AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS

Aquatic Conserv: Mar. Freshw. Ecosyst. **14**: 381–394 (2004)

Published online 1 June 2004 in Wiley InterScience
(www.interscience.wiley.com). DOI: 10.1002/aqc.623

Restoration of a small-scale forest wetland in a Belgian nature reserve: a discussion of factors determining wetland vegetation establishment

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ABSTRACT

1. The main aim of this restoration attempt within a nature reserve was to recreate sustainable conditions for wetland species, particularly aquatic plants.
2. In the process of restoration, two phases of activity were distinguished: a pre-restoration phase, during which information on land-use history and past vegetation was collected and used to establish clear restoration goals; and a restoration phase for stimulating germination and establishment of target species originating from the soil seed bank and species pool.
3. Within the first year of the study, pond digging allowed the establishment of extremely rare native species that react positively to mudflat creation and standing water availability. The results of this experiment indicate that pond digging can be a very suitable technique for re-establishing aquatic and wetland vegetation, providing that the site is well chosen.
4. An essential prerequisite for successful restoration is a study of the past vegetation of the target site and its surroundings. This work illustrates the importance of past vegetation in affecting current restoration success and provides an example of how restoration projects benefit from knowledge and understanding of both historical and present conditions.

KEY WORDS: aquatic plants; pond; mudflat colonization; water colonization; rewetting; topsoil removal; succession; seed bank

INTRODUCTION

Europe's history of settlement, permanent agriculture and industrialization has wrought huge changes on the natural ecosystems of the region and on their flora and fauna (Hails, 1996). Wetlands have come under particular pressure as the result of drainage of extensive lowland areas for agriculture and urban development, and with the regulation of major river systems for power generation, water storage,

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Received 28 July 2003
Accepted 11 January 2004

navigation and artificial flood control (Hails, 1996). Many freshwater habitats and semi-natural tall-herb humid meadows are currently listed in Annex I of the EC Habitats Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. For this reason, these plant communities are regarded as habitat types of community interest whose conservation requires the designation of special areas of conservation (SACs). A coherent European ecological network of SACs (called Natura 2000), will comprise sites hosting the natural habitat types listed in Annex I and habitats of the species listed in Annex II. This will enable the natural habitat types and the species' habitats concerned to be maintained at or, where appropriate, restored to a favourable conservation status in their natural range. As small elements of this network, ponds (i.e. small and shallow bodies of water), therefore, are important for biodiversity conservation (Biggs *et al.*, 1994). However, they have been lost on a large scale during the 20th century, with losses reaching 40–90% for various north-western European countries (Hull, 1997). Generally, wetland loss is difficult and costly to reverse (Moser *et al.*, 1996), and wetland restoration is an increasingly popular applied science and conservation tool (e.g. Jeffries, 1991; Wetzel *et al.*, 2001; Pokorny and Hauser, 2002). Degraded wetlands may still retain considerable potential, and this can be brought to the surface with proper management. However, the results of previous restoration projects have sometimes been inconsistent (Carey *et al.*, 2001). In order to understand the reasons for this, it is important to consider the limitations of ecological restoration (Bakker and Berendse, 1999), and it is essential to test hypotheses over a wide range of sites and conditions (Pywell *et al.*, 2002). This paper describes results gathered within a broader programme of restoring aquatic vegetation and wetland meadows. The lack of scientific literature on pond restoration and the limited number of comparisons of different restoration methods justified this project. Management measures are often intuitive and expertise is empirical. Because relatively little is known about the initial successional stages of most wetland communities and about the environmental conditions that promote their development, restoration managers must often make arbitrary decisions about the initial conditions for restoration (Budelsky and Galatowitsch, 2000). It is generally difficult to restore plant communities known from the past, because environmental conditions may change in an unforeseen way (Klötzli and Grootjans, 2001). Sometimes, restoration may even be impossible within reasonable time spans (Pfadenhauer and Klötzli, 1996).

This study was designed to monitor the spontaneous development of vegetation in a small, highly degraded forest wetland area after restoration. It was hoped that this would guide later management measures and build up expertise on such environments, the main objective being the restoration of wetland and aquatic vegetation. For this purpose, patterns of plant species regeneration were explored by examining: (1) the recolonization dynamics of plant species over 3 yr; and (2) how closely the emerging flora resembled that of the site before degradation.

In this context, the term 'restoration' refers to pond digging and subsequent spontaneous reflooding by groundwater and precipitation, given the assumption that aquatic plants will eventually become established.

STUDY AREA

The research was conducted in the Sonian Forest, south of Brussels (50°47′N, 4°26′E). This 4383 ha area has been proposed as a Site of Community Importance in fulfilment of the EC Habitats Directive. The study site is located in the Vuilbeek valley (10 ha), which is 2.3 km long and entirely embedded in the Sonian forest area. Historical maps from the 18th and 19th centuries clearly show a water body in this valley, and aerial photographs from 1969 show a young poplar plantation (*Populus* x *canadensis*) and a realigned brook. In this post-war period, subsistence ponds downstream were 'cleaned' and the mud was disposed of in the upper drained pond — the actual study site. The study site measured approximately 30 m × 30 m and was located within the 0.5 ha drained 'middle' pond of the Vuilbeek valley nature reserve.

MATERIAL AND METHODS

In order to gain a general idea of the potential vegetation and floristic diversity that was present before and which could reappear after restoration, all accessible literature regarding the Vuilbeek valley was analysed. This encompasses botanical and phytosociological studies of the valley from 1940 onwards.

Field work was carried out using the same method as in 1989 and during 1995–1996 to establish a baseline for the valley and for the study site. The vegetation was described using the classical phytosociological method (Braun-Blanquet, 1964). Quadrats were placed in each homogeneous vegetation unit, the size of which (1–50 m^2) varied according to the vegetation type as recommended by Kent and Coker (1992). The abundance/coverage of all species of vascular plants in the tree layer, the shrub layer and the herb layer was recorded.

All ruderal vegetation on a 20 m × 15 m area was discarded in January 1997, and an irregularly shaped pond (with gently sloping banks) was dug in frozen soil until the groundwater level was reached (maximum 1 m depth). The pond filled slowly with very clear water over 15 days to reach a size of 16 m × 9 m. This fluctuated, particularly during the dry 1997 summer, but never dried up, having a minimum water area of 13 m × 6 m. The excavated substrate was disposed of within the same valley on a nearly bare forested site that was not included in the study area. No planting or deliberate sowing was carried out in the study area. On each visit, care was taken to wear mud-free boots. The site was not fenced, but it was not readily accessible.

After the pond was dug, the water and the newly exposed mudflats were described by recording the presence of all vascular plant species and macroalgae during 3 yr (1997–1999) between June and September. Only presence/absence records were used, as the Braun-Blanquet method was not relevant because of the scarcity of the vegetation at this pioneer stage of recolonization.

Species colonization and fluctuation during the 3 yr survey were analysed according to species richness, species rarity, species functional groups (established strategies, life forms, ecology, Ellenberg values) and turnover. Species rarity index is given for northern Belgium by the arithmetical scale of Stieperaere and Fransen (1982). This scale classifies each species of the Belgian flora within one of 10 rarity levels, corresponding to a grid-cell frequency class in the atlas of Belgian and Luxembourg flora (Van Rompaey and Delvosalle, 1979). The well-known and validated indicator values of Ellenberg *et al.* (1991), but recalibrated and completed for the British flora (Hill *et al.*, 1999), were used in order to gain knowledge of species' niches, which can be used to make inferences about the environment. Indeed, species are not always constant in their ecological requirements and ought, in principle, to have different indicator values in different parts of their range (Hill *et al.*, 1999). The original Ellenberg system was defined for central Europe, and so the recalibrated values for the British Isles were used because they are more relevant for Belgium (since both these countries belong to western Europe and are phytogeographically much more similar to each other than to central Europe).

The species turnover is calculated according to the method of Barkham (1992). The total numbers of losses and gains are examined for each species group in relation to the total number of occurrences in 1997 and 1999 together. Expressed as a percentage, this gives a measure of the turnover or transience of species of a particular group. A value of 100% means that there was no instance of a species in that group occurring in both years. Species' ecological strategies (according to Grime *et al.* (1998)) were examined to help explain the role of particular species in succession (Leps *et al.*, 1982). Seed-bank types of established species were obtained from the database of Thompson *et al.* (1997). The nomenclature and species' life forms are given by Lambinon *et al.* (1992), and ecological groups were determined according to Stieperaere and Fransen (1982).

RESULTS

Literature survey

Noirfalise (1952) published five phytosociological relevés made in the 1940s in the valley. He described the area as a marshy, inundated meadow belonging to the tall herb variant of the *Carici remotae–Fraxinetum* association, with *Equisetum telmateia*, accompanied by *Rumex sanguineus*, *Carex remota* and *Carex strigosa* as characteristic species of the association. In the remaining ponds of the valley, Noirfalise and Dethioux (1977) found an aquatic flora belonging to the *Nymphaeion* association, where *Myriophyllum verticillatum*, *Lemna minor*, *Lemna trisulca*, *Nuphar lutea*, *Elodea canadensis*, *Ranunculus circinatus*, *Potamogeton natans*, *Potamogeton alpinus* and *Potamogeton crispus* were present.

De Clercq and Roelandt (1989) describe the site as a tall-herb community in a loose poplar plantation (Table 1), where the *C. remotae–Fraxinetum* has been substituted by *Urtica dioica*-dominated tall-herb vegetation with some relicts of the previous community. It is obvious that this vegetation shift results from environmental disturbance (e.g. draining), due to the stand preparation for the poplar plantation. The exotic *Populus* x *canadensis* was intended to increase the economic value of the marshland and led to a decrease in water level and to nutrient enrichment of the topsoil. From a floristic and nature management point of view, the situation before 1950 had deteriorated considerably and resulted in a very impoverished community in 1996.

Vegetation study prior to the project management measures

Surveys in 1995–1996 (Table 1) recorded a tall-herb community dominated (at 95%) by *U. dioica*, accompanied by *Galium aparine* and *Circaea lutetiana* (Weyembergh, 1996). Characteristic *C. remotae–Fraxinetum* species were absent. At this stage, the ruderal tall-herb community was considered worthless in terms of nature conservation. The groundwater level recorded between February 1995 and April 1996 showed fluctuations between 65 and 91 cm below ground level. These measurements helped determine the depth to which to dig the pond.

Vegetation study after the project management measures

The excavated depression slowly filled with water derived from groundwater and 'hanging water' (i.e. suspended water table). The water level fluctuated, but never dried up, in spite of the dry summer of 1997. The survey of the spontaneously emerging flora from June to September 1997 yielded 74 vascular plant species that could be identified unambiguously (Table 2), 21% of which were extremely rare.

Water colonization

A few months after the pond was dug, eight vascular species established in the water body (Table 2). From June onwards, a dense population of *Chara vulgaris* var. *contraria* developed. *R. circinatus* was the first seed plant to establish visibly in three large 40 cm diameter patches. From July onwards, *Potamogeton* spp. appeared: first *Potamogeton pectinatus* on the charophyte algae, followed by small colonies of *Potamogeton lucens*. About 10 individuals of *Zannichellia palustris* subsp. *palustris* were found at the margin of the charophyte mass fruiting abundantly in August. Numerous rosette-forming *Sagittaria sagittifolia* appeared at the end of June on the pond substrate (below the water level), six individuals reaching the water level by August. *Sparganium erectum* and *Alisma plantago-aquatica* established both on the mudflats and in the pond.

Table 1. Wet meadow vegetation of the study area prior to pond digging (De Clercq and Roelandt, 1989; Weyembergh, 1996). Third relevé corresponds exactly to the place where the pond was dug in 1997. Cover classes according to Braun-Blanquet (1964): r = 1 or 2 individuals; + = few individuals (<20) with cover <5%; 1 = many individuals (20–100) with cover <5%; 2 = 5–25% cover; 3 = >25–50% cover; 4 = >50–75% cover; 5 = >75–100% cover

	Distance to restoration site (m)	17	25	0	65	75	25
	Downstream (D)/upstream (U)	–	D	–	U	U	U
	Sampling surface (m^2)	25	9	50	1	5	7
	Total cover (%)	80	100	100	95	90	100
	Year	1989	1989	1989	1996	1996	1996
A	*Populus* x *canadensis*			2			
	Salix caprea			2			
a	*Salix alba*			2			
	Salix caprea			2			
	Sambucus nigra			2			
	Sambucus racemosa			2			
h	*Urtica dioica*	1	5	5	5	5	4
	Galium aparine	+	r	r	2	2	2
	Circaea lutetiana	2		r		2	1
	Cirsium oleraceum	3	r			r	r
	Impatiens parviflora	r	r		+		1
	Glechoma hederacea	1	+	1			1
	Impatiens noli-tangere	r	r	+			
	Cardamine flexuosa				1	1	+
	Cardamine hirsuta	2		+			
	Phragmites australis					1	1
	Eupatorium cannabinum	r				r	
	Myosotis scorpioides	r			1		
	Mentha aquatica	3					
	Scrophularia umbrosa	3					
	Cirsium arvense	+					
	Polygonum hydropiper	+					
	Ranunculus repens	+					
	Cirsium vulgare	r					
	Equisetum telmateia	r					
	Juncus effusus	r					
	Lysimachia vulgaris	r					
	Lythrum salicaria	r					
	Silene dioica	r					
	Rumex sanguineus	r					
	Chrysosplenium oppositifolium			+			
	Moehringia trinervia					+	
	Carex paniculata						1
	Equisetum telmateia						r
	Carex acutiformis						+

Mudflat colonization

Colonization by vascular plants on the mudflats proceeded more slowly than in the pond. In the first growing season, coverage remained below 20%, and in the zone of varying water level it did not reach 10%. Rabbits exert a strong and sometimes selective herbivorous pressure on young shoots of terrestrial plants (div. Poaceae, *Juncus* spp., *Carex* spp., *Scirpus sylvaticus*, *A. plantago-aquatica*, *S. sagittifolia*, *Epilobium* spp.)

Table 2. Vegetation dynamics recorded in the study area between 1997 and 1999. Within each group, species are ranked by decreasing frequency; x: species present; m: mudflat; w: water; rarity index 1 = extremely rare; 10 = very common. The rarest species (those with rarity index 1) are indicated in bold. T: transient (< 1 yr); SP: short-term persistent (> 1 to < 5 yr); LP: long-term persistent (> 5 yr)

Species/ecological group	Year			Colonization area	Rarity index (Belgium)	Seedbank type
	1997	1998	1999			
River-bank and freshwater plants						
Lemna minor	x	x	x	w	5	T
Potamogeton lucens	**x**	**x**	**x**	**w**	**1**	
Ranunculus circinatus	**x**	**x**	**x**	**w**	**1**	T
Carex acutiformis	x	x	x	m	3	T, SP, LP
Lycopus europaeus	x	x	x	m	7	T
Mentha aquatica	x	x	x	m	7	T, SP, LP
Phragmites australis	x	x	x	m	6	T
Sparganium erectum	x	x	x	w/m	4	T
Alisma plantago-aquatica	x	x	x	w/m	5	SP, LP
Myosotis scorpioides	**x**	**x**	**x**	**m**	**1**	T, LP
Sagittaria sagittifolia	x	x	x	w	2	
Scrophularia auriculata	x	x	x	m	4	SP, LP
Scrophularia umbrosa	**x**	**x**	**x**	**m**	**1**	SP
Veronica beccabunga	x	x	x	m	5	T, SP, LP
Epilobium parviflorum	x	x	x	m	4	T, SP
Zannichellia palustris	**x**	**x**		**w**	**1**	T, SP
Glyceria maxima		x	x	m	5	T, SP
Lythrum salicaria		x	x	m	6	T, SP, LP
Oenanthe aquatica	x	x		m	3	
Potamogeton pectinatus	**x**			**w**	**1**	T, SP
Iris pseudacorus	x			m	6	T
Scutellaria galericulata	x			m	3	T
Typha latifolia	x			m	4	T, SP, LP
Eupatorium cannabinum	x			m	6	T, SP, LP
Petasites hybridus	x			m	3	T
Salix alba plantula	x			m	5	T, LP
Glyceria fluitans			x	m	7	T, SP, LP
Carex pseudocyperus			**x**	**m**	**1**	
Glyceria notata			x	m	2	SP
Veronica anagallis-aquatica		x		m	7	SP
Angelica sylvestris			x	m	9	T, SP, LP
Plants from mesotrophic to eutrophic humid to damp grasslands						
Cirsium oleraceum	x	x	x	m	3	T
Scirpus sylvaticus		x	x	m	5	T, SP, LP
Holcus lanatus			x	m	10	T, SP, LP
Prunella vulgaris	x			m	9	T,SP,LP
Galium palustre	x			m	6	T,SP,LP
Pioneers from disturbed semi-natural habitats, on open humid soils						
Juncus effusus	x	x	x	m	9	T, SP, LP
Ranunculus repens	x	x	x	m	10	T, SP, LP
Polygonum hydropiper	x	x	x	m	8	
Cyperus fuscus	**x**	**x**	**x**	**m**	**1**	SP
Sagina apetala	**x**	**x**	**x**	**m**	**1**	T, SP
Juncus tenuis		x	x	m	5	T, SP, LP
Rorripa palustris		x	x	m	3	SP, LP
Myosoton aquaticum	x	x		m	4	
Ranunculus sceleratus	x	x		m	3	T, SP, LP

Table 2 *Continued.*

Species/ecological group	Year			Colonization area	Rarity index (Belgium)	Seedbank type
	1997	1998	1999			
Deschampsia cespitosa			x	m	8	T, SP, LP
Juncus articulatus			x	m	3	T, SP, LP
Poa trivialis			x	m	7	T, SP, LP
Juncus bufonius	x			m	7	T, SP, LP
Gnaphalium uliginosum	x			m	6	T, SP, LP
Pioneers from disturbed, artificial habitats: road verges, dry waste lands, fields						
Plantago major	x	x	x	m	10	T, SP, LP
Poa annua	x	x	x	m	10	T, SP, LP
Cirsium arvense	x	x	x	m	10	T, SP, LP
Epilobium ciliatum	**x**	**x**	**x**	**m**	**1**	SP, LP
Sonchus asper		x	x	m	9	T, SP, LP
Sonchus arvensis	x			m	6	T, SP, LP
Cirsium vulgare	x			m	9	T, SP, LP
Species from clear-felled areas						
Galium aparine	x	x	x	m	9	T, SP
Glechoma hederacea	x	x	x	m	10	T, SP, LP
Silene dioica	x	x	x	m	7	T,SP, LP
Urtica dioica	x	x	x	m	10	T, SP, LP
Sambucus nigra plantula	x		x	m	9	T, SP, LP
Forest plants						
Cardamine flexuosa	**x**	**x**	**x**	**m**	**1**	T, SP
Equisetum telmateia	**x**	**x**	**x**	**m**	**1**	
Impatiens noli-tangere	**x**	**x**	**x**	**m**	**1**	T
Circaea lutetiana	x	x	x	m	3	T
Salix caprea plantula	x	x		m	9	T
Carex pendula			**x**	**m**	**1**	SP
Carex remota			x	m	5	T, SP, LP
Festuca gigantea			x	m	5	T, SP
Chrysosplenium alternifolium	x			m	2	
Carpinus betulus plantula	x			m	8	T
Moehringia trinervia	x			m	7	T, SP
Stachys sylvatica	x			m	8	T, SP, LP

Most species established in the first year (Table 2), but also in the second and third years of succession some species with delayed germination became established (e.g. *Lythrum salicaria*, *Veronica anagallis-aquatica*, *Carex pseudocyperus*, *Scirpus sylvaticus*, *Rorippa palustris*, *Carex pendula*). In the first year of investigation (1997), many pioneer species such as *Juncus bufonius*, *Ranunculus sceleratus*, *Cyperus fuscus*, *Impatiens noli-tangere*, *Myosoton aquaticum* and *Polygonum hydropiper* developed successfully. Some competitors also re-established very rapidly, such as *Phragmites australis*, *U. dioica* and *Cirsium arvense*.

Functional groups and succession

Twelve species (or 21%) that appeared within the first year survey (Figure 1) may be considered as 'extremely rare' in the Belgian context (i.e. *C. fuscus*, *P. lucens*, *P. pectinatus*, *R. circinatus*, *Scrophularia umbrosa*, *Z. palustris*). Another two species (or 3.5%) were 'extremely rare' and seven species (or 12.5%) rare.

The remainder were moderately rare to common. The species range predominantly comprised competitors–ruderals (between 37.5 and 41%). Competitors were also rather abundant, with a proportion of 22% in the first year, progressively decreasing to 16% in the third year of succession. No stress-tolerators were found during the study. River-bank and freshwater plants were by far the most abundant species, representing between 41 and 44%. For the life forms, hemicryptophytes were present for the most part, with 43% in 1997 and 51% in 1999. During re-colonization, 23% and 20% therophytes were found in the first and the third years respectively. Hydrophytes and helophytes contributed 7% and 11% of the biological spectrum respectively. For indicator values, 4% of plants rooting under water and 7% of submerged plants were found. All other species are at least moist-site indicators. As might be expected, plants from well-lit places were predominant, with 58% in the first year of monitoring. Plants from richly fertile places were the most abundant. No indicators of infertile sites were encountered. No clear shifts could be detected in those ecological spectra during the 3 yr succession. Only for soil pH (R), a slight tendency towards higher values appeared during the re-colonization process. For the life forms and the ecological groups, temporal changes were shown more clearly by calculating the turnover rate. Table 3 presents the total number of losses and gains between 1997 and 1999 for each species group in relation to the total number of occurrences in both years together. The results suggest that hydrophytes and geophytes are relatively persistent, such as pioneers from disturbed artificial habitats and river-bank and freshwater plants, whereas other groups are more transient. Taking all species together, the turnover rate is 36.45% over the 3 yr period.

DISCUSSION

Colonization

The floristic value of pioneer communities that developed after the restoration experiment was rather unexpected, as topsoil removal without introduction of species is believed to be a very slow process of restoration (Berendse *et al*., 1992). The colonization of the pond (which had no open-water contact with a brook or other ponds, thus excluding fish-mediated zoochory or water as a vector) could be due either to diaspore immigration or long-term survival in a seed bank (the soil was exposed after at least 30 yr, but probably 50–80 yr). Human introduction, whether deliberate or by accident, is less plausible: care was taken to wear mud-free boots and the area hardly ever attracts passers-by.

Data gathered from this study show that most of the bank and water plants which appeared on the restored site have transient or short-term persistent seeds, i.e. persisting less than 5 yr (Thompson *et al*., 1997), which suggests that most of these species colonized the experimental site by seed sources in the vicinity. This is particularly likely for *P. pectinatus*, *R. circinatus* and *S. erectum*, which are known to occur less than 1 km from the study site. Transient or short-term persistent seed banks were also reported for other desirable species, such as *C. fuscus*, *Sagina apetala* and *I. noli-tangere*, which appeared from the first year of the experiment. Systematic prospecting in the 1970s yielded several records for *Z. palustris* in the Woluwe valley, of which the Vuilbeek is a tributary, but beyond the limits of the forest and 5 km further downstream (De Sloover *et al*., 1976; Tanghe and Duvigneaud, 1978). The high dispersability of *Z. palustris*, as mentioned by Arnold *et al*. (2000), suggests colonization by seed rain, but as it has not been

Figure 1. Ecological spectra of the restored area and evolution over the 3 yr study. Strategies following Grime *et al*. (1988): C = competitors; S = stress-tolerators; R = ruderals. Life forms according to Lambinon *et al*. (1992): hy = hydrophytes; hel = helophytes; t = therophytes; g = geophytes; h = hemicryptophytes; c = chamephytes; p = phanerophytes. F, L, N, R are soil moisture, light, soil nitrogen and soil reaction indices respectively, according to Hill *et al*. (1999), with 1 as the lowest level and 9 (12 for soil moisture) the highest level for the index considered. Rarity level according to Stieperaere and Fransen (1982), with 1 = extremely rare species, and 10 = very common species. Ecological groups according to Stieperaere and Fransen (1982): 1 = pioneers from disturbed, artificial, habitats; 2 = pioneers from disturbed, semi-natural habitats; 4 = river-bank and freshwater plants; 5 = plants from mesotrophic to eutrophic humid to damp grasslands; 8 = species from clear-felled areas; 9 = forest plants.

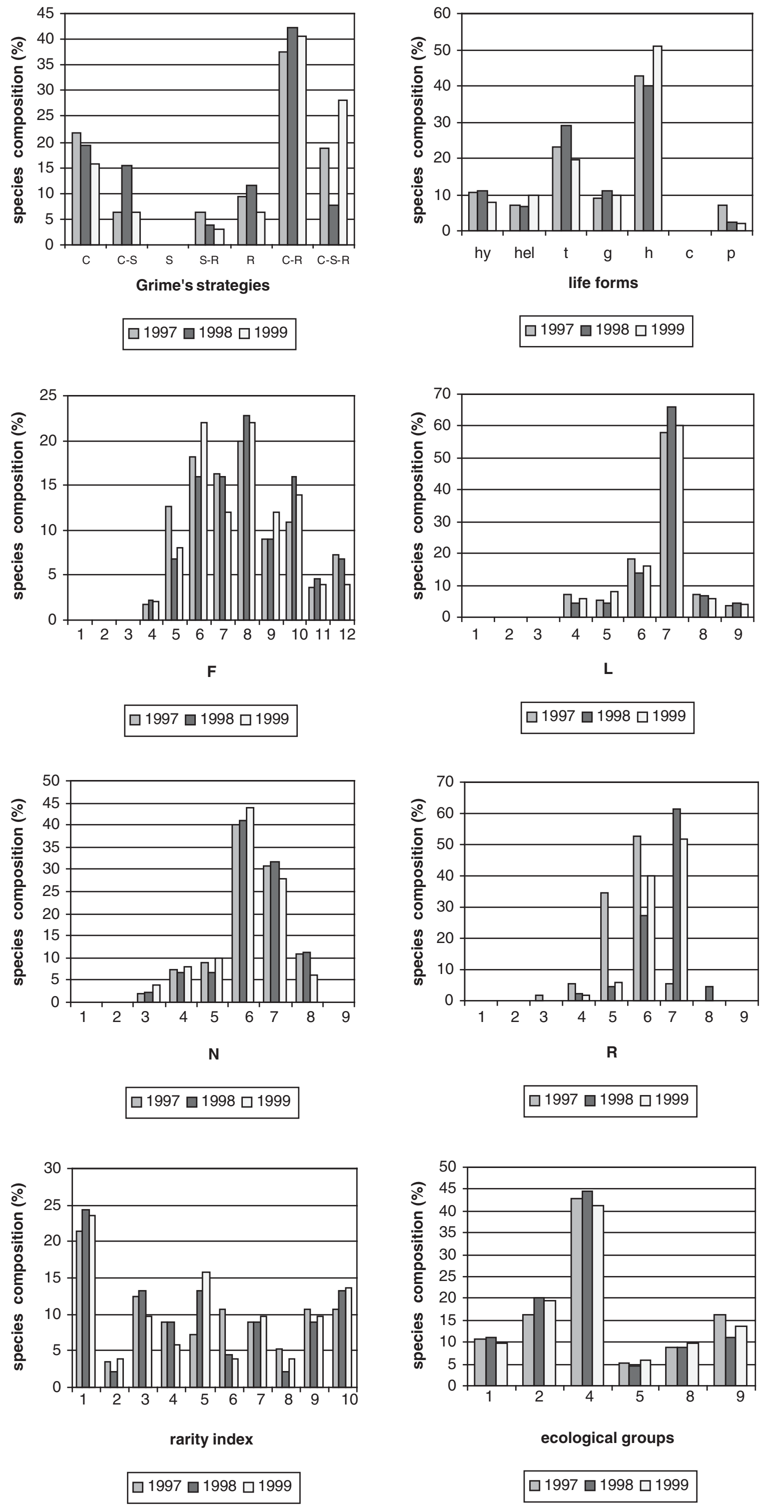
species composition (%)
C
C-S
S
S-R
R
C-R
C-S-R
Grime's strategies
1997 1998 1999
hy
hel
t
g
h
c
p
life forms
F
L
N
R
rarity index
ecological groups

Table 3. Turnover of species in the study area. A 'loss' is a species that was present in 1997 but absent in 1999. A 'gain' is a species recorded in 1999 but not in 1997

Ecological group	Total species	Total occurrences o	Losses l	Gains g	$l+g$	Turnover (%) $(l+g\times 100)/o$
Hydrophytes	6	10	2	0	2	20.00
Helophytes	7	9	2	3	5	55.56
Therophytes	15	23	5	2	7	30.43
Geophytes	6	10	1	1	2	20.00
Hemicryptophytes	35	50	9	11	20	40.00
Phanerophytes	4	5	3	0	3	60.00
Pioneers from disturbed artificial habitats	7	11	2	1	3	27.27
Pioneers from disturbed semi-natural habitats	14	19	4	5	9	47.37
River-bank and freshwater plants	30	45	9	6	15	33.33
Plants from mesotrophic to eutrophic humid to damp grasslands	5	6	2	2	4	66.67
Species from clear-felled areas	5	10	0	0	0	0.00
Forest plants	12	16	5	3	8	50.00
Total	73	107	22	17	39	36.45

recorded from the area (though sought), it may also have been brought in by endozoochory. The role of ducks in wetland seed dispersal has been highlighted by some (e.g. Mueller and van der Valk, 2002). Having passed through the gut, diaspores may still be viable, the more so if they are small and thick-walled (van der Pijl, 1972), which is the case for *Z. palustris*. The seed's rough surface and hooked beak may have enabled its transport, perhaps in mud on birds' legs or feathers. Diaspores may also have remained in the buried soil. Both long-term survival (> 100 yr) and, in contrast, failure to germinate from herbarium specimens from 1856 and 1987, have been reported (Dethioux and Noirfalise, 1986; Thompson *et al*., 1997). These conflicting results can be partly explained by the different storage conditions, as it has been shown that several wetland species lose viability if seeds are allowed to dry beyond a certain high moisture content (Budelsky and Galatowitsch, 1999). The soil that had been put down to fill in the old ponds may have brought in seeds, and it is also possible that the excavation of the substrate in January 1997 exposed layers containing seeds. The scattered distribution of *Z. palustris* in the water body supports this explanation.

The occurrence of species with wind-dispersed diaspores (*Typha latifolia*, *Epilobium* spp., *Cirsium* spp.) may be due to diaspore input from populations close to the study site, whereas species with vegetative propagation underground (e.g. *Carex acutiformis*, *P. australis*, *Glyceria maxima*) may be able to survive topsoil removal as rhizomes or stolons. Recolonization of the mudflats by common species, such as *P. hydropiper*, *Juncus effusus*, *Mentha aquatica*, *Lycopus europaeus*, etc. may be by propagation from the adjacent vegetation (border effect). Most of the other species (plants from grasslands, disturbed habitats and clear-felled areas) that newly colonized the mudflats have a long-term persistent seed bank, suggesting that the seed bank plays an important role for these species.

Establishment

Once in the restored area, propagules must find suitable conditions for establishment. The period of seedling recruitment and establishment is presumed to be most critical for community development (Grubb, 1977). A rather rapid germination rate was observed, with most of the aquatic species already identified between June and August, i.e. 5–7 months after restoration. This is consistent with the results of Vivian-Smith and Handel (1996), which showed that, in the wetland soil, species richness and plant density responded favourably to inundation. This differs from the study of Abernethy and Willby (1999), which suggested that, under permanent inundation, propagule germination and species richness are low. Most grassland species require open soil for germination and establishment (Bakker, 1989), where they experience little or no competition and where the temperature variation is higher than in closed vegetation (Thompson and Grime, 1983). Thus, the bare ground created by topsoil removal has certainly favoured the establishment of many species.

Species recolonization patterns and associated strategies are known to be related to species traits, particularly vegetative and sexual reproduction (Barrat-Segretain and Amoros, 1996). In this experiment, pond digging led to the recruitment of some ruderals, i.e. ephemeral plants of frequently disturbed productive habitats (e.g. *J. bufonius*, *R. palustris*, *R. sceleratus*). The emergence of these R-strategists is consistent with the results of Abernethy and Willby (1999), who found that, on damp mud (conditions associated with hydrological instability), the total seedling number and species richness increased significantly and that annuals and facultative ruderal species predominated. In this study, the development of some competitors (such as *Petasites hybridus*, *P. australis*, *T. latifolia*, *U. dioica*) was also noted. As their regenerative strategy is primarily by vegetative means, it is possible that the pond digging did not remove all the rhizomes that were present in the topsoil, giving a chance for their development.

Persistence

The 1999 survey showed that a substantial number of species did not persist — 23 disappeared and 33 were stable over three seasons. The results suggested that hydrophytes and geophytes were relatively persistent. For the former, this was because the pond never dried up; for the latter, this was due to their underground storage organs. Nitrophilous species that dominated the area before restoration (*U. dioica*, *Galium aparine*, *Silene dioica*, *Sambucus nigra*, *Glechoma hederacea*) re-established from the first year and persisted during the 3 yr survey, but the desired objective of no invasion of the former *U. dioica*-dominated vegetation was met. Forest plants were more transient. These are essentially species that cannot withstand full light (e.g. *Stachys sylvatica*, *Moehringia trinervia*, *C. lutetiana*, *Festuca gigantea*), so their failure to persist is not surprising. River-bank and freshwater plants persisted fairly well, except *Z. palustris* and *P. pectinatus*, which were no longer recorded, perhaps due to species traits (e.g. reproduction) or to environmental conditions. *Z. palustris* is known to be self- and cross-pollinated (Guo *et al*., 1990) and was found to be fruiting abundantly in August 1997. Thus, sexual reproduction was successful and could not have prevented its persistence. Climatic factors might have been responsible for the transient character of the species as most submerged macrophytes are sensitive to frost damage (Lohammar, 1938, cited by Ho (1979)). In the case of *P. pectinatus*, frost damage, combined with the rapid decomposition of plants in water, causes the species to behave as an annual in shallow waters in temperate climates, with buried turions as the only vegetative structure to survive winter (Lapirov and Petukhova, 1985, cited by Prejs (1987)). The disappearance of these hydrophytes may also have been caused by the low water depth or by being eaten by ducks. This is considered by some to be the most significant factor controlling the establishment of wetland species (van der Valk, 1981). This could be confirmed for *P. pectinatus*, which cannot compete well in shallow water against species that produce seeds more quickly (Van Vierssen and Verhoeven, 1983).

It is concluded that the combination of pond digging and rewetting by groundwater and precipitation, as well as the creation of mudflats by topsoil removal, seem suitable techniques for re-establishing desirable vegetation on degraded wetlands. Patterns observed in this experimental study suggest that: (1) the establishment of wetland species is limited not by the lack of diaspores but by the lack of favourable microsites for germination; (2) topsoil removal seems a better technique than mowing alone, because many plant species require open soil for germination and successful establishment where they experience no competition; (3) because several water plants do not have a long-term persistent seed bank, spontaneous recolonization is more efficient when the restored site is surrounded by (semi)-natural vegetation, which can act as a seed source; (4) vegetation re-establishment by sowing or planting need not always be considered for restoration purposes; (5) the invasion of undesirable species, such as non-natives or pioneers from disturbed artificial habitats, can be limited by maintaining the site under water (or at least wet) during the restoration process; (6) an essential prerequisite for the functioning of such a restoration practice is a study of the past vegetation of the target site; (7) the integration of the restoration site in a historic and ecologically functioning wetland network is very important.

This work shows that restoration was successful, partly because sufficient data on the original state of the area were available. This was also highlighted in the study of Brown (1998), which showed that an analysis of remnant vegetation was probably more useful for predicting restored vegetation in sites with prolonged disturbance than seed-bank analysis, which seems to be a less efficient technique. Through immigration processes and diaspore survival phenomena, a particularly interesting flora for the region and the country appeared rapidly at a small scale. No invasion of the former ruderal vegetation took place within three seasons of the survey. This situation is unlikely to persist in the long term, however, particularly in view of its strong pioneer element. Therefore, we recommend an investigation period of more than 3 yr to assess the future development of such restoration sites with respect to vegetation and soil processes. At a larger management scale (valley, forest), attempts could be made to create such restored areas consecutively at various places, leaving them to develop spontaneously afterwards.

ACKNOWLEDGEMENTS

We wish to acknowledge the National Lottery and the King Boudewijn Foundation for their financial contribution. The authorization to work in nature reserves was kindly given by the Brussels Institute of Environmental Management. Professor J.-J. Symoens, L. Vanhecke and J. Saintenoy-Simon are thanked for their help in some identifications and for providing unpublished phytogeographic data.

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