of species establishment was related to different success factors. Vegetation data were collected in the restoration site and in the adjacent salt marshes during three consecutive periods. Seed length, width and mass were used as dispersal traits, and Ellenberg moisture, salinity and nutrient indices as indicators of site suitability. Seed production in the reference site and seed bank in the restoration site were also investigated. The establishment of salt-marsh species in the restoration site was good and fast, the cover of new colonizers was unrelated to their cover in the restoration site at the first year. Seed availability appeared to be a more important factor in explaining the sequence of species establishment than salt and nutrient-limitation tolerance. Among dispersal and site traits, seed length and mass mainly indicated a relationship with new colonizers.

1 **Factors affecting the success of early salt-marsh colonizers: seed availability**  
2 **rather than site suitability and dispersal traits**

3  
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1 **Abstract**

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3 We evaluated the process of salt-marsh colonization in early successional stages and  
4 investigated how the sequence of species establishment was related to different success  
5 factors. Vegetation data were collected in the restoration site and in the adjacent salt marshes  
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13 length and mass mainly indicated a relationship with new colonizers.

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15 **Key words:** Site suitability; Seed dispersal traits; Seed availability; New colonizers

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## 1 **Introduction**

2       The successful restoration of plant communities depends on the availability of diaspores  
3 of the target species and favourable abiotic conditions for seedling establishment and growth  
4 (Bakker et al. 1996). Of all species included in local and regional floras, only some take an  
5 important part in early primary succession; such species must be capable of colonizing and  
6 reaching a large cover in the restoration site (Prach and Pysek 1999). Succession at a new site  
7 by colonization of plant species from higher spatial scales is controlled by local and regional  
8 variables (Caley and Schluter 1997; Hillebrand and Bleckner 2002; Kirmer et al. 2008). Both  
9 plant species richness and composition depend on the presence of suitable abiotic conditions  
10 (Grubb 1977; Urbanska 1997; Peach and Zedler 2006). Site conditions typical of a pioneer  
11 stand (e.g. nutrient deficiency in terrestrial habitats) were proven to be important factors for  
12 the colonization by initial adapted species (Rehounkova and Prach 2006; Kirmer et al. 2008).  
13 Physical factors, e.g. salinity, anoxia, pH or sedimentation, strongly affect the germination  
14 and recruitment of species in salt marshes, particularly at lower marsh elevations (Gray 1992;  
15 Huckle et al. 2000; Tessier et al. 2000).

16       Population dynamics of plant species at the beginning of primary succession are not  
17 only determined by local niche-based processes, but also by seed dispersal processes (Kirmer  
18 et al. 2008), which are assumed to be particularly important in late successional stages  
19 (Bossuyt and Honnay 2008). Seed availability (limitation) can be a major limiting factor in  
20 ecological restoration projects (Ozinga et al. 2004; Dausse et al. 2008). Target species can  
21 establish through dispersal from source plant communities. The degree of seed limitation is  
22 likely to depend on the abundance of adults in the local and adjacent species pool and specific  
23 dispersal traits of the plant species (Zobel 1997; Ozinga et al. 2005). It is expected that the  
24 plant species that exist in the local and regional areas would have the ability to colonize a  
25 newly available site (Wolters et al. 2005a). Distances to seed sources (Frenzen et al. 1988),

1 spatial distribution of seed sources (Wood and Del Moral 1987), neighbourhood influences  
2 (Ryser 1990) and the movement of seeds from productive areas into the new site (Shmida and  
3 Ellner 1984) are all likely important determinants of the outcome of colonization.

4 In salt-marsh restoration, the fastest development of vegetation is expected from the  
5 community species pool within a target area, either from established vegetation or the below-  
6 ground seed bank (Wolters et al. 2008). Colonization of plants from the species pool is a two-  
7 step process: seed availability and germination. Seed availability is the first step needed to  
8 establish a population from seed, but does not guarantee seed germination. Seed dispersal  
9 alone, only makes a species a member of the *potential* flora of the site, not its *actual* flora  
10 (Major and Pyott 1966). Species abundance in the local species pool was also found to be  
11 important for determining the order of colonization in salt marshes with late establishers  
12 being less abundant on the adjacent marshes than intermediate colonizers (Wolters et al.  
13 2008). Dispersal ability affects the probability of a plant species to colonize a new substrate  
14 (Wilson and Traveset 2000), initial colonizers having a high dispersal ability compared to  
15 species that would colonize later. The tidal current is the most important agent to disperse  
16 plant seeds in salt marshes. Although seeds of most salt-marsh species can immerse or float in  
17 seawater (Packham and Willis 1997), buoyancy of seeds and flotation period are different in  
18 various species, which affects the dispersal ability of salt-marsh species (Huiskes et al. 1995).  
19 Several factors affect the buoyancy of seeds, such as seed shape (defined as length / width:  
20 Grime et al. 1988) and seed mass; with increasing seed shape and seed mass, seed buoyancy  
21 is reduced (Poschlod et al. 2005). It is expected that initial colonizers in a salt marsh have  
22 seeds with a shorter length, wider width and lower seed mass than the species of later  
23 successional stages. In terrestrial habitats, species tend to present heavier seeds in late  
24 successional than in early successional ones (Fenner 1987; Leishman 1999), but few studies  
25 have examined such relationship in salt-marsh habitats. Lastly, seed germination is a complex

1 physiological process depending on many environmental conditions (Mayer and Poljakoff-  
2 Mayer 1982). It can be expected that species with high salinity tolerance germinate and  
3 establish earlier (Wolters et al. 2008). Of all species included in a regional and local flora,  
4 only some take an important part in early primary succession; such species must be capable of  
5 colonizing and reaching a large cover in a restoration site (Prach and Pysek 1999). There are  
6 few studies that have synchronically examined factors affecting mechanisms for distribution  
7 and colonization in a newly created salt marsh in Europe.

8         The present paper aims to determine the factors affecting both plant colonisation and  
9 distribution in a newly created salt marsh in the Yzer estuary, Belgium, by addressing the  
10 following questions: what seed and plant traits are important in the establishment of primary  
11 colonizers in a salt marsh restoration scheme, and is colonisation limited by seed availability  
12 or by abiotic conditions? We first tested the hypothesis that seed dispersal traits may limit  
13 plant colonisation by comparing the seed availability in the reference site and the seed bank in  
14 the restoration site. First year colonizers are hypothesized to show shorter seed length, wider  
15 seed width and lower seed mass than those colonizing in later years. We then tested the  
16 hypothesis that, beside seed availability, the success of restoration can be influenced by plant  
17 traits (as a surrogate of site suitability) by comparing the seed bank and the plant presence and  
18 cover in the restoration site. In particular highly salt and nutrient-limitation tolerant species  
19 are expected to be earlier colonizers than less salt tolerant and less nutrient-limitation tolerant  
20 species.

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## 1 **Material and Methods**

### 2 **Study area**

3       The study area is situated in the Yzer estuary, part of the IJzermonding nature reserve  
4 on the Belgian North Sea coast. A new salt marsh (ca 14ha) was created after the removal of  
5 buildings and slurry material during large nature restoration works in the period 1999-2002.  
6 (Hoffmann 2006). The objective of the restoration project was to restore beach-dune-salt-  
7 marsh ecotones from a quasi-virgin situation by the dispersal of target species from the local  
8 species pool (adjacent salt marshes and sand dunes) by natural colonization. In the newly  
9 created intertidal area (hereafter called the restoration site), gradual elevational gradients were  
10 created, ensuring inundation frequency conditions between 100% and 0% inundation. The  
11 area was exposed to tidal inundation from the beginning of 2002 onwards. This way, the  
12 unique opportunity was created to study the sequence of species establishment in relation to  
13 site suitability, seed availability, species pools and traits.

14       From a pilot study of the seed bank of some intertidal mud flats, newly created after  
15 removal of 3 to 4 meters of slurry material (Stichelmans 2002, cit. in Hoffmann and  
16 Stichelmans 2006) at the study site, we could conclude that no relevant salt- marsh species  
17 seed bank was available in the formerly buried, newly exposed mud flat soil. This indicates  
18 that the soil of the rest of the restoration site, that was buried for several decades, would also  
19 be free of salt-marsh species seeds. Colonization of the site therefore relied entirely on  
20 diaspores from external sources. In salt marshes, hydrochory has been reported as the  
21 preferential mode for seed dispersal, which is mostly of a local character, even though some  
22 seeds can disperse over long distances, up to 60 km per week (Koutstaal et al. 1987; Huiskes  
23 et al. 1995). The presence of a naturally established salt marsh in the adjacent Yzer estuary  
24 was considered here as the only local source of diaspores for the restoration site because the

1 most proximate salt-marsh areas are approx. 50 km southwest and 42 km northeast of the  
2 present study area.

3 The old adjacent natural salt marsh (hereafter called the reference site) consists of two  
4 parts (Fig. 1): a large one (O1) at the west and in free tidal current contact with the restoration  
5 site (N), and a smaller (O2) located in the south of the restoration site and separated from it by  
6 a dike (with a 7 m height), not allowing direct tidal current contact between both..

7

### 8 **Seed production in the reference site**

9 Seeds produced by salt-marsh species were collected from the reference site to estimate  
10 seed production. Three sites were randomly selected, one in the southern part (O2) and two in  
11 the west part (O1). At each site, 10 samples were randomly collected in plots of 50 \* 50 cm  
12 on four occasions between the beginning of September and the end of October, 2008. Seeds  
13 were collected before they were completely ripened and naturally dispersed. Each sample  
14 contained all flowering stems for perennials and all entire plants for annuals per quadrates 50  
15 \* 50 cm. The average total seed production was measured in each spike for grasses and each  
16 flower for flowering species. After the number of spikes and flowers was counted, we counted  
17 the number of seeds for one unit randomly chosen for each quadrate. Mean seed production  
18 by unit was estimated by using the average seed production across quadrates where the plant  
19 was present. Finally, the total seed production was calculated for the entire reference site by  
20 multiplying the number of seeds per unit, the number of units per quadrate and the total area  
21 of the site divided by the surface of the quadrate, taking into account the cover of every  
22 species in the different salt-marsh habitats.

23

### 24 **Seed bank in the restoration site**

1           The seed bank of the restoration site was sampled in 2006, four years after the site was  
2 first exposed to tidal inundation. With an auger with a diameter of 3 cm, 10 soil cores were  
3 randomly collected in close proximity of permanent plots and across the restoration site, to a  
4 depth of 15 cm, ensuring taking samples of all newly accreted marine sediments. The samples  
5 were collected in March 2006 after natural stratification during winter. The big parts of litter  
6 layer were removed in the field and samples transferred to the laboratory. The methodology  
7 of ter Heerdt et al. (1996) was used to concentrate the soil seed bank samples, which were  
8 washed through a coarse (2 mm mesh width) and a fine (0.18 mm mesh width) sieve,  
9 removing all roots and coarse vegetative parts on the first sieve, and withholding the vast  
10 majority of seeds on the second, while most of the soil material flushed away through the  
11 latter sieve. The concentrated samples were spread in a thin layer (maximum 0.4 cm thick) in  
12 40 cm \* 40 cm trays filled with sterilized potting soil. The trays were placed in a greenhouse  
13 in a random order with a natural light regime and were kept moist by regular rain water  
14 spraying. Air temperature varied between 14 °C and 25 °C throughout the experiment. 24  
15 control trays, filled with the same sterilized potting soil, were randomly placed among the  
16 seed bank trays in order to test for possible greenhouse and potting soil seed contamination.

17           Seedlings were identified as soon as possible after germination, counted and removed  
18 or, if they could not be identified immediately, transplanted to pots to allow further growth.  
19 After 6 months, when no further seedlings germinated, the trays were left to dry for two  
20 weeks. This allowed the sample to be crumbled to expose deeper buried seeds to the light.  
21 After watering the samples for another 3 weeks and controlling the light regime in 8 hr  
22 dark/16 hr light conditions, no new seedlings emerged. Finally, the residual soil was checked  
23 for remaining seeds by viewing small random samples taken from trays under a microscope  
24 and probing seeds with a needle in order to distinguish any remaining, potentially viable  
25 seeds. Since, the number of seeds that remained in the investigated soil samples was very low

1 (none in most cases, and always less than 3 per tray), we did not need to correct for remaining  
2 seeds. Mean number of seeds per m<sup>2</sup> was finally calculated from the 10 cores for each species  
3 recorded in the seed bank samples taken from the restoration site.

4

#### 5 **Vegetation cover within the restoration and reference sites**

6 Vegetation data were collected in the restoration site and adjacent reference salt marshes in  
7 permanent plots. Cover of all vascular plant species was visually estimated, using a decimal  
8 scale (Londo 1976). According to the size of the surface of the restoration site and adjacent  
9 salt marshes, 176 and 86 permanent 4 m<sup>2</sup> (2 \* 2 m) plots were collected. Vegetation was  
10 sampled in 2003, 2005 and 2007 along six randomly chosen transects, which were established  
11 perpendicular to the main elevation gradient (inundation frequency). Plots were distributed  
12 evenly across transects at 3 m intervals to account for vegetation heterogeneity across the  
13 study sites. Nomenclature followed Lambinon et al. (1998).

14

#### 15 **Plant traits and site suitability**

16 The selection of plant traits was based on previous studies by Wolters et al. (2008) and  
17 prior expectations about possible effect on the abundance of new colonizers. We selected six  
18 traits related to environmental factors and seed morphology: the Ellenberg indices for  
19 nutrients, salinity and moisture (Ellenberg et al. 1991) and three seed traits: seed length, seed  
20 width and seed mass. Seed length and width are correlated to seed shape, which is related to  
21 seed buoyancy (Poschlod et al. 2005). Ellenberg indices were used to estimate the species  
22 tolerance to environmental factors and seed traits were used to estimate the seed dispersal  
23 ability. Dispersal traits were abstracted from the Bioflor database  
24 (<http://www.ufz.de/bioflor/index.jsp>), and the Leda trait database (Knevel et al. 2003,  
25 <http://www.leda-traitbase.org/LEDA>) for salt-marsh species.

1

## 2 **Statistical analyses**

3       The average cover of each species in the restoration site and adjacent reference salt  
4 marsh were correlated by Pearson correlation index for each year separately. For analyzing  
5 changes in species cover along time, average covers of dominant species (i.e. having a cover  
6 of at least 5% during our study) were compared among years by T-tests for dependant  
7 samples for each site separately (after Bonferonni correction for multiple comparisons). Plant  
8 trait analysis was performed in order to detect the differences in trait promotion or inhibition  
9 during succession from 2003 until 2007. For each plant trait (three Ellenberg's indicators and  
10 three seed traits) weighted averages were calculated at the plot level in all three years  
11 separately, i.e. 2003, 2005 and 2007. All trait data were continuous. The species traits were  
12 compared between three years (2003, 2005 and 2007) using repeated measurements General  
13 Linear Modelling (GLM) and a pairwise LSD test. Calculations were down with SPSS 15.0.  
14 All data met normal distribution criteria according to Kolmogorov-Smirnov tests (after  
15  $\log(x+1)$  transformation for plant covers).

16

## 17 **Results**

### 18 **Seed production at the reference site**

19       Seed production as observed for different salt-marsh species is given in Table 1. In  
20 some species, no flowering stems were observed in any of the four sampling sessions. Some  
21 perennial graminoid species were contaminated by fungi. For *Aster tripolium*, each flowering  
22 branch contained on average  $85 \pm 14$  flowers. Each flower contained  $17 \pm 7.6$  seeds. For *Elymus*  
23 *athericus*, most florets were empty, but by taking into account the percentage cover of this  
24 species, total seed production is still being estimated to be no less than  $6.7 \cdot 10^5$  seeds for the

1 reference site. For *Puccinellia maritima*, flowering stems were never observed. For *Spartina*  
2 *townsendii*, most spikes were contaminated with *Claviceps purpurea* and/or empty.

3

#### 4 **Seed bank at the restoration site**

5 The number of species within the seed bank of the restoration site was limited (Table 2).  
6 The density of seeds in the seed bank in the restoration site was entirely dominated by annual  
7 species. Characteristic perennial salt-marsh species, present in the above-ground vegetation of  
8 the reference site, were not recorded within the restoration site seed bank (*Elymus athericus*,  
9 *Limonium vulgare*, *Plantago maritima*, *Puccinellia maritima*, *Salsola kali*, *Artemisia*  
10 *maritima* and *Spartina townsendii*). *Aster tripolium* and *Triglochin maritimum* were only  
11 recorded from one core with one germinating seed each. Although the pioneer species *Beta*  
12 *vulgaris* ssp. *maritima* was present in the above-ground vegetation of the reference site, it was  
13 not found in any of both seed banks, nor in the above-ground vegetation of the restoration  
14 site.

15

#### 16 **Vegetation cover within the restoration site and adjacent local salt marsh**

17 In 2003, one year after being exposed to tidal flooding, 79% of the species present in  
18 the adjacent old salt marshes germinated within the restoration site (Table 3). Species from  
19 the adjacent species pool that established during the first year were predominantly annuals.  
20 The restoration site was dominated by the annual species *Suaeda maritima*, *Atriplex* spp.,  
21 *Salsola kali* and *Salicornia europaea*. The adjacent salt marshes were dominated by the  
22 perennial species *Elymus athericus*, *Puccinellia maritima* and *Limonium vulgare*. There was  
23 no significant correlation between species cover within the restoration and the reference sites  
24 in the first year of colonization.

1 In 2005, after three years of tidal inundation, 81% species growing in the adjacent salt  
2 marshes were recorded in the restoration site. *Plantago coronopus* and *Parapholis strigosa*,  
3 absent in 2003, were recorded in 2005 within the restoration site for the first time. There was  
4 a significant correlation between species abundance within the restoration and the reference  
5 sites in 2005 ( $P < 0.01$ ,  $r = 0.50$ ).

6 In 2007, 84% species growing in the reference salt marsh were recorded in the  
7 vegetation of the restoration site. Species abundance in the new salt marsh was positively  
8 correlated to species abundance in the adjacent salt marsh ( $P < 0.01$ ,  $r = 0.44$ ). *Plantago*  
9 *maritima*, which was only present in the old salt marsh part O2 (Fig. 1), isolated from the  
10 restoration site by a dike was not found back in the investigated plots of the restoration site; it  
11 was however present with very few individuals outside the restoration site plots in 2005 and  
12 2007. *Triglochin maritimum* and *Artemisia maritima* (the latter outside sampled vegetation  
13 plots), both also restricted to the old salt-marsh part O2, remained entirely absent from the  
14 restoration site. The percentage cover of all the dominant species increased along time in the  
15 restoration whereas it remained constant in most cases in the reference site (Table 3).

16

### 17 **Plant traits**

18 Seeds of early colonizers had the shortest length and seed length increased in time  
19 (Table 4). There was no significant difference in seed width between early and later  
20 colonizing species. Seed mass was lowest in 2003 and 2005, and highest in 2007. The  
21 weighted average of Ellenberg indicator of salinity was higher in 2003 and 2005 than in 2007.  
22 There was a significant decreasing trend in Ellenberg nitrogen indicator value from 2003 to  
23 2007. The early colonizers had the highest Ellenberg nitrogen indicator value in the  
24 restoration site. No clear trend was detected for moisture indication number from 2003 to  
25 2007 (Table 4).

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## Discussion

*Limonium vulgare*, *Puccinellia maritima*, *Elymus athericus* and *Spartina townsendii* were the late colonizers of the restoration site. We conclude that viable seed availability might be the most important constraint for these species to act as early colonizers. Nonetheless, all species can disperse seeds via seawater well (Boorman 1967; Gray and Scott 1977; Adam 1990; Huiskes et al. 1995). Since the seeds of these species also did not appear in the seed bank of the restoration site neither, probably the production of viable seeds is a very probable constraint to the appearance of these species as important initial colonizers in our study area, particular those species coming from low salt-marsh zones, i.e. *Spartina townsendii*, *Limonium vulgare* and *Puccinellia maritima*. The seed production estimates confirm this statement for some species only. In this study we used both seed production per unit and dominance of plant species for estimating seed availability. Despite the fact that the number of seeds of a given species available for dispersal may vary within a given site, according the parental abundance of species (Bertness et al. 1987), we wanted to estimate the global seed production per plant species by taking into account the mean number of seed per unit and a proxy of the number of units within the entire reference site. This particularly allowed us to take into account the important cover of some species with low seed production. Indeed, *Elymus athericus* produced a relatively high seed number in the entire reference salt marshes, indicating necessity of study on seed viability for this species. Concerning inter-annual variations in seed production, we can compare our results from 2008 to those obtained within the same study site in 2006 by (Castermans 2007) for *Aster tripolium*. She found that each flowering stem contained on average 89.76 flowers and each flower contained on average 23 seeds, leading to a mean seed production with the same order of magnitude (2064 seeds per unit in 2006, standard errors are not available, vs.  $1445 \pm 650$  seeds per unit in 2008). We thus

1 argue that despite possible intra-site and inter-annual variations, our estimation of global seed  
2 production per species can be considered as a reliable general indicator of seed availability for  
3 new colonizers in the restoration site.

4 Despite the rapid colonization of most of the species recorded in the local species pool,  
5 the abundance of early colonizers in the restoration site was not related to their abundance in  
6 the adjacent salt marsh. *Elymus athericus* was dominant in the reference marshes, while, one  
7 year after creation, its cover and presence was extremely low in the restoration site.  
8 Adversely, *Suaeda maritima* was the dominant and most frequent species in the restoration  
9 site in 2003, while it appeared with very low cover values in the adjacent salt marshes. There  
10 was no correlation between the abundance of species in the restored and adjacent salt marsh in  
11 the first year of colonization, indicating that the relative cover of initial colonizers is  
12 determined by seed production rather than by standing cover in the reference sites. This again  
13 confirms the first hypothesis, indicating some species despite high abundance in the  
14 surrounding area can not be first colonizers since they can not produce sufficient viable seeds.

15 The early colonizers of the restoration site in 2003 had the shortest seed length and  
16 lowest seed mass (second hypothesis). As the ratio of length over width (seed shape) and seed  
17 mass has been proven to be negatively correlated with seed buoyancy (Poschlod et al. 2005),  
18 it can be concluded that initial colonizers had a higher buoyancy and therefore greater  
19 dispersal ability than late colonizers. In addition, it has been demonstrated that seeds of  
20 pioneer species can disperse by other mechanisms, i.e. not only as seed, but also as seedling  
21 and adult plant (Dalby 1963; Morisawa 1999; Davy et al. 2001), increasing the chance of a  
22 higher number of seeds to disperse.

23 *Salicornia*, *Salsola* and *Suaeda* were the dominant genera in the early stages of  
24 vegetation colonization within the restoration site. In our study, these genera only comprised  
25 annual species that produce large seed numbers (Wolters and Bakker 2002; Morisawa 1999;

1 Davy et al. 2001). The large seed production (production of up to one million seeds per plant  
2 in *Salsola kali*: Duke, 1983 cited by Wolters et al. 2008 and 300-30000 per m<sup>2</sup> in *Salicornia*  
3 and *Suaeda*: Wolters et al. 2008 and the results of this study), high viability (Davy et al.  
4 2001), high floatability of seeds (shortest seed length and lowest seed mass) and seedling and  
5 entire plant, may explain their rapid colonization within the first year after creating the new  
6 salt marsh.

7 Salinity was not shown to be the most important factor inhibiting the germination and  
8 establishment of species (part of the second hypothesis), since the Ellenberg index for salinity  
9 was between six and eight. If their seeds were transported to the restoration site and did not  
10 germinate, the seeds should have appeared in the seed bank. The data of the seed bank  
11 showed that some species had little or no seed bank available in the restoration site.  
12 Therefore, seed availability might be the most important factor to explain the absence of these  
13 species as initial colonizers. Nevertheless, species that colonized in 2003 and 2005, showed  
14 higher mean salt tolerance than species that colonized in 2007, indicating also higher salt  
15 tolerance for initial colonizers. Wolters et al. (2008) stated that salinity was the most  
16 important factor influencing the absence or presence of species as initial colonizers. In  
17 general, the late increase in abundance of these perennial species suggests that the increase of  
18 abundance is mainly occurring by clonal expansion.

19 Early colonizing species had the lowest nutrient Ellenberg indices. In this study, *Salsola*  
20 *kali*, with low nutrient-limitation tolerance, had a high abundance in the first year of  
21 colonization. However, previous studies showed that nutrient availability is rarely limiting in  
22 salt-marsh systems with the exception of those of barrier islands (van Wijnen and Bakker  
23 1999).

24 The presence of a salt marsh close to restoration sites appears to be a pre-requisite for  
25 rapid regeneration and colonization of new salt marsh (Wolters et al. 2008; Thom et al. 2002).

1 Indeed, creation of an intertidal area in a much more isolated restoration site in the nature  
2 reserve the Westhoek, remained devoid of salt-marsh species since its creation in 2004 (pers.  
3 obs., last author). Four years after creation, the restored Yzer marsh showed species  
4 composition similar to that of adjacent old salt marshes. The speed and rate of colonization in  
5 our study area was similar to that observed in the Sieperda tidal marsh in Scheldt estuary in  
6 the Netherlands (Eertman et al. 2002). Vegetation succession took place rapidly and within 5  
7 years, the newly created mudflat became colonized with most adjacently appearing salt-marsh  
8 species. The same pattern and progress was observed in an estuarine restoration site in the Elk  
9 River Estuary, USA (Thom et al. 2002), which was created by re-introducing a tidal  
10 inundation regime to a former embankment area. Here, the largest increase in number of  
11 species occurred 3 years after de-embankment and after 5 years species diversity was similar  
12 to an adjacent reference marsh. In our study, most species growing on the reference salt  
13 marsh were also recovered in the vegetation of the restoration site shortly after creation.

14 A review of salt-marsh restoration at different sites in north-west Europe showed that  
15 between 48% and 100% of the species present in the local species pool established in the  
16 restoration site within 1-13 years after de-embankment (Wolters et al. 2008). Compared with  
17 the regional species pool, only 26-64% of the species established in the restoration sites  
18 (Wolters et al. 2005b; Wolters 2006). Wolters et al. (2008) showed that 8 years after  
19 restoration, only 32% of the regional species pool had established in the Tollesbury  
20 restoration site and the establishment of regional salt-marsh species in new salt marsh may  
21 take several years to be reached and established. The distance between the restoration site and  
22 existing salt marshes and the number of inundations per year may be important determinants  
23 of the speed with which newly created intertidal areas are colonized. This is shown by at least  
24 three species present on the old salt-marsh part O2 (Fig. 1) of the Yzer which were not  
25 recorded in plots on the restoration site by 2007 (*Artemisia maritima*, *Plantago maritima* and

1 *Triglochin maritimum*). Since at least both last species produce sufficient seeds that can float  
2 in sea water from a few hours to several months and most seeds retain their viability in salt  
3 water and germinate when exposed to suitable conditions (Reading et al. 2008), their seeds  
4 apparently did not reach the restoration site in sufficient large numbers to allow successful  
5 colonization. The lack of colonization success of these three species is most probably caused  
6 by the low connectivity between O2 and the restoration site (cf. Fig. 1), both being separated  
7 by a narrow 7m TAW high dike (mean high water tide is approx. 4.45m TAW; mean spring  
8 tide high water reaches 4.86m TAW). We can conclude from these findings that hydrological  
9 connectivity between seed source and sink is vital for successful colonization of salt-marsh  
10 restoration sites. Even a distance of only 1 km between seed source and seed sink area, which  
11 is the approximate distance at the study site between the old salt marsh O2 and the restoration  
12 site along a strongly curved line, seems unbridgeable on the short term (six years).

13

#### 14 **Conclusions**

15 The present study showed that the development of salt-marsh target species could be  
16 restricted by limited viable seed production and unfavourable soil conditions. In its current  
17 state there is little hope that the vegetation of the restoration site will evolve towards a  
18 complete range of salt-marsh vegetation on the short run. It seems some species such as  
19 *Artemisia maritima*, *Plantago maritima* and *Triglochin maritimum* would benefit from  
20 (artificial) seed introduction in the restoration site. Some species such as *Spartina townsendii*  
21 may not be able to perform as a pioneer species in the restoration site even if safe sites and a  
22 proper elevation level (i.e. inundation frequency) would be available. Nevertheless, it would  
23 be able to expand substantially by rhizome dispersal, followed by vegetative expansion  
24 (Garbutt and Wolters 2008). The successful establishment and spread of this species has been  
25 well documented and was largely attributable to the species' rapid dispersal by rhizome  
26 pieces, perennial life-history and the colonization of mudflats formally unoccupied by salt-

1 marsh plants (Gray et al. 1990). This study confirms the importance of a salt marsh nearby to  
2 a restoration site and the importance of a continuous, short and straightforward water bridge  
3 between seed source and sink.

4

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14

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- 15

1 **Table 1.** Seed production in different salt-marsh species at the study site.

Species	Unit	Seeds/unit	Seeds/reference site/year
<i>Aster tripolium</i>	flowering stem	1445±650	18.2*10 <sup>8</sup>
<i>Atriplex littoralis</i>	individual	111±29	4.1*10 <sup>6</sup>
<i>Atriplex prostrata</i>	individual	365±78	1.3 * 10 <sup>7</sup>
<i>Elymus athericus</i>	spike	0.8±1.4	6.7 * 10 <sup>5</sup>
<i>Limonium vulgare</i>	flowering stem	322±284	6.0 * 10 <sup>8</sup>
<i>Puccinellia maritima</i>	plant	0	0
<i>Salicornia europaea</i>	individual	62±56	8.6 * 10 <sup>8</sup>
<i>Spartina townsendii</i>	spike	0	0
<i>Suaeda maritima</i>	individual	146±158	4.9 * 10 <sup>8</sup>
<i>Triglochin maritimum</i>	flowering stem	12±15	6.7 * 10 <sup>5</sup>

2

3 **Table 2.** Seed density (germinating seeds/m<sup>2</sup>) for salt-marsh species in the restoration site in 2006,  
 4 four years after the site was first exposed to tidal inundation, also to be considered as the first exposure  
 5 period to seed rain. The average of seed density was estimated in 0-15 cm depth.

Species	Seed density (mean ± s.e.)
<i>Aster tripolium</i>	3.13±3.13
<i>Atriplex littoralis</i>	48.47±28.85
<i>Atriplex prostrata</i>	69.36±34.95
<i>Chenopodium rubrum</i>	971.53±424.49
<i>Glaux maritima</i>	5.61±5.61
<i>Salicornia</i> sp.	3431.62±1580.22
<i>Spergularia</i> spp.	651.89±315.85
<i>Suaeda maritima</i>	201±63.25
<i>Triglochin maritimum</i>	2.46±2.46

6

1 **Table 3.** Average ( $\pm$  s.e.) species cover (%) in restoration and reference sites between 2003  
2 and 2007. a, b and c indicate significant differences between years and within each site for  
3 dominant species (bold in the table; according to t-test for dependant samples, after  
4 Bonferonni correction for multiple comparisons). Salt-marsh species not present in the plots  
5 but present at the site are given too. (\*): present in the reference site but not (yet) within the  
6 permanent plots; (\*\*) present in the restoration site but not (yet) in the permanent plots.

Species	Restoration site			Reference site		
	2003	2005	2007	2003	2005	2007
<i>Agrostis stolonifera</i>	2.02 $\pm$ 0.81	1.89 $\pm$ 0.47	2.26 $\pm$ 0.54	0.21 $\pm$ 0.10	0.36 $\pm$ 0.17	0.41 $\pm$ 0.2
<i>Artemisia maritima</i> (*)	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Aster tripolium</i> (**)	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	2.51 $\pm$ 0.84	2.38 $\pm$ 0.74	3.01 $\pm$ 1.14
<i>Atriplex littoralis</i>	0.91 $\pm$ 0.41	0.20 $\pm$ 0.07	0.05 $\pm$ 0.02	1.24 $\pm$ 1.07	0.09 $\pm$ 0.03	0.09 $\pm$ 0.03
<i>Atriplex prostrata</i>	1.29 $\pm$ 0.52	0.72 $\pm$ 0.25	0.13 $\pm$ 0.02	0.95 $\pm$ 0.70	0.22 $\pm$ 0.05	0.07 $\pm$ 0.03
<i>Beta vulgaris ssp. maritima</i>	0.04 $\pm$ 0.02	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01	0.07 $\pm$ 0.04	0.07 $\pm$ 0.04	0.05 $\pm$ 0.02
<i>Cakile maritima</i>	0.02 $\pm$ 0.01	0.01 $\pm$ 0.01	0.08 $\pm$ 0.06	0.02 $\pm$ 0.02	0.00 $\pm$ 0.00	0.01 $\pm$ 0.01
<b><i>Carex arenaria</i></b>	0.19 $\pm$ 0.04 <b>a</b>	3.36 $\pm$ 0.99 <b>b</b>	5.57 $\pm$ 1.15 <b>c</b>	0.09 $\pm$ 0.03 <b>a</b>	1.53 $\pm$ 0.91 <b>a</b>	2.00 $\pm$ 0.84 <b>a</b>
<i>Chenopodium album</i>	0.06 $\pm$ 0.02	0.07 $\pm$ 0.02	0.03 $\pm$ 0.01	0.00 $\pm$ 0.00	0.04 $\pm$ 0.02	0.00 $\pm$ 0.00
<i>Chenopodium glaucum</i>	0.00 $\pm$ 0.00	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.01 $\pm$ 0.01
<i>Chenopodium rubrum</i>	0.31 $\pm$ 0.05	0.15 $\pm$ 0.06	0.02 $\pm$ 0.01	0.12 $\pm$ 0.04	0.01 $\pm$ 0.01	0.00 $\pm$ 0.00
<i>Cirsium arvense</i>	0.36 $\pm$ 0.14	0.88 $\pm$ 0.25	0.57 $\pm$ 0.19	0.26 $\pm$ 0.11	0.24 $\pm$ 0.08	0.51 $\pm$ 0.35
<i>Diplotaxis tenuifolia</i>	0.21 $\pm$ 0.06	0.12 $\pm$ 0.03	0.00 $\pm$ 0.00	0.01 $\pm$ 0.01	0.05 $\pm$ 0.02	0.01 $\pm$ 0.01
<b><i>Elymus athericus</i></b>	0.36 $\pm$ 0.23 <b>a</b>	1.82 $\pm$ 0.72 <b>b</b>	3.36 $\pm$ 1.05 <b>c</b>	24.01 $\pm$ 3.77 <b>a</b>	25.74 $\pm$ 3.67 <b>ab</b>	33.72 $\pm$ 4.46 <b>b</b>
<i>Erigeron canadensis</i>	0.01 $\pm$ 0.01	0.40 $\pm$ 0.19	0.60 $\pm$ 0.19	0.01 $\pm$ 0.01	0.02 $\pm$ 0.02	0.16 $\pm$ 0.04
<i>Festuca rubra</i>	0.02 $\pm$ 0.01	0.22 $\pm$ 0.11	1.14 $\pm$ 0.35	0.43 $\pm$ 0.2	0.64 $\pm$ 0.30	1.72 $\pm$ 0.60
<i>Glaux maritima</i>	0.00 $\pm$ 0.00	0.03 $\pm$ 0.01	0.30 $\pm$ 0.10	0.19 $\pm$ 0.11	0.76 $\pm$ 0.60	0.28 $\pm$ 0.16
<i>Halimione portulacoides</i>	0.01 $\pm$ 0.01	0.00 $\pm$ 0.00	0.01 $\pm$ 0.01	0.07 $\pm$ 0.04	0.25 $\pm$ 0.13	0.34 $\pm$ 0.17
<i>Juncus gerardii</i> (**)	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	1.21 $\pm$ 1.06
<b><i>Limonium vulgare</i></b>	0.07 $\pm$ 0.04 <b>a</b>	0.13 $\pm$ 0.02 <b>b</b>	0.35 $\pm$ 0.04 <b>c</b>	5.74 $\pm$ 1.87 <b>a</b>	5.66 $\pm$ 1.71 <b>a</b>	5.14 $\pm$ 1.73 <b>a</b>

<i>Parapholis strigosa</i>	0.00±0.00a	0.20±0.11b	7.90±0.95c	0.31±0.17a	0.02±0.02a	0.55±0.28a
<i>Phragmetis australis</i>	0.01±0.01	0.02±0.01	1.02±0.51	0.02±0.02	0.06±0.02	0.14±0.06
<i>Plantago coronopus</i>	0.01±0.01	0.18±0.06	0.56±0.15	0.43±0.18	0.09±0.04	0.07±0.03
<i>Plantago maritima</i>	0.00±0.00	0.00±0.00	0.00±0.00	0.14±0.14	0.04±0.03	0.07±0.03
<i>Puccinellia maritima</i>	0.01±0.01a	0.45±0.11b	3.77±0.69c	1.78±0.54a	5.31±1.32b	6.29±1.37b
<i>Sagina apetala</i>	0.01±0.01	0.03±0.01	0.26±0.14	0.01±0.01	0.02±0.02	0.01±0.01
<i>Sagina maritima</i> (*)(**)	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
<i>Salicornia europaea</i>	1.93±0.23	11.35±1.33	8.69±1.18	3.57±1.18a	4.99±1.51a	3.33±1.21a
<i>Salicornia procumbens</i>	0.00±0.00	3.39±0.79	3.37±0.84	0.00±0.00	2.35±0.89	1.06±0.46
<i>Salsola kali</i>	1.66±0.29	0.51±0.14	0.15±0.03	1.13±0.32	0.39±0.24	0.12±0.03
<i>Scirpus maritimus</i>	0.00±0.00	0.00±0.00	0.00±0.00	0.05±0.05	0.01±0.01	0.12±0.12
<i>Sedum acre</i>	0.03±0.01	0.36±0.18	0.86±0.35	0.1±0.04	0.26±0.13	0.42±0.35
<i>Sonchus arvensis</i>	0.01±0.01	0.09±0.06	0.07±0.06	0.00±0.00	0.01±0.01	0.01±0.01
<i>Spartina townsendii</i>	0.02±0.01	0.18±0.13	0.15±0.08	3.70±1.40	4.99±1.7	4.47±1.63
<i>Spergularia marina</i>	0.00±0.00	0.93±0.25	2.22±0.35	0.00±0.00	0.09±0.03	0.34±0.12
<i>Spergularia media</i> ssp. <i>angustata</i>	0.03±0.01	0.11±0.04	0.53±0.11	1.00±0.25	0.53±0.09	0.20±0.04
<i>Suaeda maritima</i>	4.10±0.60a	12.47±1.16b	21.11±1.88c	3.31±0.82a	2.59±0.66a	2.00±0.43a
<i>Triglochin maritimum</i>	0.00±0.00	0.00±0.00	0.00±0.00	0.81±0.42	1.86±0.83	1.72±0.84

1

2

3 **Table 4.** Repeated measurements (GLM) for plant traits during succession from 2003 to 2007

4 in the restoration site. a, b and c indicate the significant differences of traits between years.

Plant traits	Average 2003	Average 2005	Average 2007	df	F	P-value
Nitrogen (indicator)	5.98±0.12a	5.23±0.11b	5.05±0.12c	2	25.73	<0.001
Moisture (indicator)	6.84±0.10a	6.91±0.12a	6.94±0.11a	2	0.42	0.341
Salinity (indicator)	6.29±0.22a	6.17±0.23a	6.08±0.22b	2	2.17	0.056
Seed length (mm)	1.59±0.03a	1.69±0.05b	2.02±0.03c	2	46.18	<0.001
Seed width (mm)	1.09±0.02a	1.06±0.02a	1.04±0.02a	2	2.13	0.122
Seed mass (mg)	0.55±0.03a	0.61±0.04a	0.74±0.04b	2	420.23	<0.001

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1 **Fig. 1.** Position of the restoration site (newly created salt marsh: N) and the reference site (old  
2 salt marshes: O1 and O2).

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