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Potential role of propagule banks in the development of aquatic vegetation in backwaters along navigation canals

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Abstract

The diversity and abundance of plant species in propagule banks of backwaters along two navigation canals in The Netherlands were studied in order to assess the relationship with the standing vegetation and the potential role of propagule banks in the establishment of (submerged) aquatic vegetation. At five sites, varying in vegetation composition and age, 180 samples were collected: 100 from surface sediment and 80 from the interface between original soil and sediment (=subsediment). In total, 113 species emerged of which *Juncus* spp. and *Lythrum salicaria* L. were the most abundant. Seven submerged species occurred at low densities. On average, there were 10.8–17.8 species l^{-1} in the surface sediment, and 8.5–10.2 l^{-1} in the subsediment. The mean number of propagules in samples ranged from fewer than 200 l^{-1} in 3-year-old to over 3000 l^{-1} in 10-year-old sites. There was little correspondence between propagule bank and standing vegetation. Vegetation establishment 2 months after sediment removal in six plots revealed 10 species; submerged species, however, hardly occurred. It is concluded that propagule banks cannot play a significant role in the (re-)establishment of diverse submerged aquatic vegetation along these canals. After creation of bare sites as a result of cutting and dredging in narrow zones along the water line, however, propagule banks may contribute to the development of species-rich emergent vegetation.

Keywords: Submerged macrophytes; Seed bank; Re-vegetation; Canal bank restoration

1. Introduction

In navigation canals in North West Europe, diverse aquatic vegetation is eliminated from the main water body by boat-induced disturbance (Haslam, 1987; Murphy et al., 1995).

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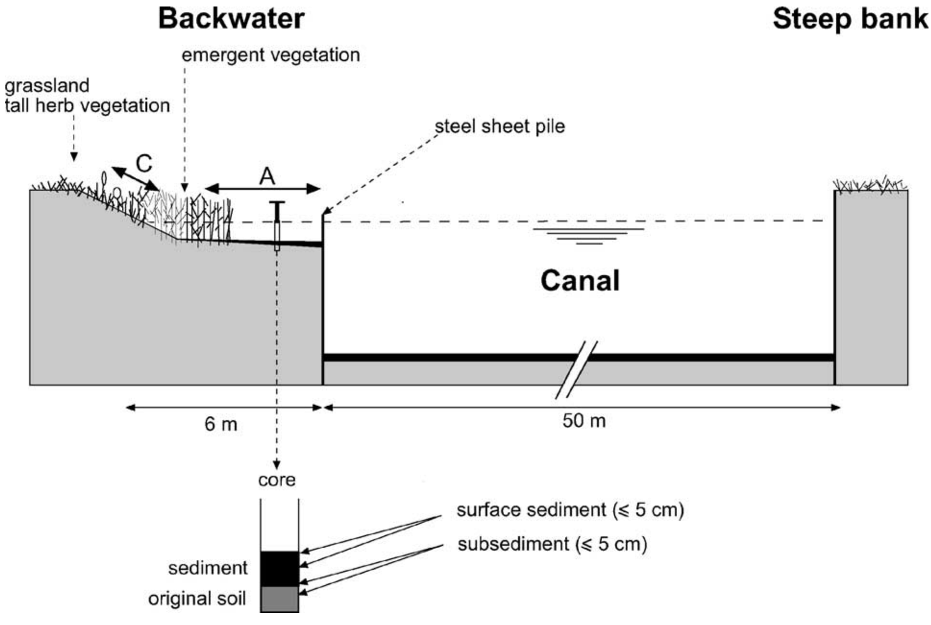

Fig. 1. Schematic cross-section of the canal with a backwater (left). Behind steel sheet piles a 0.5–1.0 m deep zone is constructed which forms a potential habitat for aquatic plants absent from a traditional steep bank (right). The positions of an aquatic plot A in which the aquatic vegetation and propagule bank were sampled, and a canal-side plot C in which the bank vegetation was recorded, are indicated.

Specially constructed shallow zones and other backwater areas, such as lock side ponds and branches, however, have potential for the development of macrophyte communities (Willby and Eaton, 1996; Boedeltje et al., 2001). Backwaters have been created along various canals in The Netherlands with the aim of ecologically enhancing intensively navigated waterways. These backwaters consist of shallow water zones, partly or fully separated from the deep canal by a dam or sheet piles and on the landward side graduating into a gently sloping, unprotected bank (Fig. 1; Boedeltje et al., 2001).

In backwaters connected to the main canal, the establishment of target communities consisting of rooting, submerged or floating-leaved macrophytes is to a large extent inhibited by boat-induced wave action, in particular around gaps in the dam or sheet piles (cf. Vermaat and De Bruyne, 1993). In less dynamic parts of backwaters however, rooting submerged macrophytes may become established. Nevertheless, their occurrence appears to be transient mainly because of high turbidity and sediment accumulation (Willby and Eaton, 1996; Boedeltje et al., 2001). Ultimately, a rapid succession towards dense, species-poor stands of *Phragmites australis* (Cav.) Steud., *Phalaris arundinacea* L. and *Glyceria maxima* (Hartm.) Holmb. predominates in this habitat.

In view of the important role of rooting macrophytes in the structure and functioning of freshwater ecosystems (Jeppesen et al., 1997), it is worthwhile considering the creation of habitat conditions in canal backwaters that will be favourable especially for this group of species. Therefore, measures to reduce turbidity and sedimentation rates, cutting of dense reed stands and removal of accumulated anoxic sediments are required (e.g. Holmes and Hanbury, 1995). Currently, sediment removal is being planned from 10 to 15 years old artificial backwaters along navigation canals in The Netherlands. The success of this restoration effort will depend both on the availability of propagules of aquatic species through dispersal into this habitat and from the propagule bank (Harper, 1977) and on the suitability of the habitat for the establishment of species. The present study focuses on the potential importance of the propagule bank.

Nicholson and Keddy (1983), Grillas et al. (1993) and Bekker et al. (1999) have shown that the number of species and the number of seeds declines with depth in marsh and lake sediments and dune slacks. Deeper sediment layers in backwaters might therefore not contain viable propagule banks. In that case, preserving parts of surface sediment layers could be an option to encourage re-vegetation after dredging, providing these layers actually contain the target species.

The present paper has two main objectives. The first is to examine the diversity and abundance of the propagule banks of surface sediment and subsediment layers in backwaters along the Twente Canals, The Netherlands and to compare the species composition of the propagule banks with the standing vegetation of water and adjacent canal sides. The second is to predict seedling recruitment from the subsediment propagule bank and to compare its potential flora with the actual aquatic vegetation 2 months after experimental sediment removal.

2. Methods

2.1. Study area

The study was conducted at five sites in backwaters along the Twente Canals (65 km long, 40–60 m wide, 3.5–5.0 m deep) in The Netherlands (Table 1). These backwaters consist of unprotected slopes, which gradually change from dry land into 0.6–1.0 m deep aquatic zones. Steel sheet piles, which rise 30–50 cm above water level, separate these zones from the main water body (Fig. 1). However, each zone is connected to the canal via gaps in the sheet piles. The backwaters are eutrophic (NO_3^-–N: 110–370 μmol l^{-1}; PO_4^{3-}: 0.9–1.3 μmol l^{-1}), turbid (Secchi-depth 40–50 cm) and have a high total alkalinity (3.3–4.0 meq. l^{-1}) (Boedeltje et al., 2001). The study sites along the canals represent all sections of shallow zones constructed in 1989, 1994 and 1996, respectively (Table 1).

2.2. Sampling vegetation and propagule bank

In July and August 1998, the aquatic vegetation was recorded. At each site, 10 plots (25 m^2) were randomly selected and clearly marked. The minimum distance of any plot from the water's edge was 1 m (Fig. 1). In June 1999, the canal-side vegetation was analysed in a 25 m × 1 m plot (Fig. 1), bordering on each aquatic plot. Each plot was subdivided into 10 subplots of 2.5 m^2, and within each of these, the percentage cover of every species was recorded. These data provided frequency values, ranging from 0 to 100 for each species within a site, and cover percentages of individual species and vegetation layers (free-floating, submerged, and emergent) for each plot.

Table 1
Characteristics of the backwaters at the study sites (1–5) and mean vegetation cover per site ($n = 10$)

No.	Location	Age (1999)	Total length (km)	Original basis	Mean total sediment thickness (cm)	Width (m)	Mean depth (m)	Mean cover (%) of vegetation		
								Free-floating	Submerged	Emergent
1	52°10′N6°22′W	3	3.0	Loam	2.0a	5.0	0.8	0.6a	17.5a	0.0a
2	52°11′N6°28′W	3	3.4	Sand	2.1a	8.0	0.5	1.0a	6.3a	0.0a
3	52°13′N6°33′W	5	3.2	Geotextile	5.0b	2.7	0.3	0.6a	4.1a	22.1b
4	52°19′N6°37′W	10	3.6	Sand	4.2ab	2.5	0.8	0.9a	22.1a	11.2ab
5	52°19′N6°37′W	10	3.6	Sand	10.7c	2.5	0.5	54.4b	20.1a	65.4c

Different letters in the same column indicate significant differences ($P < 0.05$) of the mean cover and mean sediment thickness between the sites (ANOVA, followed by a Tukey-test). Mean sediment thickness and depth: $n = 50$ and 30, respectively, for each site. N.B. Site 4 had been dredged 1 year before the investigation started.

In six out of ten plots (25 m^2) of site 5, the emergent vegetation was cut and the 7–15 cm thick sediment layers were removed by mechanical dredging in June 1999. To prevent edge effects, these procedures were extended for 50 m from both sides of each plot. In addition, the canal sides were mown. To study the potential recruitment of aquatic species from the subsediment propagule bank, the vegetation in these dredged plots was recorded again in August 1999.

Propagule bank samples were taken in February 1999 and stored dark at 4 °C until the start of the germination experiments in May 1999. From each aquatic plot, two replicated composite samples, comprising 5–15 cores (100 cm × 20 cm) each, were taken using a Vrij–Wit–Auger (Van Duin, 1992). The cores were divided into two layers: surface sediment and subsediment (Fig. 1). From the black coloured surface sediment, the upper layer ($\leqslant$ 5 cm) was taken; the collected subsediment consisted of the original, grey, sandy soil (0–3 cm) and 2 cm of overlying sediment. From each pooled and mixed layer of a replicate, 1 l was then extracted. At site 3 only, the subsediment could not be collected, because geotextile (Ivens, 1993) covered the original soil.

Sampling per volume unit instead of surface area was chosen, because of the wide variation in sediment thickness between and within the study sites. A total of 180 samples of 1 l were collected: 100 consisting of surface sediment and 80 of subsediment. Propagule density is expressed as the number of propagules per litre, or as the number of propagules per m^2 in a 1 mm thick layer for the subsediment. By using the mean sediment thickness (Table 1) it is possible to estimate the propagule density of the sediment layer at each study site.

The samples were treated according to the seedling emergence technique of Ter Heerdt et al. (1996). First they were sieved (mesh width 0.212 mm) to remove fine soil material and dead organic parts. Potentially viable vegetative parts (tubers, turions, fronds) however, were kept in the samples. Next they were spread out in a thin layer (<5 mm) on trays filled with a mixture of equal parts of sterilised sand and potting soil and set to germinate in a greenhouse under waterlogged conditions (water level 0–1 cm below soil surface) for 16 weeks (Boedeltje et al., 2002). Air temperature in the greenhouse was 25 °C or more between 06:00 and 21:00 h and 15 °C between 21:00 and 06:00 h. A photoperiod between 06:00 and 21:00 h was maintained throughout the germination period with 400 W overhead growth lights.

Seedlings were identified, counted and removed from the trays. All were identified to species with the exception of *Callitriche*, *Juncus*, *Salix* and *Typha* seedlings, which were identified only to genus because of their abundance and the difficulty of discriminating between species in the seedling stage. However, samples of these taxa were transplanted in potting soil to get an impression of species' occurrence. Nomenclature follows Van der Meijden (1996). Because of the huge number of *Juncus* seedlings (over 7000 individuals per tray), they were estimated by counting 1/4 of a tray and multiplying by 4, if necessary.

Checking 10% of the samples afterwards under a binocular microscope showed that only about 1% of *Juncus* spp. did not germinate. No viable propagules of other species were found. Species that produce spores or seeds <0.212 mm long, such as *Equisetum* species, were excluded from the total data set, although they were present in the vegetation.

2.3. Data analysis

Prior to statistical analyses, data were arcsine-square-root (percentages) or log transformed (other data) whenever necessary to improve normality (Sokal and Rohlf, 1994). The over-all quantitative comparison of the propagule bank to the standing vegetation was based on a Detrended Correspondence Analysis (DCA) applying CANOCO 4.0 (Ter Braak and Šmilauer, 1998). Sørensen's index of similarity (Sørensen, 1948) was used to compare qualitatively the composition of the propagule bank to the standing aquatic and canal-side vegetation at each site. Similarity calculations were performed with Vegron v. 7.0 (Fresco et al., 2002). Differences in mean similarity, species and propagule numbers between surface and subsediment were examined using a nested one-way analysis of variance. In the analyses, performed with the SPSS statistical package v. 11.0, the effect of soil layers (surface sediment and subsediment) was nested within sites.

3. Results

3.1. Vegetation survey

Within the aquatic vegetation, the records of sites 1 and 2 are clearly separated from those of the other sites in the DCA-ordination diagram (Fig. 2). Sites 1 and 2 are characterized by the occurrence of *Ceratophyllum demersum* L. and *Potamogeton pectinatus* L. and the low abundance of emergent species (Table 1; Appendix A). Site 2 differs from site 1 by the lower incidence of *Callitriche* spp., *C. demersum* and *Elodea nuttallii* (Planch.). Site 3 had a low cover of emergent (*P. australis*) vegetation (Table 1) with occasionally submerged *Callitriche* spp. (Appendix A). Site 4 which was dredged a year before the investigation started, had a sparse cover of emergent species with *Potamogeton pusillus* L. and *E. nuttallii* frequently occurring in the submerged vegetation (Appendix A). Site 5 had the highest cover of emergent and floating-leaved species (Table 1) with *P. australis*, *Lemna minor* L., *Spirodela polyrhiza* (L.) Schleid. and *Callitriche* spp. as the dominant species (Appendix A).

Within the canal-side vegetation, the records are poorly separated from each other in the DCA-ordination diagram (Fig. 2). In general, this vegetation is dominated by emergent aquatics (*Epilobium hirsutum* L., *P. australis*, *P. arundinacea*) and terrestrial species (e.g. *Calystegia sepium* (L.) R.Br., *Cirsium arvense* (L.) Scop., *Holcus mollis* L. and *Urtica dioica* L.; see Appendix A).

3.2. Diversity and abundance of the propagule banks

Overall, 113 species emerged from the propagule bank samples, featuring floating-leaved, submerged and emergent aquatic species, species of exposed mud and of various terrestrial habitats. Nine taxa accounted for 99% of the total number of 272,000 germinated propagules: *Juncus* spp. (88.04%), *Lythrum salicaria* (7.07%), *L. minor* (1.93%), *S. polyrhiza* (0.61%), *Urtica dioica* (0.52%), *P. australis* (0.21%), *Eupatorium cannabinum* L. (0.18%), *Typha* spp. (0.18%), *Epilobium hirsutum* (0.16%) and *Callitriche* spp. (0.15%). Apart from

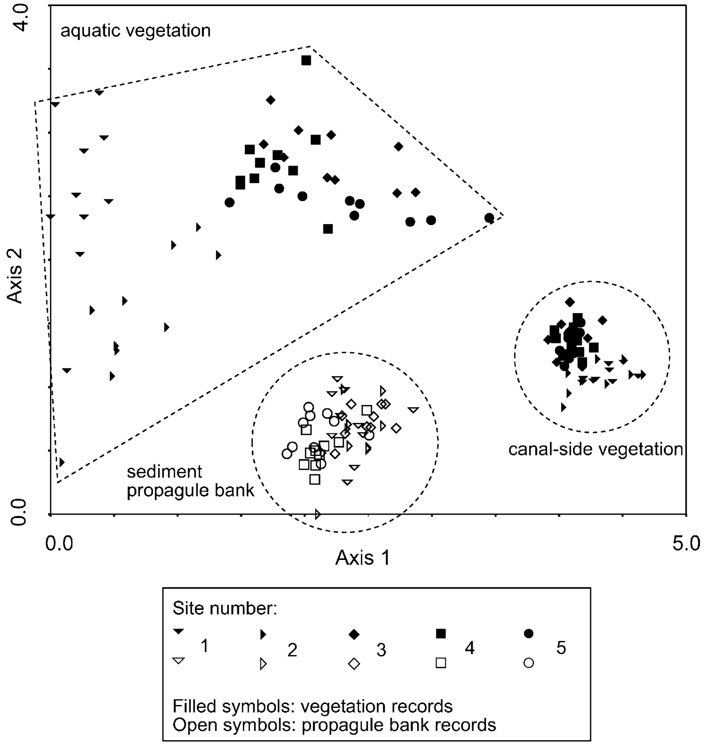

Fig. 2. DCA-ordination diagram for the first two axes showing the relative positions of the propagule bank records of the surface sediment layer together with the vegetation records, based on species frequencies, of the aquatic vegetation and the canal-side vegetation of the five study sites. Each symbol of the propagule bank records represents the two added replicates of one plot. Symbols of the vegetation represent the ten plots of each study site. The eigenvalues of the axes 1 and 2 are 0.63 and 0.22, respectively. The results of ordination the records from the subsediment propagule bank and the vegetation gave a similar diagram (results not shown).

Callitriche spp., total propagule numbers of the submerged (target) species present at the sites were low: *Callitriche* spp. (412), *Chara contraria* A. Braun ex Kütz (10), *Hottonia palustris* L. (3), *P. pectinatus* (27), *P. pusillus* (2), *Persicaria amphibia* (L.) Gray (3), *Ranunculus peltatus* Schrank (1). The average number of species found in the surface sediment (10.8–17.8 l^{-1}) was significantly higher than in the subsediment (8.5–10.2 l^{-1}) and no site-related effect could be detected (Table 2). Aquatic species found exclusively in the surface sediment were *Carex remota* L., *Myosotis scorpioides* L., *Veronica beccabunga* L. *Hottonia palustris*, *Potamogeton pusillus*, and *Ranunculus peltatus*.

In contrast, the mean number of propagules per litre sediment did not differ significantly between layers, but varied significantly between sites, ranging from 76 to 198 at sites 1 and 2 to 2323–3874 at sites 4 and 5 (Table 2, Appendix A). However, several species present in both soil layers occurred in significantly higher numbers in the surface sediment compared with the subsediment: these included *Callitriche* spp., *Lycopus europaeus* L., *Phalaris arundinacea*, and *P. australis* (Table 2, Appendix A).

Table 2
Summary of *F*-values from nested ANOVAS for mean number of species and propagules l^{-1}, for mean Sørensen's similarity between species composition of the surface sediment propagule bank (p.b.) and vegetation and for species that showed significant differences between sites or layers (surface sediment and subsediment)

	Site			Layer within site			Residual	
	SS	d.f.	P	SS	d.f.	P	SS	d.f.
Mean number of species l^{-1}	95.6	3	0.852	492	4	**0.000**	1515	152
Mean number of propagules l^{-1}	3.45×10^8	3	**0.007**	2.26×10^7	4	0.075	3.96×10^8	152
Mean similarity (p.b.–aq. veg.)	193	3	0.418	215	4	0.061	1635	72
Mean similarity (p.b.–can.-side veg.)	72.6	3	0.675	176	4	0.298	2535	72
Agrostis stolonifera	0.55	3	0.893	3.7	4	**0.035**	20.4	61
Alisma plantago-aquatica	91.1	2	**0.045**	13.1	3	0.588	413	61
Artemisia vulgaris	6.4	3	0.801	25.2	4	**0.035**	156	68
Callitriche spp.	966	3	0.274	684	4	**0.003**	4237	108
Eupatorium cannabinum	432	3	0.383	434	4	**0.001**	2547	124
Juncus spp.	2.78×10^8	3	**0.003**	1.17×10^7	4	0.294	3.56×10^9	152
Lemna minor	0.29×10^6	3	**0.032**	44454	4	0.651	2.16×10^6	120
Lycopus europaeus	66.1	3	0.308	52.5	4	**0.006**	443	128
Lythrum salicaria	2.25×10^6	3	0.300	1.74×10^6	4	**0.000**	1.02×10^7	128
Phalaris arundinacea	24.8	3	0.533	38.8	4	**0.012**	80.8	32
Phragmites australis	188	3	0.586	344	4	**0.000**	835	128
Ranunculus sceleratus	163	3	**0.042**	29.7	4	0.535	1320	140
Spirodela polyrhiza	37587	3	**0.015**	3715	4	0.554	87931	72
Urtica dioica	1025	3	0.545	1657	4	**0.000**	8525	152

Main effects are site and layer within site. Significant values are indicated in bold.

3.3. Relationship between propagule bank and vegetation

The DCA-ordination diagram (Fig. 2) shows that the vegetation and propagule bank are clearly separated along axes 1 and 2. It means that there was low correspondence between the species composition of the propagule bank and the vegetation. Mean Sørensen's similarity between the species composition of the surface propagule bank and the aquatic vegetation ($10.9\pm0.6\%$ S.E.) was significantly (ANOVA, $P < 0.05$) lower than between this propagule bank and the canal-side vegetation ($20.8\% \pm 0.9$ S.E.). Neither site nor layer effect could be detected on mean similarity between vegetation and propagule banks (Table 2).

No seedlings were found of *Elodea nuttallii*, *Ceratophyllum demersum*, *Aegopodium podagraria* L., *Anthriscus sylvestris* (L.) Hoffm., *Calystegia sepium*, *Galium aparine* L., *Elytrigia repens* (L.) Nevski and *Rubus* spp., despite their high abundances in the vegetation. Several species were more abundant in the vegetation than in the propagule bank (Appendix A). On the other hand, a few species, notably *Juncus* spp., *Lythrum salicaria* and *Typha* spp., were much more abundant in the propagule bank than in the vegetation. Several species, for instance *Chara contraria*, *Atriplex prostrata* DC., *Chenopodium rubrum* L., *Hydrocotyle vulgaris* L., *Isolepsis setacea* (L.) R.Br. and *Gnaphalium uliginosum* L., were present in the propagule bank and not in the vegetation.

3.4. Predicted and actual vegetation after sediment removal

Three months before removal of the surface sediment layer, the subsediment propagule bank in six plots of site 5 consisted of submerged, free-floating and emergent aquatics, mud-dwelling species and terrestrial plants (Table 3). Because of their germination requirements, it was predicted that only submerged, free-floating and some of the emergent species would be able to establish from the propagule bank under 60–100 cm water, the depth of the dredged area (Table 3). Moreover, establishment was predicted from vegetative parts of species that occurred abundantly in the standing aquatic vegetation before dredging, in particular *Callitriche* spp., *E. nuttalli*, *Phalaris arundinacea* and *P. australis* (Table 3).

Two months after dredging, 10 species had become established in the aquatic plots in low densities (Table 3). *E. nuttallii*, *P. arundinacea* and *P. australis* were vegetative remnants of the former vegetation. Except for *Potamogeton pusillus* and *Butomus umbellatus* L., all other species had been found in the subsediment propagule bank. Mud-dwelling and terrestrial species were lacking, as was expected.

4. Discussion

4.1. Diversity and abundance of the propagule bank

In the present study, 113 species emerged from the propagule bank samples. This number appears high compared with other aquatic soils that have been investigated, applying seedling-emergence methods. Ivens (1994) recorded 33 species in the upper 5 cm of emerged soils of backwaters along canals and rivers. In the seed banks of prairie glacial marshes 29–45 species were found (Van der Valk and Davis, 1978,1979), of freshwater riverine swamps 59 (Schneider and Sharitz, 1986), of lakeshores 41 (Keddy and Reznicek, 1982), of lake sediments 12 (De Winton et al., 2000), of floating fens 48 (Van der Valk and Verhoeven, 1988), freshwater tidal wetlands 55 (Leck and Simpson, 1987) and in cut-off channels along rivers 17 (Combroux et al., 2001). However, it should be noted that it is difficult to make absolute comparisons between our data and the results of other propagule bank studies because of differences in methodology (hydrological regime and handling of samples). Possible explanations for the species-richness of the propagule banks in our study are (1) the proximity of species-rich canal sides as a seed source, (2) species-rich drift material entering the backwaters from the main canals (Boedeltje, unpublished) and (3) the use of an improved seedling emergence method (Ter Heerdt et al., 1996).

Despite the overall species-richness, the numbers of individuals of submerged target species (e.g. *Potamogeton* spp.) in the propagule banks were extremely low. No sexual reproduction was observed (Boedeltje, unpublished data) in submerged species, such as *Ceratophyllum demersum*, *Myriophyllum spicatum*, and *Potamogeton pectinatus* which may account for the absence of seedlings of these species in the trays. Tubers mainly accounted

Table 3
Mean species frequency and cover percentage in the vegetation and species composition of the subsediment propagule bank of six 10-year-old aquatic plots of 25 m^{-2} before dredging, possible germination/establishment from this propagule bank or from remaining vegetation in shallow (1–20 cm) and deep (60–100 cm) water and predicted and observed aquatic vegetation composition 2 months after dredging the plots

Classification and species	Mean species frequency (*f*) and cover % (*c*%) per plot 1 year before dredging		Mean number of propagules in a 1 mm thick layer per plot in the subsediment propagule bank	Possibility of germination from the propagule bank (*p*) or establishment from remaining parts of the standing vegetation (*v*) according to references		Predicted presence in the plots, 2 months after dredging based on development from the propagule bank (*p*) or from vegetative parts (*v*)	Observed mean species frequency (*f*) and cover % (*c*%) per plot, 2 months after dredging	
	f	*c*%		In shallow water	In deep water		*f*	*c*%
Submerged aquatics								
Callitriche obtusangula	22	4	90	(+): $2^{v}3^{p}$	(+): 2^{v}	x (p+v)	43	4
E. nuttallii	25	1	0	(+): $2^{v}6^{v}$	(+): 6^{v}	x (v)	37	13
Potamogeton pusillus	0	0	0	(+): $1^{v}12^{p}$			13	<1
Free-floating aquatics				(+): 17				
Lemna minor	57	11	3452	(+): $14^{v}18^{v}$	(+): 14^{v}	x (v)	78	3
Lemna trisulca	18	4	46	(+): $14^{v}18^{v}$	(+): 14^{v}	x (v)	43	2
Spirodela polyrhiza	52	54	502	(+): $13^{v}14^{v}$	(+): 14^{v}	x (v)	35	<1
Emergent aquatics				(+): 17				
Alisma plantago-aquatica	2	<1	2	(+): $8^{p}11^{p}15^{p}$			2	<1
Carex acuta	15	2	8	(+): 15^{p}			0	0
Butomus umbellatus	0	0	0	(+): 11^{p}			2	<1
Epilobium hirsutum	5	<1	10				0	0
Eupatorium cannabinum	2	<1	46				0	0
Glyceria maxima	8	2	0	(+): 2^{v}		? (v)	0	0
Hydrocotyle vulgaris	0	0	2				0	0
Iris pseudacorus	2	<1	0	(−): 7^{p}			0	0
Lycopus europaeus	10	<1	25				0	0
Lysimachia vulgaris	2	<1	0				0	0
Lythrum salicaria	3	<1	3290	(+): 3^{p}			0	0
Mentha aquatica	8	<1	0	(+): 1^{v}			0	0
Phalaris arundinacea	72	15	0	(+): $2^{v}7^{p}15^{p}$		x (v)	2	<1
Phragmites australis	100	46	25	(+): 2^{v} (−): 7^{p}		x (v)	65	3

Poa palustris	0	0	2	(+): 15^{p}	0	0
Rorippa amphibia	3	<1	0	(+): 2^{v}	0	0
Schoenoplectus lacustris	2	<1	0	(+): 7^{p}	0	0
Typha latifolia	2	<1	67	(+): $7^{p}9^{p}16^{p}$	0	0
Scirpus sylvaticus	0	0	4		0	0
Mud-dwelling species				(−): $5^{p}7^{p}$		
Ranunculus sceleratus	0	0	23		0	0
Veronica catenata	0	0	2		0	0
Bidens frondosa	0	0	2		0	0
Agrostis stolonifera	0	0	2		0	0
Terrestrial species				(−): $5^{p}7^{p}$		
Calystegia sepium	43	3	0		0	0
Juncus spp.	0	0	76204	(+): $3^{p}1^{p}$	0	0
Alnus glutinosa	0	0	4		0	0
Chamerion angustifolium	0	0	2		0	0
Conyza canadensis	0	0	2	(−): 5^{p}	0	0
Epilobium tetragonum	0	0	8		0	0
Holcus lanatus	0	0	2	(−): 5^{p}	0	0
Plantago major	0	0	2		0	0
Polygonum aviculare	0	0	2	(−): 5^{p}	0	0
Rumex crispus	0	0	4	(−): 5^{p}	0	0
Rumex obtusifolius	0	0	2		0	0
Salix spp.	0	0	35		0	0
Solanum dulcamara	3	<1	0	(+): 10^{p}	0	0
Scrophularia nodosa	0	0	2		0	0
Tanacetum vulgare	0	0	23		0	0
Urtica dioica	0	0	148		0	0

Column for possibility of germination or establishment: blank: not documented; (+): possible; (−): not possible. Column for predicted presence: blank: absent; (×): present; (?): uncertain, because of low density or frequency. References: 1: Barrat-Segretain et al. (1999); 2: Boedeltje (unpublished); 3: Boedeltje et al. (2002); 4: Brock et al. (1989); 5: Casanova and Brock (2001); 6: Cook and Urmi-König (1985); 7: Coops and Van der Velde (1995); 8: Keddy and Ellis (1985); 9: Leck and Simpson (1987); 10: Morinaga (1926); 11: Muenscher (1936a); 12: Muenscher (1936b); 13: Perry (1968); 14: Preston and Croft (1997); 15: Skoglund and Hytteborn (1990); 16: Smith and Kadlec (1983); 17: Van der Valk (1981); 18: Van der Valk and Davis (1978).

for the appearance of *P. pectinatus*. However, the density of tubers of this species was low compared with that in other areas (Van Wijk, 1989).

Based on mean emergence from the samples, propagule density ranged from 3500 m^{-2} in 2 cm thick sediment of three-year-old plots (site 1), to 33,300 m^{-2} in 5 cm thick sediment of the five-year-old plots (site 3), to 320,900 m^{-2} in 10 cm thick sediment of undredged, 10-year-old plots (site 5). The numbers in the oldest zones are among the highest recorded in aquatic soils (Van der Valk and Verhoeven, 1988; Leck, 1989; Bonis et al., 1995). Similarly to other studies (Van der Valk and Davis, 1979; Bekker et al., 1999), species numbers decreased with depth. Although the total number of propagules did not significantly decline with depth, as was observed in other studies (Nicholson and Keddy, 1983; Leck and Simpson, 1987; Grillas et al., 1993), several species had significantly larger numbers of propagules in the surface sediment when compared to the subsediment.

4.2. Relationship between propagule bank and vegetation

The small overlap in vegetation and propagule bank agrees with the findings in previous studies in (tidal) wetlands (e.g. Smith and Kadlec, 1983; Leck and Simpson, 1987; Van der Valk and Verhoeven, 1988; Skoglund and Hytteborn, 1990; Wilson et al., 1993; Combroux et al., 2001). However, in some other wetland studies (Keddy and Reznicek, 1982; Leck and Simpson, 1987; Grillas et al., 1993) a close correspondence between propagule bank and vegetation was observed. The low similarity between the entire propagule bank and the established vegetation found in this study may be the result of a variety of factors, of which five are briefly discussed.

Firstly, for some species that were locally abundant in the aquatic vegetation and absent from the propagule bank, seed production was lacking or not observed: *Ceratophyllum demersum*, *Myriophyllum spicatum*, *Elodea nuttallii*, and *Potamogeton pectinatus*. This observation agrees with the results of Westcott et al. (1996) who found that *Ceratophyllum demersum* and *Potamogeton* spp. were rare as seeds, despite their common occurrence in the vegetation.

Secondly, some species, such as *Aegopodium podagraria*, *Filipendula ulmaria* (L.) Maxim. and *Vicia cracca* L., frequently found in the canal-side vegetation, do not form a persistent seed bank (Thompson et al., 1997).

A third factor might be connected with dispersal and buoyancy of seeds. The terrestrial vegetation along the bank was recorded in a strip 1 m wide. Therefore, the probability is relatively small that seeds of species occurring in the upper part of this area (e.g. *Arrhenatherum elatius* (L.) J. & C. Presl, *Rubus caesius* L., *Festuca rubra* L.) reach the water body and subsequently the propagule bank. Moreover, seeds of common canal-side species, such as *Aegopodium podagraria*, *Angelica sylvestris* and *Elytrigia repens*, immediately sink when released on water (Boedeltje, unpublished). In contrast, the seeds of other species (e.g. *Calystegia sepium* and *Iris pseudacorus* L.) can float for more than 4 months (Boedeltje, unpublished) and might be dispersed into the main body of the canal, eaten by waterfowl, or deposited with drift material into emergent bank vegetation instead of sinking to the sediment (cf. Skoglund and Hytteborn, 1990). Propagule dispersal from other areas into the canal and later into backwaters also might have influenced the composition of the propagule bank (Van der Valk and Davis, 1979).

Fourthly, only a small proportion of the propagule banks could be sampled and propagules of less common species were probably missed, in particular because strong horizontal micro-variations in propagule density in aquatic habitats may occur (Grillas et al., 1993; Bonis et al., 1995).

Fifthly, some species, although rare in the vegetation, produce numerous long-living seeds. For example, *Lythrum salicaria* was the second most abundant species in the propagule banks, but mature plants were absent at sites 1 and 2 and uncommon at the other ones. Thompson et al. (1987) estimated the mean number of seeds produced per plant at 2,700,000. Moreover, these seeds appear to be persistent (Thompson et al., 1997).

4.3. Potential role of propagule banks for the development of diverse submerged aquatic vegetation

Because of the presence of few submerged species and low propagule density of these species in the samples, it is concluded that subsediment propagule banks in backwaters along the studied navigation canals cannot play a significant role in the (re-)establishment of diverse submerged vegetation after sediment removal. Although some submerged species (*Potamogeton pusillus*, *Hottonia palustris*, *Ranunculus peltatus*) were restricted to the surface sediment, their propagule densities were so low that it is similarly unlikely that this layer can contribute to the development of diverse submerged vegetation. Emergent aquatics, mud-dwelling annuals and terrestrial species, which are major components of the propagule banks, will emerge only under low water level conditions (Van der Valk, 1981; Brock and Casanova, 1997; Keddy, 2000; Casanova and Brock, 2001; Smith et al., 2002). In navigation canals no water level fluctuations are allowed, so these conditions are met only in a narrow zone at the water line. Especially after creation of bare sites as a result of cutting and dredging, propagule banks may contribute to the development of species-rich emergent vegetation in these transition zones, as was observed along the dredged aquatic plots (results not shown).

When comparing the propagule bank and actual vegetation 2 months after sediment removal (Table 3), we assumed that dispersal had not occurred. Nevertheless, dispersal might have accounted for the establishment of *Potamogeton pusillus* and *Butomus umbellatus*, both apparently absent from the propagule bank, and can lead to further establishment of aquatic species over the following years under favourable habitat conditions.

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Appendix A

Total propagule numbers in each sediment layer, species' frequency in the vegetation and propagule bank characteristics of the sites. Number of replicates (of 1 l) for each site is 20 for propagule bank analysis and 10 for vegetation. The subsediment could not be studied at site 3 (geotextile). Different letters in the same row indicate significant differences ($P < 0.05$) of the mean frequency per species (group) between sites tested for each vegetation (ANOVA, followed by a Tukey-test). If no letters are indicated in a vegetation row, no test was performed because of low numbers. Aquatic species were included in the table if cumulative propagule numbers were ⩾20 in one layer. If the numbers in both layers were <20, an aquatic species was nevertheless included if cumulative frequency in the vegetation was ⩾50. For other species these numbers were 50 and 150, respectively. The complete list is available at the first author.

Species, characteristics	Propagules in surface sediment (study site)					Propagules in subsediment (study site)				Water vegetation frequency (study site)					Bank vegetation frequency (study site)				
	1	2	3	4	5	1	2	4	5	1	2	3	4	5	1	2	3	4	5
Free-floating aquatics																			
Lemna minor	299	106	108	393	1513	8	131	25	2662	23a	85b	27a	67ab	71ab	0	0	0	0	0
Lemna trisulca	0	0	0	55	18	0	0	39	28	3a	10ab	2a	57b	22ab	0	0	0	0	0
Spirodela polyrhiza	2	33	40	147	840	15	10	21	548	3a	62b	2a	40ab	65b	0	0	0	0	0
Submerged aquatics																			
Callitriche spp.	23	5	29	63	208	8	3	10	63	57bc	1a	66c	29ab	30abc	0a	0a	0a	6a	36b
Ceratophyllum demersum	0	0	0	0	0	0	0	0	0	46c	16b	1a	0a	0a	0	0	0	0	0
Elodea nuttallii	0	0	0	0	0	0	0	0	0	86c	21ab	9a	66bc	18a	0	0	0	0	0
Persicaria amphibia	1	0	0	0	0	0	2	0	0	0	0	5	1	0	20a	6a	20a	18a	3a
Potamogeton pectinatus	4	3	1	0	0	8	11	0	0	8ab	20b	0a	0a	0a	0	0	0	0	0
Potamogeton pusillus	0	0	0	1	1	0	0	0	0	5a	2a	2a	49b	12ab	0	0	0	0	0
Emergent aquatics																			
Alisma plantago-aquatic	3	0	21	22	29	5	0	11	18	0a	1a	14bc	23c	1ab	4a	1a	3a	23b	21b
Carex acuta	0	0	1	4	19	0	0	1	16	0a	0a	2a	1a	14b	1a	0a	10a	13ab	48b
Epilobium hirsutum	58	53	204	22	39	22	20	1	5	0	0	2	0	3	67b	78b	26a	20a	22a
Eupatorium cannabinum	5	13	178	72	156	3	5	28	33	0	0	0	0	1	19a	36a	70b	49ab	77b
Iris pseudacorus	0	0	0	3	0	0	0	1	0	0	0	0	1	1	12abc	1a	7ab	30c	19bc
Lycopus europaeus	12	7	29	30	54	7	7	8	18	0a	0a	0a	0a	9b	34abc	28ab	28a	50bc	72c
Lythrum salicaria	44	22	1580	10329	3280	17	10	2129	1831	0	0	4	16	3	6a	5a	41b	79b	63b
Myosotis scorpioides	1	2	0	0	1	0	0	0	0	0	0	1	0	0	2a	19b	10a	6a	25b
Phalaris arundinacea	4	2	7	11	19	1	1	4	2	0a	0a	4a	8a	56b	48a	57a	33a	51a	66a
Phragmites australis	19	14	298	116	65	3	15	16	16	0a	0a	93bc	83b	100c	93a	96a	100a	100a	99a
Scirpus sylvaticus	3	0	11	44	20	2	0	18	24	0	0	0	0	0	3	0	3	9	15
Typha spp.	7	1	22	213	121	11	2	69	45	0	0	1	4	13	0a	0a	4ab	10b	8ab
Veronica beccabunga	0	0	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Mud-dwelling and terrestrial species																			
Aegopodium podagraria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29b	10a	52b	50b	70b
Artemisia vulgaris	9	4	13	17	15	1	2	1	4	0	0	0	0	0	27ab	5a	5a	9a	45b
Calystegia sepium	0	0	0	0	0	0	0	0	0	0a	0a	9ab	4a	30b	77a	83ab	100b	98b	95ab
Cirsium arvense	0	2	6	1	0	2	0	0	0	0	0	0	0	0	74b	51ab	25a	49ab	35ab
Elytrigia repens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	73b	43ab	33ab	40ab	34a
Epilobium ciliatum	7	10	8	2	6	9	11	2	3	0	0	0	0	0	0	0	0	0	6
Epilobium tetragonum	17	13	11	6	2	7	15	1	16	0	0	0	0	0	0a	13b	0a	0a	0a
Holcus mollis	0	0	1	1	1	0	0	0	0	0	0	0	0	0	47b	46b	14a	67b	26ab
Juncus spp.	2616	3382	9996	57815	63795	1106	2444	39265	59139	0	0	0	0	0	55ab	63ab	24a	58ab	48ab
Poa trivialis	4	20	43	12	3	5	11	4	0	0	0	0	0	0	75b	67ab	42a	41a	56a
Ranunculus sceleratus	80	17	18	14	12	54	36	15	14	0	0	0	0	0	1a	0a	0a	10ab	24b
Rorippa palustris	41	19	10	6	3	26	58	2	3	0	0	0	0	0	0	0	0	0	5
Rumex crispus	43	0	7	0	3	11	1	4	2	0	0	0	0	0	11b	2ab	0a	4ab	15b
Tanacetum vulgare	2	2	26	17	36	0	1	3	11	0	0	0	0	0	9a	9a	14ab	12ab	20ab
Urtica dioica	85	56	402	255	265	103	70	68	104	0	0	0	0	0	39a	44a	86b	68ab	86b
Mean number of species plot^{-1}										7.0ab	5.8a	7.3ab	9.4b	9.4b	39.7bc	35.2ab	30.8a	41.0bc	48.3c
Propagule bank characteristics																			
Mean number of species l^{-1}	13.1	10.8	17.8	13.9	12.5	8.7	8.5	9.4	10.2										
Mean number of propagules l^{-1}	177	198	666	3874	3209	76	148	2323	2940										
Total emerged propagules	3545	3948	13312	69742	70605	1522	2974	41807	64671										

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