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The importance of seed bank knowledge for the restoration of coastal plant communities – a case study of salt marshes and dune slacks at the Belgian coast

Beatrijs Bossuyt[1], Els Stichelmans[1] and Maurice Hoffmann[1,2]

[1] Terrestrial Ecology Unit, Department of Biology, University of Ghent
Ledeganckstraat 35, B-9000 Ghent, Belgium
E-mail: Beatrijs.Bossuyt@UGent.be

[2] Research Group Landscape Ecology and Nature Management, Institute of Nature Conservation
Kliniekstraat 25, B-1070 Brussels, Belgium

Abstract

Knowledge on seed bank density and species composition is crucial for predicting the probability that target species will establish in the plant community on a restored site. A general overview of data available for plant species occurring in coastal plant communities showed that information on seed persistence is up to now very limited. The available data suggest that restoration of coastal plant communities cannot rely on the seed bank, except for annual species of salt marshes, and that the seed bank is to a large extent composed of species of nutrient rich habitats. This was confirmed by two case studies in dune slacks and salt marshes on the Belgian coast. Seed density in dune slacks was found to be relatively high, but the seed bank contained almost exclusively seeds of species of nutrient rich habitats, resulting in a very low similarity ratio between seed bank and vegetation. Germination from the seed bank would rather hamper the establishment of target species because competitive pressure imposed by fast growing species of nutrient rich habitats would increase. In salt marshes, the similarity between seed bank and vegetation was higher, because there is a higher contribution of typical salt marsh species in the seed bank, although not all target species are equally represented. To allow predictions of future species composition on restored sites, seed bank studies should be an essential part of each coastal restoration project.

Keywords: Ecological group; Seed longevity index; Seed persistence; Target species; Dune slack; Salt marsh.

Introduction

Coastal plant communities, such as salt marshes, dune slacks and dune grasslands, contain several species that are endangered in a West-European context (Bakker *et al*. 2002, Grootjans *et al*. 1999). To avoid extinctions of these populations, it will be necessary to conserve the remaining habitats, and to restore habitats and disappeared plant communities. On restored sites, target species can establish in the plant community through dispersal from source plant communities, or through germination from viable seeds in the soil seed bank (Bakker and Berendse, 1999). This soil seed bank can also contain seeds of non target species, which may rather hamper the establishment of target species by interspecific competition (Bossuyt *et al*., 2002). Knowledge of the seed bank composition of the site to be restored and the seed persistence characteristics of plant species of the target communities is hence essential to predict restoration success.

This knowledge is however very limited for coastal plant communities (Bekker *et al.*, 1999; Owen *et al.,* 2001; Wolters and Bakker, 2002). Some studies on temperate salt marshes concluded that the seed bank contained mainly annual species, and that the dominant perennial species in the vegetation were not present in the seed bank (Ungar and Woodell, 1993; Ungar and Woodell, 1996; Egan and Ungar, 2000; Wolters and Bakker, 2002). This results in a low similarity between seed bank and vegetation. Seed densities in temperate salt marshes ranged from 936 to 15,605 seeds.m^{-2}, with mainly seeds of *Juncus gerardii, Glaux maritima, Salicornia* sp. *Spergularia maritima* and *Suaeda maritima* (Ungar and Woodell 1993; 1996; Egan and Ungar, 2000; Wolters and Bakker, 2002). In contrast, studies on arctic salt marshes found a dominance in the seed bank of perennial graminoid species and a higher seed density, up to 83,953 seeds.m^{-2} (Jutila, 1998; Chang *et al*., 2001; Jutila, 2001).

In dune slacks and dune grasslands, the seed bank is mainly composed of non target species of nutrient rich habitats (Bekker *et al*., 1999; Owen *et al.,* 2001; Bossuyt and Hermy, 2004). Seed densities in dune slacks increased with increasing slack age, up to 14,646 seeds.m^{-2} (Bekker *et al.,* 1999; Bossuyt and Hermy, 2004), while seed densities in dune grassland were found to be very low (three seeds. m^{-2}) (Owen *et al.,* 2001). Also in early successional dune habitats where there is still frequent sand movement by wind erosion, the seed bank is as good as absent (eight seeds.m^{-2}) (Looney and Gibson, 1995).

From the results of these studies, it seems that relying on germination from the seed bank for restoration of coastal plant communities is at least to be questioned. A general overview and comparison of the possibilities in different coastal plant communities is however still lacking. Therefore, the objectives of this study are:

- providing a general overview of the data available on seed persistence characteristics of species of coastal plant communities;
- comparing seed bank and vegetation composition in two plant communities at the Belgian coast: dune slacks and salt marshes;
- discussing the potential of the seed bank for restoration possibilities of coastal plant communities.

Material and methods

General overview of seed bank knowledge

We derived a list of 274 diagnostic and differentiating species occurring in coastal plant communities based on Schaminée *et al.* (1996; 1998) and Stortelder *et al.* (1999). For each of the 274 species the number of records available in the database of Thompson *et al.* (1997) was calculated. For species with at least five records, we calculated the average seed longevity index (SLI) (Bekker *et al*., 1998). The seed longevity index varies between 0 and 1 and is a measure for the longevity of the seeds in the soil. Then, all species were assigned to one of the seven following ecological groups, based on Cosyns *et al.* (1994): species of beaches and dunes with sand movement, species of mud flats and tidal salt marshes, species of nutrient rich marshes and grasslands, species of medium nutrient rich grasslands, species of nutrient poor calcareous rich marshes and grasslands, species of nutrient poor marshes and grasslands with acid soils, species of forest edges and clearings and species of shrub and forest vegetations. For each ecological group, we calculated the average number of records available and the average SLI for species for which at least five records are available.

Case studies

The study area for the dune slack seed bank study consisted of two nature reserves [Ter Yde (260ha) and the Westhoek (340 ha)] near the western Belgian coastline. In each reserve, the management aims at the conservation and restoration of dune slack vegetation. Management measures include mechanical removal of *Hippophae rhamnoides* shrubs, mowing, grazing and in some cases small scale sod cutting or topsoil removal. Dune slack vegetation consists of a mixture of forb and graminoid species, in a matrix of small shrubs. For each slack in the region, information concerning date of origin was available.

We selected 20 slacks in different successional stages, ranging from 5 to 55 years. Vegetation data were collected during the summer of 2001 in a variable number of 1x1m plots in each slack. In each plot, the cover of all species was estimated with a decimal scale. A total of 228 plots was surveyed. Seed bank data were collected by a seedling germination method in October 2002. In each slack, again a variable number of randomly positioned 1x1m plots was sampled. In each plot, 10 samples were taken at random with an auger of 3.5cm diameter down to 10cm depth, after removal of the litter layer. A total of 134 plots was sampled for seed bank analysis. The soil samples were sown and brought into favourable conditions for germination, and the germinated seedlings were identified and counted. For four age classes of dune slacks (less than 10 years old, 10-20 years, 20-30 years and more than 30 years), we calculated the contribution of the seven ecological groups in the vegetation and the seed bank, by dividing the sum of the cover or the number of seeds of the species of each ecological group in each plot by the total cover or number of seeds found in that plot. We also calculated a similarity ratio (van Tongeren, 1995) between vegetation and seed bank for each age class, based on relative abundance values.

Salt marsh data were collected in the nature reserve the Yzermonding (128ha). A restoration project of estuarine habitats has been realized between 1999 and 2003, creating an intertidal area of ca. 28ha with potential estuarine mudflat and salt marsh. To estimate seed bank potentials, vegetation and seed bank data of the relict salt marsh area of 4ha were collected in 2001 in 30 plots, divided over six vegetation types (see Table II). In each plot, the cover of all species was estimated with a decimal scale. Seed bank data were also collected by a seedling germination method, analogous to the study in the dune slacks. In the salt marshes, 20 soil samples of the upper 7cm of the soil were taken in each plot with an auger of 5cm diameter. In a similar way as described above, we calculated the contribution of the seven ecological groups in the vegetation in the seed bank for the six vegetation types. Here also, the similarity ratio coefficient between seed bank and vegetation was calculated for each vegetation type.

Results

General overview of seed bank knowledge

From the 274 diagnostic and differentiating species described from coastal plant communities, species of nutrient rich marshes and grasslands are the best represented in the database of Thompson *et al.* (1977), with an average of 21 records for 61 species (Fig. 1). In contrast, very few information is available of species of beach habitat, salt marshes, medium nutrient rich grasslands and forest and shrub vegetation, with on average less than five records in the database. This means that the seed longevity index can not be calculated for the majority of the species growing in these habitats.

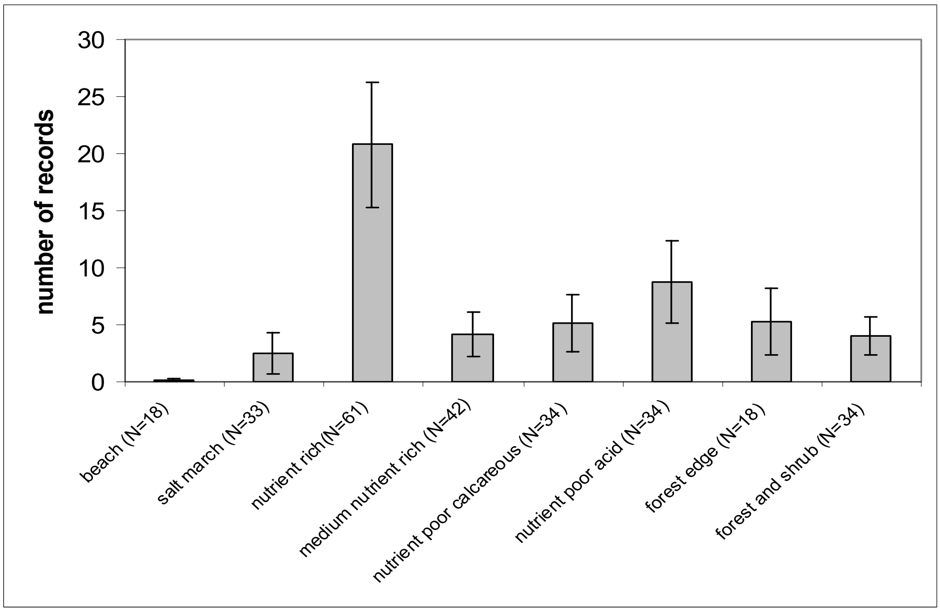

Fig. 1. Average number of seed bank records in the database of Thompson et al. *(1997) for species of seven ecological groups, considered diagnostic or differentiating for coastal plant communities. The 95% confidence interval is indicated.*

The average seed longevity index was highest for species of salt marshes, species of nutrient poor acid habitats and species of nutrient rich and medium nutrient rich grassland and marshes (Fig. 2). The seed longevity index was lower for species of nutrient poor, calcareous rich habitats and forest edges, although the differences were not significant, and very low for forest and shrub species.

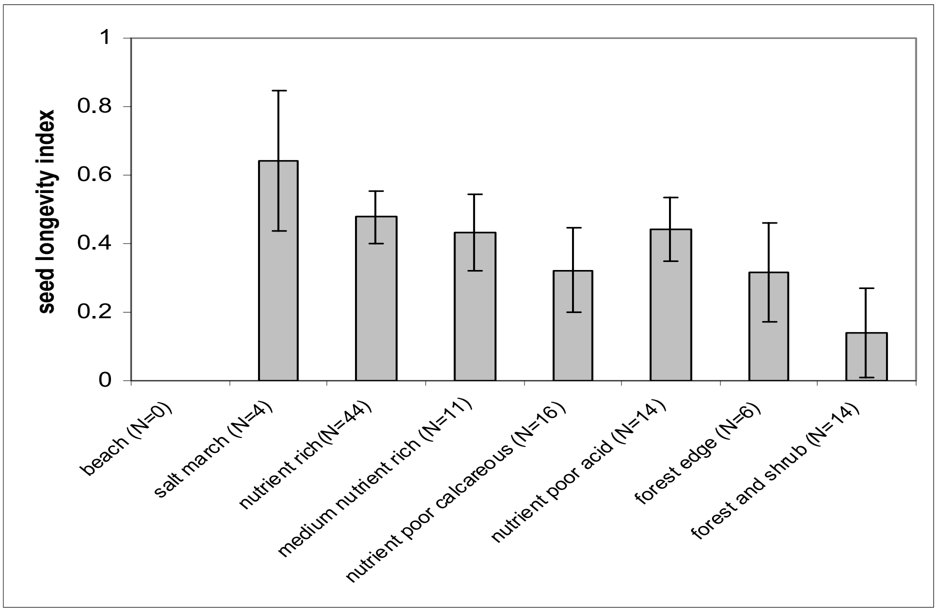

Fig. 2. Average seed longevity index for species of seven ecological groups considered diagnostic or differentiating for coastal plant communities. The 95% confidence interval is indicated.

Case studies

There were 132 species recorded in the vegetation of the dune slack plots and 56 species germinated from the dune slack seed bank samples, of which 52 occurred both in vegetation and seed bank. The total number of seedlings found corresponded with an overall seedling density of 2345 seeds.m^{-2}, ranging from 339 seeds.m^{-2} in the youngest slack to 9160 seeds.m^{-2}. The most abundant species in the seed bank were *Juncus articulatus* (578 seeds.m^{-2}), *Urtica dioica* (267 seeds.m^{-2}), *Eupatorium cannabinum* (205 seeds.m^{-2}), *Lythrum salicaria* (232 seeds.m^{-2}) and *Mentha aquatica* (173 seeds.m^{-2}).

Species of nutrient rich marshes and grasslands made up approximately 50% of the cover in the vegetation, while their seeds counted for 68 up to 98% of the total seed content of the seed bank, depending on the age class (Table I). Species of medium nutrient rich and nutrient poor calcareous grassland and marshes have also an important contribution in the vegetation, while they are badly represented in the seed bank, although their importance in the seed bank increases with slack age. The specific target dune slack species belong to these ecological groups. The similarity ratio coefficient between seed bank and vegetation was very low, and increased with increasing slack age, up to 0.08.

Table I. Relative abundance (%) of species of seven ecological groups in the vegetation and the seed bank of dune slacks of four age classes

	Vegetation				Seed bank			
Age class (years)	< 10	10-20	20-30	> 30	< 10	10-20	20-30	> 30
Number of slacks	N=4	N=3	N=8	N=5	N=4	N=3	N=8	N=5
Beach	0	1	1	0	0	0	0	0
Salt march	0	0	0	0	0	0	0	0
Nutrient rich	48	44	49	47	96	81	68	86
Medium nutrient rich	15	30	18	19	3	13	3	2
Nutrient poor calcareous	17	9	10	14	0	0	1	6
Nutrient poor acid	9	7	10	8	0	2	5	4
Forest edge	6	6	7	7	1	5	22	1
Forest and shrub	4	4	4	4	0	0	0	0
Similarity ratio	0.04	0.05	0.07	0.08				

Table II. Relative abundance (%) of species of seven ecological groups in the vegetation and the seed bank of six plant community types in salt marshes

Vegetation type	SSt (N=5)	TSb (N=11)	TSm (N=2)	PPu (N=4)	Aae (N=5)	AAl (N=3)
			Vegetation			
Beach	0	5	11	13	29	26
Salt marsh	100	92	81	79	44	21
Nutrient rich	0	3	8	7	19	46
Medium nutrient rich	0	0	0	1	3	3
Nutrient poor calcareous	0	0	0	1	4	4
Nutrient poor acid	0	0	0	0	0	0
Forest edge	0	0	0	0	0	0
Forest and shrub	0	0	0	0	0	0
			Seed bank			
Beach	0	0	0	1	6	2
Salt marsh	13	55	47	52	47	17
Nutrient rich	80	41	39	20	32	60
Medium nutrient rich	0	0	1	0	5	14
Nutrient poor calcareous	0	1	1	1	2	7
Nutrient poor acid	0	0	0	0	0	0
Forest edge	7	3	11	26	8	1
Forest and shrub	0	0	0	0	0	0
Similarity ratio	0.12	0.66	0.38	0.11	0.07	0.14

SSt = Spartinion - *Spartinetum townsendii*; TSb = Thero-Salicornion - *Salicornietum brachystachyae*; TSm = Thero-Salicornion - *Suaedetum maritimae*; PPu = *Puccinellion maritimae - Puccinellietum maritimae* ; AAe = *Armerion maritimae – Atriplici-Elytrigietum pungentis*;
AAl = *Atriplicion littoralis - Atriplicetum littoralis.*

In the vegetation of the salt marshes (Table II), 67 species were recorded, while overall seed density in the soils was 3014 seeds.m^{-2}, divided over 85 species. The most abundant species were *Salicornia* sp. (516 seeds.m^{-2}), *Spergularia* sp. (391 seeds.m^{-2}), *Chenopodium rubrum* (315 seeds.m^{-2}), *Sagina maritima* (295 seeds.m^{-2}) and *Spergularia marina* (204 seeds/m²). In four of the six vegetation types (SSt, TSb, TSm and PPu), species of salt marshes had a very important contribution in the vegetation. In three of these vegetation types, these species also contributed to a large extent to the seed bank, up to 55%. The rest of the seed bank was mainly composed of species of nutrient rich marshes and grasslands. In the AAe and AAl vegetation type, species of beaches and habitats with moving sands have a contribution of 30%, but seeds of these species were not abundantly present in the seed bank. In these vegetation types, species of nutrient rich marshes and grasslands become also more important, both in the vegetation and in the seed bank. In general, the similarity ratio coefficient between seed bank and vegetation was higher than for dune slacks, ranging between 0.07 up to 0.66 in the TSb vegetation type.

Discussion

An analysis of the seed bank records available in the databank of Thompson *et al.* (1997) showed that there are indeed few data available on seed persistence of plant species considered diagnostic or differentiating for coastal plant communities. In particular for species of beaches and habitats with moving sand, there are almost no data records, and a minimum of five records (necessary to calculate longevity index) was available for only four species of salt marshes (*Spergularia maritima, Salicornia europaea, Glaux maritima* and *Juncus gerardii*). In contrast, for the non specific common species of nutrient rich habitats, a seed longevity index could in most cases be calculated. A lack of general seed bank knowledge means that it is difficult to predict seed densities and species composition in the soil of a particular site to be restored.

The limited data that are available for salt marsh species indicated that most annual species of salt marshes have a persistent seed bank, since the average seed longevity index for these four species reaches a value of 0.62. Species of calcareous rich habitats, medium nutrient rich habitats, beaches and habitats with moving sand have a low seed longevity index, confirming the results of seed bank studies in grasslands (Davies and Waite, 1998; Willems and Bik, 1998; Bossuyt and Hermy, 2003). Some authors suggested that the transient character of seeds of dune grassland species may be the result of the stable, reliable and safe nature of dune grassland habitats with a high probability of successful germination and establishment, so that there is evolutionary no need for developing dispersal strategies in time (Owen *et al*., 2001). On the other hand, the substrate in dunes with a high level of sand movement is very dynamic and is not expected to favor seed dormancy (Looney and Gibson, 1995). Besides, it may be that the sandy soils are not a suitable medium for the development of prolonged dormancy, due to an excess of aeration (Owen *et al.,* 2001). This, however, contrasts with the observation that seeds of species growing on nutrient poor and acid soils that are in most cases sandy (*e.g*. heathlands), have a relatively high seed longevity index (Bossuyt and Hermy, 2003), which is also confirmed here. In general, species of forest and shrub vegetation have a very low seed longevity index (Bossuyt and Hermy, 2001). The highest seed longevity index is found for species of nutrient rich habitats. This means that the high seed density of these species in the soil of coastal habitats is likely to hamper or disturb the wanted restoration process. These species are often fast growing and competitive and may hence increase the competitive pressure on the target species. These general findings are confirmed by the results of the case studies. A relatively high seed density was found in dune slack habitats, and seed density increased in the course of succession. However, a very large percentage of the seeds concerned species of nutrient rich habitats, and the seed density of target species was very low. This is also indicated by the very low similarity ratio coefficient between seed bank and vegetation. Germination from the seed bank on restored sites, *e.g.* after cutting of shrub vegetation, will hence mainly result in the establishment of non target species, while target species will have to establish after dispersal from other source populations. Also in salt marshes, a high seed density was found and a relatively high proportion consisted of seeds of salt marsh specific species, which resulted in a higher similarity ratio coefficient between seed bank and vegetation. Not all target species are however equally represented, since it concerns mainly annual species and seeds of perennial salt marsh species, such as *Puccinellia* sp., are absent (Ungar and Woodell, 1993; Ungar and Woodell, 1996; Egan and Ungar, 2000). This means that the similarity ratio coefficient is especially high in vegetation types with a high contribution of annual species such as Thero-Salicornion communities. Species of beaches and habitats with moving sands were indeed not found in the soil seed bank, even if they had a high cover in the vegetation, which indicates that these species (e.g. *Salsola kali, Elymus athericus* and *Beta vulgaris* spp *maritima* but with the exception of *Atriplex littoralis*) do not produce persistent seeds. The contribution of seeds of species of nutrient rich habitats is also high in the salt marshes. This should however be less problematic than in dune slacks or grasslands, since germination and establishment of these species may be very difficult in this stress imposing environment (Wolters and Bakker, 2002).

It is clear that the amount of data available up to now on seed persistence of coastal plant communities is very limited. Moreover, the available data suggest that in most cases, restoration of coastal plant communities cannot rely on the soil seed bank (Bekker *et al.,* 1999; Owen *et al.,* 2001; Bakker *et al*., 2002; Wolters and Bakker, 2002). This means that there is still a need for a general insight into seed bank dynamics of coastal plant communities through general seed bank research. This also implies that a study of the seed bank density and species composition should be integrated in each particular restoration project. The results of seed bank studies will allow a better prediction of future plant community composition and of the probability that target species will establish through germination from the soil seed bank.

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