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Macrophyte succession in floodplain lakes

spatio-temporal patterns in relation to

river hydrology, lake morphology and management



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Chapter 1

Introduction

G.J. Van Geest

Introduction

In the coming decades, the floodplain landscape along the Lower Rhine in The Netherlands will change drastically because of measures proposed to increase discharge capacity of the river. Large parts of the floodplain area will be transformed into extensively grazed wetland areas, especially as the result of large-scale excavations (1 – 2 m) of floodplains (Smits *et al.*, 2000). However, scientific insight into the effects of these measures on the ecology of floodplain lakes is still poor. The purpose of this thesis is to identify the effects of hydrological dynamics, lake morphometry, and lake age on macrophyte abundance, composition and succession in shallow floodplain lakes along the Lower Rhine. Based on the results of this study, guidelines can be proposed on position, shape, and character of future water bodies that will be created as part of large-scale flood accommodation works in the floodplains.

Research on macrophytes has a long history and addresses a broad range of environmental factors. Several studies have shown the importance of water depth and transparency (Canfield *et al.*, 1985; Chambers & Kalff, 1985a; Skubinna, Coon & Batterson, 1995), slope (Duarte & Kalff, 1986), and sediment characteristics (Chambers & Kalff, 1985b). Additionally, it has become clear over the past decade that submerged macrophytes play a key role in the regulation of ecosystem processes, particularly in shallow lakes (Jeppesen, Søndergaard & Christoffersen, 1997). This insight has sparked extensive recent work on the dynamics of vegetation in a wide range of shallow lakes (Scheffer, 1998). In these studies however, the role of fluctuations in water level is hardly addressed.

Previous studies in floodplain lakes predominantly stress the role of river-flooding as the major driving force for vegetation abundance and composition (Junk, Bayley & Sparks, 1989; Van den Brink *et al.*, 1991; Amoros & Bornette, 1999). Recently, the importance of low river water-levels for the ecological functioning of rivers has also been recognized (McMahon & Finlayson, 2003). In addition, the age of lakes, surrounding land use, and seepage from hill slope aquifers have been found to affect successional stage and nutrient content of the water in floodplain water bodies (Bornette, Amoros & Lamouroux, 1998).

To evaluate the importance of river dynamics, water bodies may be placed into a “hydrological connectivity gradient”, representing the relative influence of river dynamics on the ecosystem of floodplain water bodies. Along this gradient, large shifts in occurrence and abundance of species occur. In floodplains along the Lower Rhine, species richness of macrophytes, algae, zooplankton and macro-invertebrates has been shown to decrease with increasing connectivity (Van den Brink, 1994). Along the River Danube, highest species richness of macrozoobenthos, Odonata and macrophytes occurred at

intermediate connectivity, whereas the species richness of amphibians and fish peaked in water bodies with the lowest and highest connectivity, respectively (Tockner *et al.*, 1999). Consequently, rivers with a relatively intact hydrological connectivity gradient exhibit a high biodiversity on both spatial and temporal scales.

Nowadays, many rivers are strongly regulated to facilitate navigation in the main channel or agriculture in the floodplains, and to safeguard the hinterland from flooding. As a result, the course of the river has been fixed and floodplains have become disconnected from the main channel by construction of embankments. As a result, large parts of the former hydrological connectivity gradient have disappeared from floodplains, resulting in a reduced biodiversity and disrupted successional pathways.

Over the past decade, interest grew in restoring connectivity gradients in floodplains along regulated rivers. In 1985 and 1992, plans were initiated to restore habitat conditions in floodplains along the Lower Rhine in The Netherlands ('Black Stork'; De Bruin *et al.*, 1987; 'Living Rivers'; WWF, 1993). Both plans provided space for natural morphological processes, such as erosion and sedimentation, and restoration of lost habitats such as floodplain forests, low-flow secondary channels, and large woody debris. At present, these plans have been integrated with programmes to sustain safe flood levels along the Lower Rhine in the future. The Dutch government formulated the programme 'Ruimte voor Rijntakken' ('Room for Rhine branches'), which combines measures to increase river discharge capacity with programmes for river rehabilitation. The proposed measures include the removal of minor embankments or other obstacles in the winter bed, construction of secondary side channels, and large scale lowering of the floodplains.

Because flood prevention is the primary goal for management of the Lower Rhine, the programme 'Room for Rhine branches' sets limits to the potential for nature development in floodplains. Consequently, large-scale development of vegetation types with a high hydraulic resistance (like floodplain forest) is not allowed. As an alternative, large parts of the floodplains will be transformed into extensive wetland areas (Smits, 2000), especially by means of large-scale excavation of floodplains where clay layers of up to 1 – 2 meters will be removed. The resulting floodplains will be more frequently flooded, and highly connected to the river. Scientific insight into the effects of such an increased connectivity on the ecology of floodplain lakes is poor. Van den Brink (1994) showed that highly connected lakes are characterized by vegetation-poor water with low species richness of macrophytes and invertebrates. Although the water quality of the Rhine has improved considerably since the studies of Van den Brink (1994), there is a general fear that many of these lakes will end as algae dominated, vegetation-poor water with a low ecological diversity.

In 1998, the Dutch Institute for Inland Water Management and Waste Water Treatment (RIZA) in cooperation with Wageningen University started the OER project, viz. **Onderzoek Ecologie Rivierplassen** (Research on Ecology of Floodplain lakes). The OER-project aimed at unraveling the dominant steering factors of ecosystem development in floodplain lakes along the Lower Rhine (Coops *et al.*, 2000). In a multidisciplinary approach, the importance of geomorphological conditions (lake morphometry, levee height), abiotic processes (groundwater-flow, flooding, nutrients), and biotic interactions (e.g. role of fish on phytoplankton) on ecosystem development in floodplain lakes was investigated. This information would help in designing of position and morphology of future water bodies in floodplains along the Lower Rhine.

Research questions

With respect to the dynamics of macrophyte communities in floodplain lakes along the Lower Rhine, two questions constitute the central theme in the present thesis:

- What are the factors determining macrophyte composition and succession in floodplain lakes along the Lower Rhine?
- How should position, morphology, and character of future water bodies in the Lower Rhine floodplains be designed?

The study focused on floodplain lakes along the Lower Rhine branches, which may be periodically flooded by the river, but are never permanently connected to the main channel. Floodplains along the river Meuse were not taken into account. The river Meuse and Lower Rhine differ in discharge regime, origin of water, and water quality, which makes it difficult to extrapolate the results.

Introduction to the chapters

Chapter 2 describes the relationship between variation in river water level and fluctuations in lake water-level through groundwater flow. In the same chapter, the relationship between water-level fluctuations and macrophyte species richness is explored. In *Chapter 3*, the observed successional sequence of submerged vegetation, nymphaeids and helophyte dominance in lakes is related to environmental variables regarding hydrological connectivity, lake morphometry, lake age and land use on adjacent land. In *Chapter 4*, the hypothesis is tested that the reduced amplitude of water-level fluctuations with lake age drives succession from desiccation-tolerant species in young lakes to desiccation-sensitive species in old lakes. In addition, the effect of stabilized water levels on macrophyte species richness in lakes along the Neder-Rijn is assessed. *Chapter 5* highlights the importance of short-term interannual variation in river water-level on macrophyte occurrence. In *Chapter 6*, the data of aquatic-vegetation inventories made over five decades in floodplain lakes along the Lower Rhine is related to incidence of

summer floods and drawdown events. In *Chapter 7*, the hypothesis is tested that drawdown stimulates the germination of *Chara* in subsequent growing season. In *Chapter 8*, the conclusions of this study are summarized. In addition, the most important findings are put in perspective to the results of other studies.

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Sampling of sediment composition in the lakes
Photo: John van Schie (RIZA)

Chapter 2

Water-level fluctuations affect macrophyte richness in floodplain lakes

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Abstract

The characteristic ecology of floodplain lakes is in part due to their relatively strong water-level fluctuations. We analyzed the factors determining water-level fluctuations in 100 floodplain lakes (during non-flooded conditions) in the active floodplains of the Lower Rhine in the Netherlands. Furthermore, we explored the relationship between water-level fluctuations and macrophyte species richness, and analyzed the suitability of artificially created lakes for macrophyte vegetation. During non-flooded conditions along the Rhine, lake water-level fluctuations are largely driven by groundwater connection to the river. Hence, water-level fluctuations are largest in lakes close to the main channel in strongly fluctuating sectors of the river and smallest in isolated lakes. Additionally, water-level fluctuations are usually small in old lakes, mainly due to reduced groundwater hydraulic conductivity resulting from accumulated clay and silt on the lake bottom. Species richness of floating-leaved and emergent macrophytes was reduced at both small and large water-level fluctuations, whereas species richness of submerged macrophytes was reduced at small water-level fluctuations only. In addition, species richness of submerged macrophytes was higher in lakes that experienced drawdown, whereas no similar pattern was detected for floating-leaved and emergent macrophytes. The decline in amplitude of lake water-level with lake age implies that the number of hydrological dynamic lakes will decrease over time. Therefore, we propose that along regulated rivers, excavation of new lakes is essential to conserve the successional sequence of floodplain water bodies including conditions of high biodiversity. Shallow, moderately isolated lakes, of which bottom is exposed occasionally, have the highest potential for creating macrophyte-rich floodplain lakes along large lowland rivers. The water-level regime of such lakes can in part be designed, through choice of the location along the river, the distance away from the river and the depth profile of the lake.

Introduction

Water bodies in floodplains are usually characterized by abundant and species-rich macrophyte vegetation (Bornette *et al.*, 1998; Coops *et al.*, 1999). Several studies stress the effects of timing and duration of flooding for macrophyte composition and succession in floodplain lakes (Van Geest *et al.*, 2003; Henry *et al.*, 1994; Bornette *et al.*, 1994; Bornette *et al.*, 1998; Van den Brink, 1994). However, far less attention has been paid to the effects of low river water levels on macrophyte composition and succession. Several studies have shown that temporary declines in water-level may enhance macrophyte abundance (e.g. Havens *et al.*, 2004). In large river floodplains, such declines are largely the result of natural fluctuations in river discharge. During low river water-levels, there is no surface connection between the main channel and lakes. Under these conditions, the impact of the river's water-level regime on lake water-levels depends on the conductivity of the soil to groundwater flow, called 'hydraulic conductivity' (Brunke & Gonser, 1997). During low river water-levels, infiltration of lake water into the alluvial aquifer may result in a decline of lake water-levels (Figure 1), until in certain cases the lake bottom becomes exposed (drawdown). The latter may have a strong effect on vegetation composition and succession (Wilcox & Meeker, 1991).

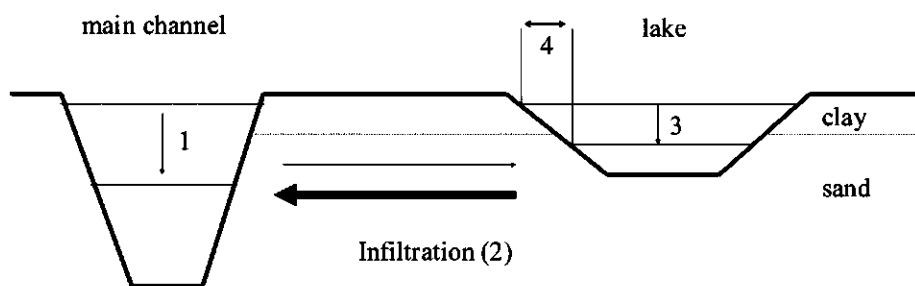


Figure 1. Pathways for groundwater flow between a floodplain lake and the main channel during non-flooded conditions. During low water levels in the river (1), infiltration of lake water to the river (2) will result in a decrease in the lake water-level (3), potentially resulting in sediment exposure (4) (drawdown).

Human interference has changed the water-level fluctuations in water bodies along many rivers. Along the Lower Rhine, major effects on the water-level regime were the result of embankment, normalization of the main channel, and regulation of the river discharge regime. Coinciding, a great loss of macrophytes has occurred, which has often been attributed to the effects of eutrophication (Blindow, 1992; Kowalczewski & Ozimek, 1993; Van den Brink, 1994), but may also be the result of hydrological alterations (Blindow *et al.*, 1993). Along the Lower Rhine, both extreme summer inundations (Brock *et al.*, 1987; Coops & Van Geest, in press) and stabilization of the river water-level during

low river discharge (Van Geest *et al.*, in press) have resulted in a reduced species richness of aquatic macrophytes.

One of the objectives of rehabilitation along regulated rivers is recovery of macrophyte-rich lakes. Especially when new water bodies are created or measures are taken that change the connectivity within the floodplain, understanding of the relationship between the river's water level regime and water-level fluctuations in floodplain lakes may help in the design of macrophyte-rich lakes.

In this paper, we evaluate how water-level fluctuations in 100 lakes along the Lower Rhine in the Netherlands are related to the water-level regime in the main channel (during non-flooded conditions) and variables affecting the hydraulic conductivity of the soil. Subsequently, we analyzed the relationship between water-level fluctuations and macrophyte species richness. Finally, we explored the suitability of artificial created lakes for macrophyte vegetation.

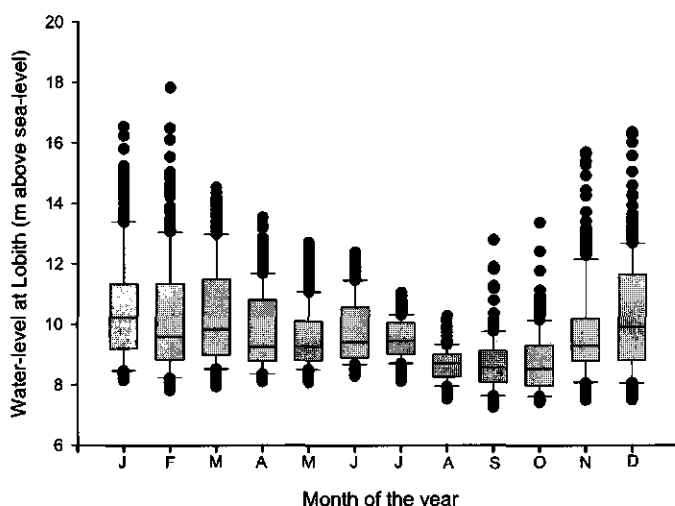


Figure 2. Monthly water-level of the Lower Rhine at Lobith in the period 1990 – 1999. Each box represents the average, and the 5, 25, 75, 95 percentile values. Dots indicate individual water-level measurements lower or higher than the 5 and 95 percentile value, respectively.

Study area

The Rhine, from its source in Switzerland to the outflow to the North Sea, is 1320 km long and has a catchment area of 185,000 km² (Lelek, 1989), of which 25,000 km² is situated in the Netherlands. Where the Rhine enters The Netherlands, the discharge varies roughly between 800 and 12,000 m³ s⁻¹, resulting in a difference between the minimum and maximum water level of up to 8 metres at Lobith (Figure 2) (Middelkoop, 1997). Typically, the highest river discharges occur during December – March and the lowest in August – October (Buijse *et al.*, 2002). After crossing the border of The Netherlands, the Lower Rhine splits into three branches, the Waal, IJssel, and Neder-Rijn. Due to the construction of major embankments, the active floodplain has been reduced to a narrow stripe of only a few kilometres wide. No weirs are present along the Waal and IJssel, whereas the lower water levels of the Neder-Rijn have become regulated after the construction of three weirs in the 1960's. All weirs are closed only below the mean river discharge of the Rhine (2,200 m³ s⁻¹). Hence, in the Neder-Rijn the construction of weirs did not result in changes in the flooding regime, whereas the natural water-level regime with occasional low river water levels has been replaced by an artificial distribution with higher minimum water levels than would be expected naturally. Consequently, water levels do rarely fall below a fixed level in the Neder-Rijn and the floodplain lakes alike. Indeed, lake drawdown was strongly reduced along the impounded Neder-Rijn, whereas drawdown occurred frequently in lakes along the unimpounded Waal and IJssel (Figure 3), especially in young lakes.

Table 1. Number of lakes, minimum, maximum, and 25, 50 and 75 percentile values of environmental variables

	N	min.	25%	50%	75%	max.
Decrease in water level lake (m)	100	-0.35	0.24	0.55	0.81	1.60
Decrease in water level river (m)	100	0.07	1.03	1.79	2.70	2.77
Distance lake – main channel (m)	100	10	80	225	528	1400
Mean lake depth (m)	100	0.13	0.66	0.99	1.42	5.16
Lake surface area (ha)	100	0.01	0.19	0.73	2.13	44.6
Inundation duration (d.y ⁻¹)	100	1	11	11	35	258
Lake age (y)	100	1	40	85	250	≥ 300

In 1999, a set of 100 floodplain lakes in the active floodplains along the Lower Rhine in The Netherlands was selected in such a way that they formed a representative cross-section of shallow lakes along the Lower Rhine, and covered a range in potentially important factors for hydrology and aquatic vegetation such as distance to the river, lake age, and inundation duration (Table 1). All lakes were characterized by periodic inundation by the river through surface overflow, yet none of the lakes were year-round connected to the river. The water-level regime of the Lower Rhine during July – October 1999 was typical for the water-level regime during these months over the last decade (Figure 2).

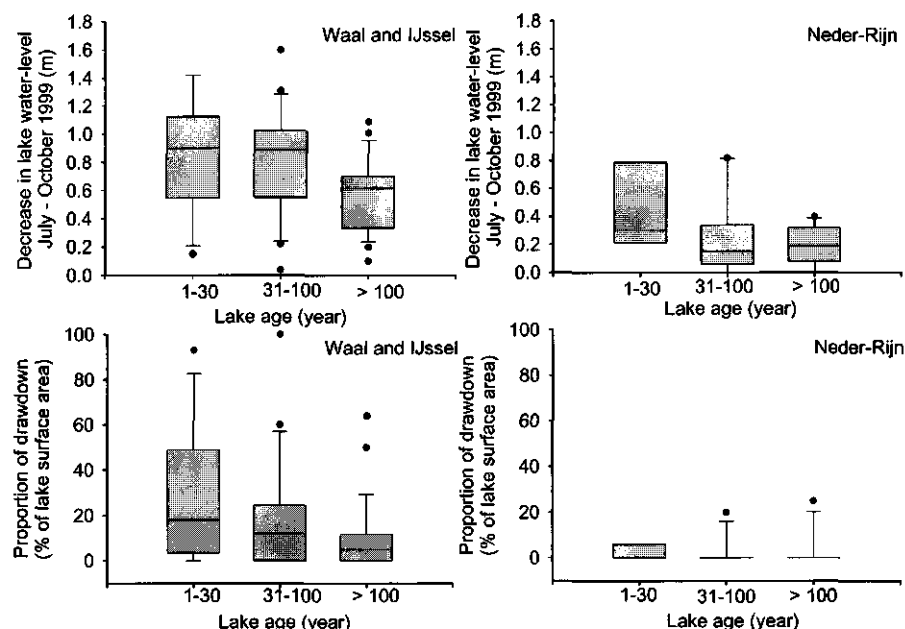


Figure 3. Decrease in lake water-level and drawdown area in relation to lake age along the unimpounded branches Waal and IJssel, and impounded branch Neder-Rijn. Each box represents the average, 5, 25, 75, and the 95 percentile values. Dots indicate individual water-level measurements lower or higher than the 5 and 95 percentile value, respectively.

Materials & methods

Daily Rhine water-level data, obtained from RIZA (Institute for Inland Water Management and Waste Water Treatment), were used to determine the maximum (R_{\max}) and minimum water level (R_{\min}) of the river in the interval 1 July – 31 October 1999. The difference in water level [$R_{\max} - R_{\min}$] at the location in the river corresponding to each lake was calculated using hydrological dependence lines for the three river branches. We measured water depth in cm at several locations in each lake in July 1999. The lake water level in July and October 1999 was measured from a marked rod placed in each lake. Based on these data, the difference in lake water level between July and October 1999 (WL_{J-O}) was calculated. The drawdown area is defined as the percentage of the surface area of the lake bottom in July that became exposed in October.

In all lakes, 2-10 sediment samples were investigated at several locations. The presence of sand and clay in the upper 0.5 m of each sample of the sediment was determined visually from each core. In the dataset, the presence or absence of sand and clay in the upper 10 cm was recorded. For all lakes, surface area, inundation duration and shortest distance

between the lake and the main channel were estimated using the River Information System (GIS data base of RIZA). Inundation duration is defined as the long-term (1900 – 1995) average number of days per year during which the floodplain lakes are connected to the main channel through surface connection. The approximate age of lakes was established using various historical topographical maps (Topografische Dienst, Emmen, The Netherlands). Reliable estimates of the age could be made for lakes ≤ 300 years old; lakes > 300 years were classified as 300 years old. Due to the lower availability of older maps, the uncertainty of the lake age estimation was ± 1 year for lakes < 20 y (1980), $\pm 3 - 7$ years for lakes aged 20 – 90 y (1980 – 1910), and $\pm 10 - 25$ years for lakes aged > 90 y (prior to 1910).

Macrophyte vegetation was sampled in July and early August 1999, coinciding with the period for optimal development of macrophyte vegetation. The area covered by each vegetation type proportional to the total area of the lake was determined by combining visual estimates and collection by rake from a boat. Species composition of submerged, floating-leaved, and helophyte vegetation of the whole lake area was surveyed intensively until no additional species were found in about ten minutes. The abundance of the species present were expressed on the Tansley-scale (rare, occasional, frequent, abundant, dominant), which for statistical analysis was converted to an ordinal scale ranging from 1 to 5, respectively. Furthermore, we gathered additional data for the years 1992 – 2003 regarding vegetation development in lakes that were excavated in recent rehabilitation projects (referred to as rehabilitation lakes; $N = 6$). All rehabilitation lakes were < 10 years in 1999.

We used multiple stepwise linear regression analysis (Jongman *et al.*, 1995) to evaluate the relationship between WL_{I-O} and seven abiotic variables (Table 2). Inundation duration, lake age, mean lake depth, and surface area were $\ln(x)$ transformed to meet assumptions for multiple linear regression. Both forward and backward stepwise regressions were carried out to check for model stability, using statistical package SPSS version 7.5 (Norusis, 1997). Variables were excluded from the model if they were correlated to other independent variables that were included in the model. In such cases, we performed alternative analyses to check if the excluded variable could contribute significantly to the model when its correlated variable was removed. Data regarding species richness of macrophytes were first checked for homoscedasticity and normality, and subsequently tested by means of a t-test, or one-way analysis of variance (ANOVA) followed by post-hoc comparison (Tukey HSD).

Table 2. Seven independent variables used in multiple stepwise linear regression analyses to predict the decrease in water level in the floodplain lakes between July and October 1999; ^a = ln(x)-transformed

Variable	Unit	Comments
Decrease in water level river	m	the difference between the maximum water level in the main channel in July and the minimum water level in July, 1 st – October, 31 st 1999
Shortest distance between lake and main channel	m	
Mean lake depth ^a	m	calculated from 5 – 31 measurements in each lake
Inundation duration ^a	d.y ⁻¹	long term average 1900–1995
Surface area ^a	ha	surface area of lake at start of growing season
Lake age ^a	y	for accuracy: see Methods
Sand		presence or absence of sand in the upper 10 cm of lake sediment

Table 3. Results of forward stepwise regression analysis for decrease in water level in floodplain lakes between July and October 1999 ($R^2_{adj.} = 0.62$; Std. Error of the Estimate = 0.25). Backward stepwise regression analysis gave similar results. ^a = ln(x)-transformed. Note that the decrease in lake water-levels is sensitive to the duration of the period that the river water-level is lower than the water level in lakes. Therefore, the formula presented in this table is only valid for water-level regimes of the river that are comparable to the period July – October 1999. In years with different duration of low river water-levels, a stepwise regression analysis between WL_{J-O} and abiotic variables listed in Table 2 may yield different results.

Variable	Unstandardized Coefficient \pm S.E.	P	Standardized Coefficient
Water-level river	0.319 \pm 0.033	<0.0001	0.697
Distance lake-river	-3.82.10 ⁻⁴ \pm 0.000	<0.0001	-0.259
Lake depth ^a	0.157 \pm 0.049	<0.01	0.242
Lake age ^a	-4.70.10 ⁻² \pm 0.016	<0.01	-0.189
Lake surface area ^a	-3.47.10 ⁻² \pm 0.017	<0.05	-0.144
Constant	0.273 \pm 0.090	<0.01	

Results

The lakes sampled in the Lower Rhine floodplains varied in distance to the main channel (10 – 1400 m), mean depth (0.13 – 5.16 m), surface area (0.01 – 45 ha), age ($1 - \geq 300$ y) (Table 1), while lake sediments consisted mainly of clay and sand (present in 91 and 42% of the lakes, respectively); gravel was almost absent. Four lakes along the impounded Neder-Rijn showed some increase in water level between July and October 1999; in the remaining 96 lakes the water level declined (up to 1.60 m difference) over this period.

The decline in lake water-level was positively related to differences in water-level in the main channel and mean lake depth, and negatively related to lake age, distance to the main channel, and surface area of the lakes ($R^2_{\text{adj.}} = 0.62$, Table 3, Figure 3). The relationship with lake age and depth could be caused by the sediment composition of the lakes, as lakes with sandy sediments were significantly younger (t-test; $p < 0.01$) and deeper (t-test; $p < 0.05$). Indeed, when the variables 'mean lake depth' and 'lake age' were excluded from the analysis, the decline of the water-level in the lakes during the growing season was positively related to differences in water level in the main channel and presence of sand, and negatively related to the distance to the main channel ($R^2_{\text{adj.}} = 0.58$; results not shown).

The species richness of submerged macrophytes and helophytes, as well as total number of macrophyte species, was significantly related to the amplitude of water-level fluctuations (ANOVA, $p = 0.008$, 0.0139, and 0.013, respectively, $F_6 = 2.89$, 3.11, and 2.85, respectively). For submerged macrophytes and total number of macrophytes, species richness was lower at fluctuations within the range ≤ 0.2 m compared to 0.4 – 0.6 m (in both cases $p < 0.05$; Tukey HSD; Figure 4). For helophytes, species richness was significantly higher at fluctuations of 0.4 – 0.6 m compared to 1.0 – 1.2 m ($p < 0.05$, Tukey HSD, Figure 4). For floating-leaved macrophytes, no significant pattern between species richness and amplitude of water-level fluctuations was detected (ANOVA; $p = 0.051$), although there was a trend for increased species richness at 0.4 – 0.6 m (Figure 4). In addition, lakes with partial drawdown exhibited a significant higher species richness of submerged macrophytes compared to lakes with no drawdown (t-test; $p = 0.006$; Figure 5). By contrast, drawdown was not significantly related to species richness of floating-leaved macrophytes, and helophytes (t-test; $p = 0.88$ and 0.37, respectively; Figure 5).

Rehabilitation lakes were readily colonized by various submerged macrophytes in the years after excavation. In the first four years, species such as *Chara vulgaris*, *Potamogeton pusillus*, and *Elodea nuttallii* dominated these lakes. Remarkably, after this first stage of submerged macrophyte dominance, all rehabilitation lakes lost their aquatic vegetation within a few years (Table 4).

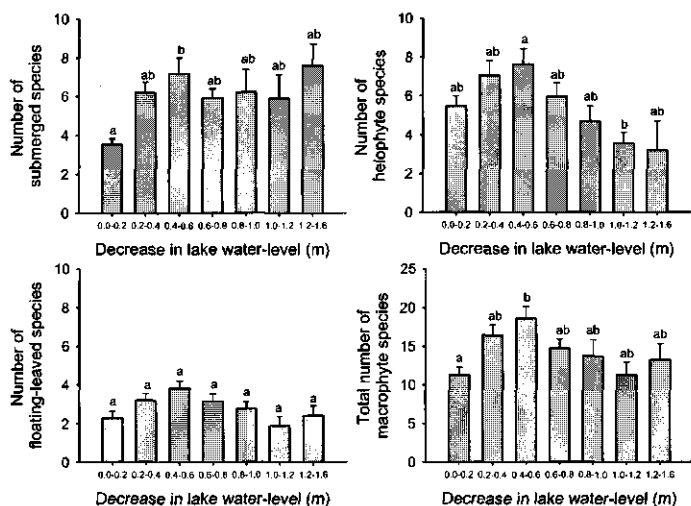


Figure 4. Frequency distribution of species richness of submerged, floating-leaved, helophytes and total number of macrophytes in lakes (\pm standard error) in relation to decline in lake water-level between July – October 1999. Data for lakes along the impounded Neder-Rijn with an increase in water-level during July – October 1999 ($n=4$) were excluded. Significant differences are indicated with different letters (post-hoc comparison with Tukey HSD test, $p < 0.05$).

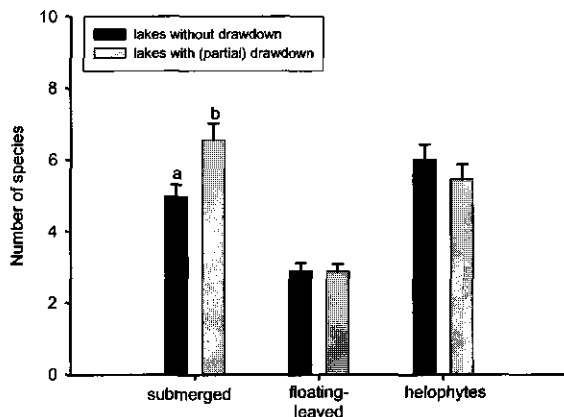


Figure 5. Frequency distribution of species richness of submerged, floating-leaved, and helophyte macrophytes in lakes (\pm standard error) with and without drawdown (n lakes = 48 and 49, respectively). Data for lakes along the impounded Neder-Rijn with an increase in water-level during July – October 1999 ($n=4$) were excluded. Significant differences are indicated for submerged macrophytes; for floating-leaved macrophytes and helophytes, no significant differences were detected.

Table 4. Vegetation development in rehabilitation lakes in the first year after excavation. Nymphaeids were absent in all years. Data based on own results, Coops *et al.* (1993) and Lauwaars *et al.* (1997). “?” = not measured.

Floodplain/year of excavation	Year	Submerged veg. cover	Number of species
Afferden-Deest (1998)	1998	10	6
	1999	< 1	2
	2000	34	3
	2001	14	5
	2002	< 1	?
	2003	< 1	?
Blauwe Kamer (1992)	1993	≥ 50	10
	1994	15	3
	1995	≥ 50	9
	1999	42	8
	2000	8	7
	2001	< 1	7
	2002	< 1	4
	2003	< 1	?
Duurse Waarden (1989)	1989	≥ 50	3
	1993	≥ 50	4
	1999	< 1	4
Koppelerwaard (1996)	1999	100	6
	2000	67	4
	2001	< 1	4
	2002	< 1	?
	2003	< 1	?
Lent (1997)	1998	≥ 50	?
	1999	10	4
	2000	< 1	?
	2001	< 1	?
	2002	< 1	?
	2003	30	?
Wageningen (1998)	1998	≥ 50	?
	1999	60	4
	2000	23	?
	2001	7	?
	2002	10	?
	2003	< 1	?

Discussion

Our results indicate that the amplitude of water-level fluctuations during non-flooded conditions strongly depends on the water-level regime in the main channel, and variables related to the hydraulic conductivity of the soil. Generally, hydraulic conductivity (and hence amplitude of lake water-levels) decreases with increasing distance to the main channel. Furthermore, coarse-textured soils (e.g. sand) have a much higher hydraulic conductivity to groundwater flow, and will support a higher groundwater exchange between the lake and the main channel compared to fine-textured soils (e.g. clay, silt) (Wood & Armitage, 1997). Therefore, shallow lakes that are totally embedded in the clayey top layers of floodplains will show relative small water-level fluctuations during low river stage. By contrast, deeper lakes in general often contact the sandy subsoil, implying a rather unrestricted groundwater contact to the river, which results in larger water-level fluctuations. With increasing lake age, organic matter and fine deposited materials accumulate in the lake sediment. This results in a decreased hydraulic conductivity of the lake bottom, which explains the decrease in water-level fluctuations with lake age (Table 3). In highly dynamic rivers, fine lake sediments may be removed by scouring floods (Henry *et al.*, 1994). However, because such floods are absent along the Lower Rhine (Middelkoop, 1997), temporary removal of lake sediment through scouring is prevented. The negative relationship between decline in lake water-level and surface area is somewhat unexpected and may have been caused by the fact that in large lakes, water levels are to some extent regulated by sluices or other artificial structures.

The amplitude of water-level fluctuations may strongly determine the development of macrophytes in floodplain lakes. In lakes with small water-level fluctuations, drawdown may not occur. Drawdown strongly affects macrophyte composition, because drawdown is a prerequisite for successful germination and survival of various macrophytes (Bonis & Grillas, 2002; Coops & Van der Velde, 1995; Keddy & Constabel, 1986; Smits *et al.*, 1989). In addition, disturbances caused by drawdown may prevent competitive dominance, thereby increasing species richness (Hill *et al.*, 1998). Consequently, species richness of macrophytes is enhanced by increasing amplitude of water-level fluctuations. However, large water-level fluctuations may eliminate species that are sensitive to prolonged submersion, such as certain helophyte species (Brock *et al.*, 1987). Furthermore, increasing water-level fluctuations may result in complete lake drawdown, thereby eliminating desiccation-sensitive species that were otherwise able to survive in deeper lake parts. Consequently, species richness of macrophytes tended to peak at intermediate amplitude of water-level fluctuations in our dataset (Figure 4). Also for cut-off channels along the river Doubs in France, macrophyte species was positively related to the occurrence of drawdown (Bornette *et al.*, 2001).

The decrease in water-level fluctuations with lake age may be a major determinant of aquatic vegetation succession, as macrophyte dominance shifts from desiccation-tolerant species in young lakes to desiccation-sensitive species in old lakes (Van Geest *et al.*, in press). *Chara* spp., the dominant species in young lakes with regular drawdown along the Lower Rhine, is a highly desiccation-tolerant species since their oospores may survive long periods of complete dried-out conditions (Proctor, 1967). After submersion of the sediment, *Chara* spp. may rapidly germinate from seed banks and become dominant in lakes (Bonis *et al.*, 1995). For *Nuphar lutea*, in contrast, several years without drawdown are needed to allow establishment in lakes, due to the high vulnerability of both seeds and juvenile plants to desiccation (Smits *et al.*, 1989).

The decline in amplitude of lake water-level with lake age implies that the number of hydrologically dynamic lakes will decrease over time. Moreover, on the long term all floodplain lakes will disappear due to siltation and terrestrialization processes. Our results indicate that a decrease in the number of hydrological dynamic lakes may have considerable consequences for species richness of aquatic water bodies in floodplains. This would imply that – where possible – erosive processes in the floodplain must be allowed, which may create new lakes or remove fine lake sediments. As such processes are not likely to re-appear, sediment removal in existing lakes or excavation of new lakes is essential to conserve the successional sequence of floodplain water bodies including conditions of high biodiversity.

In our floodplains, many of the recently excavated rehabilitation lakes were rapidly colonized by submerged species such as *Chara vulgaris*, *Potamogeton pusillus* or *Elodea nuttallii*. Remarkably, almost all rehabilitation lakes lost their submerged macrophytes in recent years. Coinciding, a strong decline in the number of submerged species occurred in these lakes, as cover and species richness of submerged macrophytes were significantly correlated in our dataset (Spearman $r = 0.33$; $p < 0.001$). The loss of submerged macrophytes in the rehabilitation lakes may be caused by the drawdown regime of these lakes. For lakes along the Lower Rhine, submerged macrophyte cover is strongly stimulated by drawdown events in previous years (Coops & Van Geest, in press; Van Geest, unpublished data). For rehabilitation lakes, the year of excavation can be regarded as a 'drawdown' year, because entering groundwater is pumped out during the process of digging. Consequently, lake sediments become exposed, which may stimulate conditions for submerged macrophyte growth after subsequent filling (Giles, 1987). The subsequent loss of submerged macrophytes may be caused by the absence of lake drawdown in recent years (Coops & Van Geest, in press). Along the Lower Rhine, the number of lakes with drawdown may vary strongly from one year to another, because of large inter-annual variation in river water-level (Coops & Van Geest, in press). Indeed, for a set of 70 lakes along the Lower Rhine, the occurrence of lake drawdown was strongly reduced during

years after 1998, and coincided with a strong decrease in the number of lakes dominated by submerged vegetation (Chapter 5). Therefore, we expect that along the Lower Rhine, only rehabilitation lakes that have regularly exposed sediments will have high cover values and species richness of submerged macrophytes.

In the floodplains along the Lower Rhine in The Netherlands, numerous water bodies will be excavated over the coming decades in a campaign aimed at enhancing the water discharge capacity as well as for ecological rehabilitation (Smits *et al.*, 2000; Duel *et al.*, 2001). This program provides many opportunities for ecological rehabilitation. Understanding the optimal water-level regime of new water bodies from the point of view of ecological values implies that an effective design of such water bodies may be chosen. Particularly relevant factors in the design appeared to be the location along the river, distance to the main channel, depth profile and bottom sediment type and their inter-relationships with water-level fluctuations. Obviously, there is little hope of restoring fluctuating water levels in lakes along impounded branches. When lakes are excavated along river stretches with highly stabilized water levels during low river discharge, the lake-water level will remain stable regardless of their distance to the river, depth or age.

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Chapter 3

Vegetation abundance in lowland floodplain lakes determined by surface area, age and connectivity

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Abstract

We analysed the vegetation structure of 215 lakes in the floodplain of the lower river Rhine in relation to environmental variables related to hydrological connectivity, lake morphometry, lake age and land use on adjacent land. The frequency distribution of the cover of submerged macrophytes was not normal, implying that submerged macrophytes in any one lake were either scarce or abundant. Clear water lakes with dominance of submerged macrophytes occurred over a wide range of total P concentration (0.020 to 0.40 mg total P L⁻¹). Multiple logistic regression indicated that the probability of dominance by submerged macrophytes decreased markedly with the surface area, depth and age of the lakes. The surface area effect occurred independently of the depth. Further, there was a negative relationship between submerged macrophyte dominance and the long-term annual duration of inundation by the river. Nymphaeid cover showed a distinct optimum with respect to mean lake depth, being almost absent in lakes shallower than 0.5 m. In contrast to what was found for submerged plants, the probability of occurrence of nymphaeids increased with lake age. The probability of helophyte occurrence increased with lake age, and decreased with the presence of trees, cattle grazing, surface area, use of manure and mean lake depth. In all cases the critical level of one factor (e.g. mean lake depth) depended on other factors (e.g. surface area or age of lake). Thus, in the present study, small lakes tended to remain dominated by submerged macrophytes up to a greater depth than large lakes, and helophytes colonised smaller lakes in an earlier phase. The effect of inundation by the river was modest. This could be because most of our lakes are rarely inundated during the growing season and experience only moderate current velocities while flooded. The results have practical implications for future management of floodplains for conservation purposes. In new water bodies, macrophyte domination will be promoted if many small shallow lakes, rather than few large deep ones, are excavated.

Introduction

In recent years interest has grown in restoring floodplain function by reconnecting the floodplain with the main channel of regulated rivers. However, scientific insight into the effects of such increased 'connectivity' on the ecology of formerly isolated floodplain lakes is still poor. Previous work on the composition and succession of aquatic vegetation in floodplain water bodies predominantly stresses the role of river-related hydrological dynamics as the major driving force for vegetation abundance and composition (Junk, Bayley & Sparks, 1989; Van den Brink *et al.*, 1991; Amoros & Bornette, 1999). However, various other abiotic variables may strongly influence the aquatic vegetation. The age of lakes, surrounding land use and seepage from hill slope aquifers have been found to affect the successional stage and nutrient content of the water along the River Rhône (Bornette, Amoros & Lamouroux, 1998). Geomorphological conditions have been addressed as an important factor determining the impact of inundations. The erosive power of the overflowing water is high in straight, formerly-braided channels, resulting in sediment scouring and macrophyte removal. This creates recruitment opportunities for new plant individuals. In contrast, oxbow lakes with high sinuosity experience only moderate erosive forces, resulting in a very soft substratum of organic matter, which impedes recruitment of new individuals (Henry, Amoros & Bornette, 1996).

Research on macrophytes other than in floodplains has a long history and addresses a much broader range of environmental factors. Many studies stress the importance of water depth and transparency (Canfield *et al.*, 1985; Chambers & Kalff, 1985a; Skubinna, Coon & Batterson, 1995), but also the effects of slope (Duarte & Kalff, 1986a), wave action (Strand & Weisner, 1996), bird grazing (Lauridsen, Jeppesen & Andersen, 1993), periphyton (Weisner, Strand & Sandsten, 1997), and sediment characteristics (Chambers & Kalff, 1985b) have been shown to be important in many lakes. It has also become clear over the past decade that submerged macrophytes play a key role in the regulation of ecosystem processes, particularly in shallow lakes (Jeppesen, Søndergaard & Christoffersen, 1997). This insight has sparked extensive recent work on the dynamics of vegetation in a wide range of shallow lakes (Scheffer, 1998). In these studies however, the role of fluctuations in water level is hardly addressed.

The objective of the present study is to unravel the combined effects of hydrological dynamics, lake morphometry, lake age and land use on macrophyte occurrence in a large set of shallow floodplain lakes along the Lower Rhine.

Methods

The aquatic vegetation of a total of 215 shallow lakes was sampled in the Lower Rhine floodplains in the Netherlands in 1999 (100) and 2000 (115), including 93 lakes in which the plankton and water quality were analysed in parallel (Roozen *et al.*, 2003). All lakes were characterised by periodic inundation by the river via surface overflow, yet none of the lakes were permanently connected to the river during the growing season. Lakes were selected *a priori* so that they covered the natural range in potentially important factors such as inundation duration, surface area, lake age, decrease in water level during the growing season, distance to the main channel, and land use on the adjacent land.

Sampling of vegetation

In July and August 1999, submerged and floating vegetation was sampled in 917 quadrats distributed over 100 of the 215 water bodies. Each sample was taken in a quadrat containing a homogeneous vegetation type. The surface area of the quadrats varied from 1 m² for submersed vegetation up to 4 m² for nymphaeids. In each lake, the number of quadrats located in submerged and nymphaeid vegetation and areas poor in vegetation was chosen in proportion to the estimated area occupied by these types. The number of quadrats per lake varied between 4 and 31, depending on the complexity of the vegetation structure and surface area of the lake. Submerged plants were collected using a rake. The percentage cover projected on the bottom was visually estimated for each species using a seven-point scale (< 1%, 1-5%; 6-15%, 16-25%; 26-50%; 51-75%, 76-100%). In each quadrat, the total percentage cover of submerged plants, floating plants, helophytes and filamentous algae was estimated. The surface area covered by submerged and nymphaeid vegetation and the percentage of vegetation-poor area in the whole lake was calculated based on cover percentages and transformed to the lake surface area. Additionally, the cover of large emergent species (helophytes such as *Typha* and *Phragmites*) was estimated separately as a percentage of the surface area of the lake in July. In July and August 2000 the remaining 115 lakes were studied following an almost identical procedure. However, the smallest lakes were now surveyed by wading rather than by boat. In the small lakes no quadrats were sampled, but the total cover of different vegetation types and unvegetated areas was visually estimated.

Abiotic variables

Table 1 gives an overview of the abiotic variables measured and their ranges, the number of lakes sampled and year of sampling. For all lakes, estimates of inundation duration, surface area, and shoreline length were obtained from GIS-maps (RIZA, Arnhem, The Netherlands). Inundation duration is defined as the long term (1900 – 1995) average number of days per year during which the floodplain lakes were connected with the main channel. The relative shoreline length was calculated by the ratio of shoreline length to surface area. The drawdown area was estimated visually in the field and is defined as the percentage of the surface area of the lake bottom in July which became exposed in

October. The approximate age of lakes was derived from historic topographical maps. Reliable estimates of the age of the lakes could be made up to 300 years; older lakes were classified being 300 years. The uncertainty of the lake age estimation was about one year for lakes with an age between 1 – 20 years, 3 - 7 years for lakes with an age between 20 – 90 years, and 10 - 25 years for lakes older than 90 years. During the fieldwork the prevailing land use in the adjacent floodplain (presence of trees, cattle access, use of manure) was recorded. For these variables the following categories were used: presence of trees: (0, shoreline length for < 25% covered by trees; 0.5, shoreline covered for 25 – 75% by trees; 1, shoreline covered > 75% by trees); cattle grazing: (0, cattle access to 0 – 25% of perimeter; 0.5, 25 – 75% of perimeter; 1, > 75% of perimeter; use of manure: (0, no manuring of adjacent land; 0.5, > 0 – 50% of adjacent land; 1, 51-100% of adjacent land).

Table 1. Number of lakes, minimum, maximum and 25, 50 and 75 percentile values of environmental variables; a): only sampled in 1999; other variables were determined in both 1999 and 2000

	N lakes	min.	25%	50%	75%	max.
Inundation duration (d.y ⁻¹)	215	1	11	11	35	258
Drawdown area (%)	215	0	0	0	10	100
Water level drop May – Oct (m) ^{a)}	99	0.10	0.49	0.94	1.35	2.30
Surface area (ha)	215	0.01	0.19	0.73	2.13	44.6
Mean lake depth (m)	215	0.13	0.66	0.99	1.42	5.16
Relative shoreline length (m ⁻¹)	215	146	440	726	1208	11905
Age (y)	215	1	40	85	250	300
Presence of clay ^{a)}	99	0.0	1.0	1.0	1.0	1.0
Presence of sand ^{a)}	99	0.0	0.0	0.0	1.0	1.0
Presence of trees	215	0.0	0.0	0.0	0.5	1.0
Use of manure	215	0.0	0.0	0.5	1.0	1.0
Cattle grazing	215	0.0	0.0	0.5	1.0	1.0
Total N (mg L ⁻¹)	94	0.48	0.93	1.12	1.46	3.63
Total P (mg L ⁻¹)	94	0.02	0.12	0.18	0.24	1.27

For the 100 floodplain lakes sampled in 1999, the texture of the upper 0 – 0.5 m (in some cases extended to 1.0 m) of the sediment was visually determined from a core. In most lakes, two to ten sediment cores were taken: at least one in the centre and one on the shoreline. In the dataset the presence of sand and clay in the upper 10 cm of the cores was documented for each lake. From the other 115 lakes sampled in 2000, no data for sediment composition were obtained. For 93 of the 100 floodplain lakes sampled in 1999, samples for total N and total P in the water phase were taken according to Roozen *et al.* (2003).

For the 100 floodplain lakes sampled in 1999, water depth was measured at several (5 - 31) locations in each lake. To obtain an estimate of the decline in water level in these

lakes during the growing season, additional measurements were made in July, August and October 1999. Based on these data, mean lake depth in July and drawdown area of the lakes at the end of the growing season, when the lowest level occurred (October), was calculated. In the additional 115 lakes, the area of the lake bottom exposed was estimated visually in October 2000. A rough estimate of the water level in May was obtained from the vegetation zonation on the shoreline.

Data analysis

The percentage cover of submerged, floating-leaved and helophyte vegetation relative to the total water surface area in July was used in the analyses for each lake. The nymphaeids were the only floating-leaved plants included in the analysis, because non-rooted floating-leaved species like *Hydrocharis morsus-ranae* L. were very rare and lemniids dominated only at the end of the growing season (i.e. after the sampling period) in a few lakes. Filamentous algae were also rare and were therefore excluded from the analysis. We checked for normality of distribution of the cover-values of the vegetation growth forms by means of the Kolmogorov-Smirnov test.

Correlations among abiotic and biotic variables were determined using a Spearman rank correlation test. Because abundance of vegetation growth forms tended to fall into two distinct classes (abundant or rare/absent, see Results), we used multiple logistic regression (Jongman *et al.*, 1995) to evaluate the relationship between the probability of being abundant for different vegetation growth forms and abiotic environmental variables. The general expression for this probability is:

$$P(x) = \frac{\exp(b_0 + b_1x_1 + b_2x_2)}{1 + \exp(b_0 + b_1x_1 + b_2x_2)}$$

where b_0 , b_1 , and b_2 are regression coefficients. The parameters were estimated by means of the maximum-likelihood principle. Eight independent variables were used in the multiple logistic regression analysis (Table 2). Inundation duration, drawdown area, surface area, mean lake depth and lake age were $\ln(x+1)$ -transformed. For each analysis both forward and backward multiple logistic regressions were done. Further, in cases where independent variables were excluded from the model, but were correlated to other independent variables that were included, we performed alternative analyses to check if the excluded variable could contribute significantly to the model if its correlated 'competitor' was removed. We also checked if the year of sampling influenced the results by including this variable in the multiple logistic regression analysis.

Table 2. Eight independent variables used in multiple logistic regression analysis to predict submerged vegetation dominance, and nymphaeid and helophyte occurrence; ^a = $\ln(x+1)$ -transformed

Variable	unit	comments
Inundation duration ^a	d.y ⁻¹	long term average 1900 – 1995
Drawdown area ^a	%	% of lake surface area in October that has been drawn down compared to the surface area in July
Lake surface area ^a	ha	surface area of lake at start of growing season
Mean lake depth ^a	m	calculated from 5 – 31 measurements in each lake
Age ^a	y	for accuracy: see Methods
Use of manure	categories	see Methods
Presence of trees	categories	see Methods
Cattle grazing	categories	see Methods

Results

The lakes varied widely in inundation duration (< 2 up to > 150 days y⁻¹), surface area (0.01 – 45 ha), mean depth (0.13 – 5.16 m), age (1 up to ≥ 300 years), and concentrations of total N (0.48 – 3.6 mg L⁻¹) and total P (0.024 – 1.3 mg L⁻¹) (Table 1). Submerged macrophyte cover was negatively correlated with mean lake depth, surface area, inundation duration and lake age and positively with relative shoreline length and drawdown area (Table 3). Nymphaeid cover was positively correlated with lake age (Table 3, Fig. 1), showed an optimum at 0.5 to 1.0 m with respect to mean lake depth (Fig. 3), and was negatively correlated with the occurrence of sandy bottoms (Table 3). Helophyte cover was negatively correlated with the decline in water level through the growing season, mean lake depth, surface area and, positively, with lake age (Fig. 1) and relative shoreline length (Table 3).

Many variables in the dataset were correlated (Table 3). Such multi-collinearity occurred among morphometric variables like mean lake depth, surface area and relative shoreline length, as well as indicators of abundance of submerged macrophytes, nymphaeids and helophytes. Therefore, the correlations with macrophyte abundance cannot be evaluated straightforwardly. After arc-sin transformation of the percentage cover of the three growth forms, all of them still deviated significantly from a normal distribution ($p < 0.001$). Indeed, there was a tendency for each of these three groups to be either rare or abundant in a lake. The frequency distribution of the cover of submerged macrophytes in the lakes was particularly bimodal (Fig. 2). In view of this we categorised lakes into rich or poor for submerged macrophyte, nymphaeid and helophyte cover, and used multiple logistic regression for further analysis. For both nymphaeids and helophytes the cut level for

Table 3. Spearman rank correlations among macrophyte cover and abiotic variables in 215 floodplain lakes along the river Rhine

	Cover submersed (%)	Cover nymph. (%)	Cover Heloph. (%)	Extinction (1/m)	Inundation duration (day y ⁻¹)	Drop in water-level May-Oct (m)	Draw down area (%)	Mean lake depth (m)	Surface area (ha)	Rel. shoreline length (m ⁻¹)	Age (y)	Pres. sand	Pres. clay	Pres. trees	Cattle grazing
Cover nymphacids	-0.027														
Cover helophytes	0.320**	0.297**													
Extinction ^b	-0.409**	0.069	0.096												
Inundation duration	-0.161*	0.119	-0.023	0.388**											
Drop in water-level May-Oct ^c	-0.231*	-0.094	-0.335**	-0.197	0.009										
Drawdown area ^a	0.176**	0.020	0.051	-0.239*	0.074	0.525**									
Mean lake depth ^a	-0.446**	0.066	-0.329**	-0.124	-0.017	0.392**	-0.217**								
Surface area ^a	-0.460**	0.036	-0.319**	-0.107	-0.169*	0.276**	-0.112	0.536**							
Rel. shoreline length ^a	0.401**	0.012	0.326**	0.184	0.195**	-0.268**	0.041	-0.517**	-0.904**						
Age ^a	-0.158*	0.427**	0.349**	0.451**	0.223**	-0.298**	0.072	0.278**	-0.103	0.205**					
Presence sand ^c	-0.150	-0.294**	-0.230*	-0.076	0.005	0.263**	-0.092	-0.127	0.324**	-0.273**	-0.405**				
Presence clay ^c	-0.101	0.212*	0.190	0.178	0.237*	-0.092	-0.081	-0.127	-0.020	-0.011	0.350**	-0.226*			
Presence trees	-0.183**	-0.116	-0.125	-0.173	0.056	0.077	0.020	0.123	0.157*	-0.153*	-0.124	-0.121	0.077		
Cattle grazing	0.036	0.054	-0.093	0.199	0.239**	-0.030	0.150*	-0.106	-0.069	0.049	0.207**	0.104	0.138	-0.273**	
Use of manure	0.004	0.049	-0.010	0.134	0.157*	0.067	0.090	-0.010	-0.173**	0.125	0.280**	-0.102	0.199*	-0.170*	0.304**

* $P < 0.05$; ** $P < 0.01$; ^a $\ln(x+1)$ -transformed values; ^bsampled in 71 lakes; ^csampled in 99 lakes

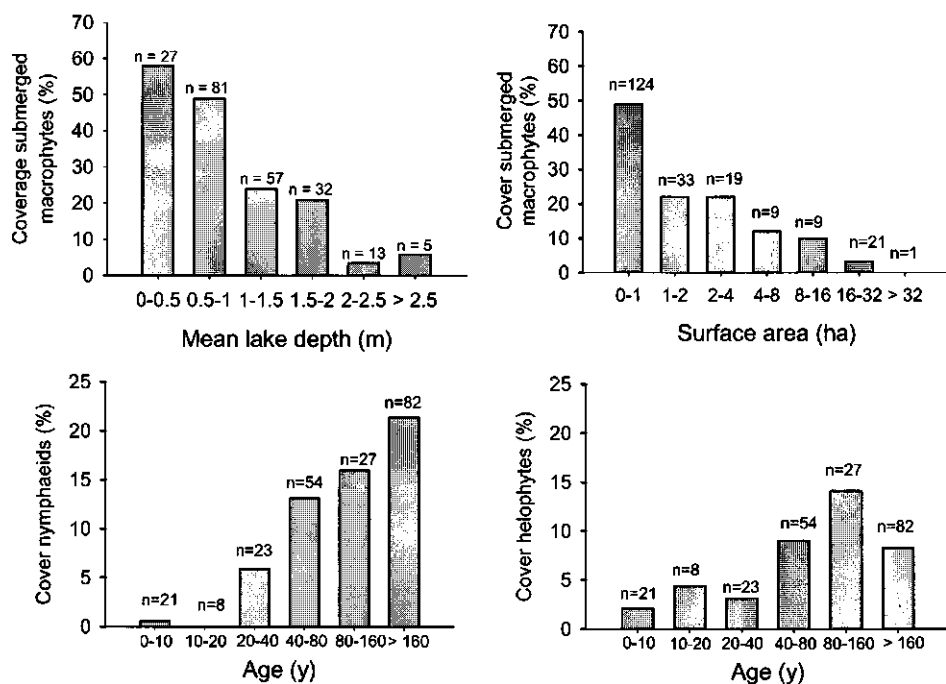


Figure 1. Cover of submerged macrophytes, nymphaeids and helophytes in relation to age, mean depth and surface area of the lakes

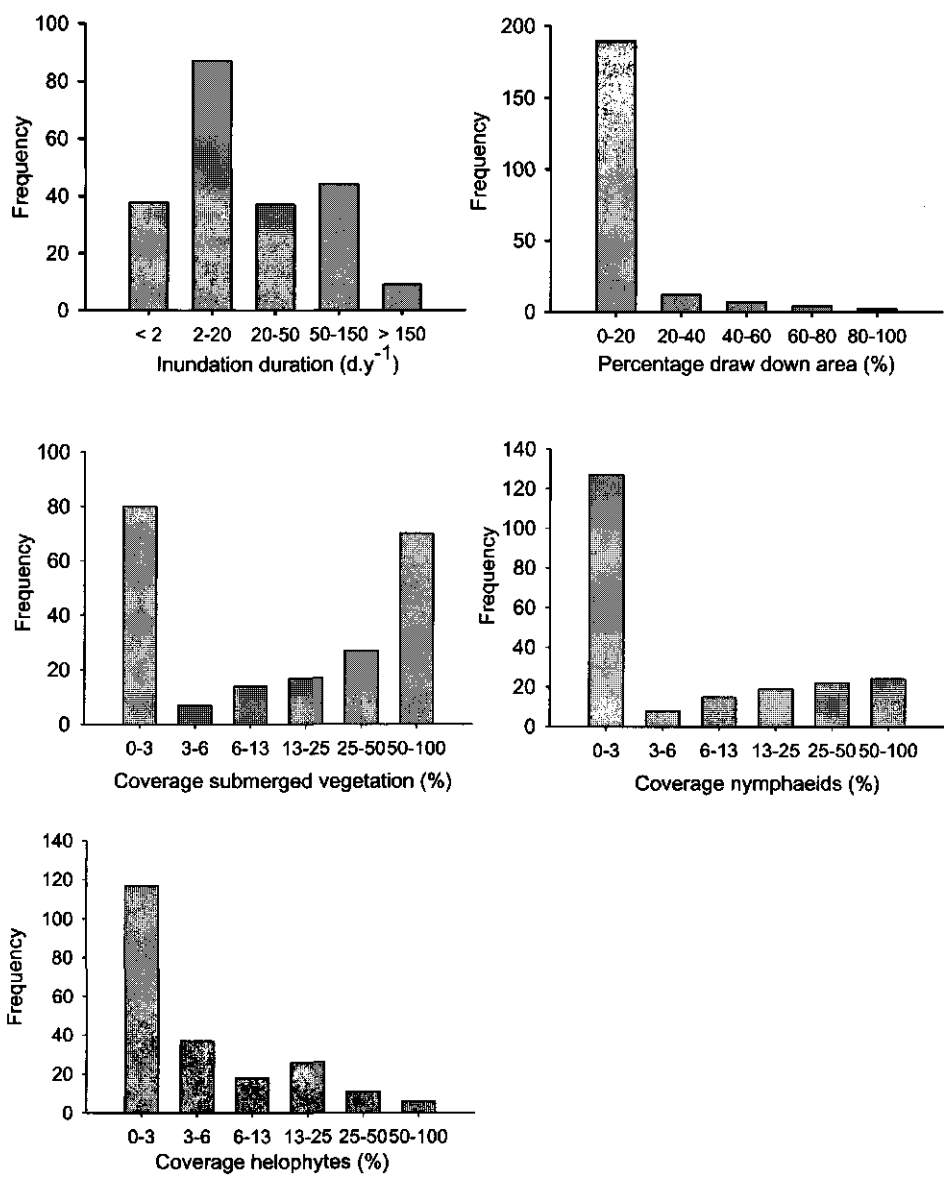


Figure 2. Frequency distributions of the cover of submerged macrophytes, nymphaeids and helophytes, and the percentage drawdown area and inundation duration. Total number of lakes in survey = 215

separating vegetation cover into two classes was taken at 1%. Based on the shape of the curve for submerged macrophytes (Fig. 2), the data were analysed for cut levels of, respectively, 20, 30, 40 and 50%.

We used multiple logistic regression to analyse the combined effect of independent variables on the probability of dominance of submerged macrophytes, and the occurrence of nymphaeids or helophytes. First, we used the abiotic variables listed in Table 2 together with Secchi-depth as explanatory variables. In these analyses a) the probability of dominance by submerged macrophytes was positively related to Secchi-depth and negatively related to mean lake depth, b) the probability of nymphaeid occurrence was positively related to Secchi-depth and lake age, and c) the probability of helophyte occurrence was positively related to lake age and Secchi-depth, and negatively related to mean lake depth and the presence of trees (Table 4). However, because water transparency might be rather the effect than the cause of aquatic vegetation abundance during the sampling period of our lakes (see Discussion), we kept the variable 'Secchi-depth' out of further logistic regression analyses. During subsequent logistic regression analyses, only the abiotic variables listed in Table 2 were included. In all cases backward and forward multiple logistic regression gave similar results. For each group the results of backward analysis are presented in Table 5.

The probability of submerged macrophyte dominance decreased with increasing surface area, mean lake depth, lake age and inundation duration (Figs. 1 & 4; Table 5a). Surface area and mean depth of the lakes explained the largest proportion of the variance, whereas age and inundation duration were less important, although highly significant (Table 5a). The general shape of the fitted response of submerged macrophytes to mean lake depth and surface area corresponded well to patterns shown by quadrats of the raw data, indicating that the logistic regression model is well suited to describe the pattern (Fig. 4).

Note that the quadrats of the raw interpolated data confirmed that (as assumed in the models) the effects of different factors are multiplicative. This implies that, for instance, the critical depth for macrophytes depends on the age and size of a lake. In small lakes submerged macrophytes dominated at greater depth than in large lakes (Fig. 4). Further, small old lakes were more often dominated by submerged macrophytes than large old lakes (Fig. 4), and small lakes with high inundation duration were more often dominated by submerged macrophytes than large lakes with high inundation duration (results not shown).

Because surface area was correlated with relative shoreline length (Table 3), we offered the latter variable as a substitute for surface area in an alternative regression analysis. Indeed, in the absence of surface area, relative shoreline length was included as a highly significant variable in the model equation ($p < 0.001$). This means that the negative

correlation between surface area and submersed vegetation dominance can also be explained as a positive correlation between relative shoreline length and submerged vegetation dominance or a combination of both abiotic variables. We also checked if the variable mean lake depth could be substituted for the correlated variable percentage drawdown area (Table 3). However, the latter variable did not contribute to the model significantly.

Nymphaeid occurrence was positively related to lake age and mean lake depth (Table 5b). The quadratic term in the model implies an optimum of nymphaeids roughly at 1.5 m with respect to mean lake depth (Fig. 3).

In alternative analyses, the independent variable age in the model was substituted by relative shoreline length and inundation duration, respectively, as these variables were correlated with lake age (Table 3). The regression for relative shoreline length was not significant, whereas the correlation for inundation duration was significant ($p < 0.01$), indicating that a high inundation duration may have a positive effect on nymphaeid occurrence.

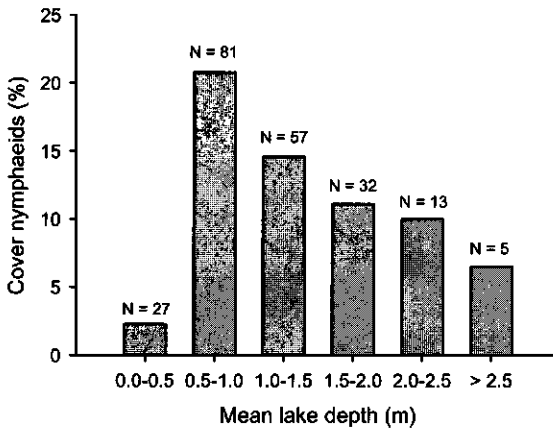


Figure 3. Average cover of nymphaeids in relation to mean depth per lake

Table 4. Results of backward logistic regression analyses for dominance of submerged vegetation (cut level of cover 20%) and occurrence of nymphaeids and helophytes (cut level of cover 1%). In these analyses Secchi-depth is included as abiotic variable in addition to the variables listed in Table 2; ^a) : $\ln(x+1)$ -transformed

A. Dependent variable: submerged vegetation dominance

Variable	Coefficient \pm S.E.	p	R
Mean lake depth ^a	-7.4846 \pm 1.8573	< 0.001	-0.3658
Secchi-depth	0.0702 \pm 0.0168	< 0.0001	0.3801

B. Dependent variable: nymphaeid occurrence

Variable	Coefficient \pm S.E.	p	R
Age ^a	1.3594 \pm 0.3277	0.0001	0.3794
Secchi-depth	0.0254 \pm 0.0102	0.0310	0.1981
Constant	-7.2095 \pm 1.9237	0.0002	

C. Dependent variable: helophyte occurrence

Variable	Coefficient \pm S.E.	p	R
Age ^a	1.3570 \pm 0.3716	< 0.001	0.3260
Mean lake depth ^a	-4.7845 \pm 1.2994	< 0.001	-0.3292
Secchi-depth	0.0519 \pm 0.0145	< 0.001	0.3199
Presence of trees	-1.7456 \pm 0.8836	< 0.05	-0.1336

Helophyte occurrence was found to increase with age and decrease with the presence of trees, cattle grazing, surface area, use of manure and mean lake depth in multiple logistic regression (Fig. 4; Table 5c). As for submerged macrophytes, the effects of these variables were multiplicative. For instance, in small lakes helophytes occurred at younger age than in large lakes (Fig. 4), and in shallower lakes helophytes occurred at younger age than in deep lakes (not shown). In an alternative analysis, the variable surface area was substituted by the strongly correlated variable relative shoreline length (Table 3). As with submerged macrophytes, this variable was accepted as highly significant in the model equation ($p < 0.001$), indicating that helophyte occurrence could be affected by a surface area per se or by relative shoreline length. We also checked if the variable age could be substituted for the correlated variables inundation duration and relative shoreline length (Table 3). However, neither of these substitutions contributed significantly to the model.

Table 5. Results of backward logistic regression analysis for dominance of submerged vegetation (cut level of cover 20%) and occurrence of nymphaeids and helophytes (cut level of cover 1%); In these analyses only abiotic variables listed in table 2 are included (Secchi-depth is excluded) ^a) = $\ln(x+1)$ -transformed; ²) = the square-value of variable

A. Dependent variable: submerged vegetation dominance

Variable	Coefficient \pm S.E.	p	R
Surface area ^a	-1.4994 \pm 0.3528	0.0001	-0.2322
Mean lake depth ^a	-2.7894 \pm 0.7694	0.0003	-0.1934
Age ^a	-0.4271 \pm 0.1453	0.0033	-0.1493
Inundation duration ^a	-0.3869 \pm 0.1329	0.0036	-0.1474
Constant	6.0926 \pm 1.0015	0.0001	

B. Dependent variable: nymphaeid occurrence

Variable	Coefficient \pm S.E.	p	R
Age ^a	0.9080 \pm 0.1655	0.0001	0.3075
Mean lake depth ^a	7.1784 \pm 2.3792	0.0026	0.1546
Mean lake depth ^{2a}	-3.7647 \pm 1.4711	0.0105	-0.1237
Constant	-7.6505 \pm 1.3464	0.0001	

C. Dependent variable: helophyte occurrence

Variable	Coefficient \pm S.E.	p	R
Age ^a	1.0279 \pm 0.1711	0.0001	0.3404
Presence of trees	-1.5689 \pm 0.4993	0.0017	-0.1636
Cattle grazing	-1.4571 \pm 0.4549	0.0014	-0.1676
Surface area ^a	-0.7398 \pm 0.2706	0.0063	-0.1364
Use of manure	-0.9295 \pm 0.4230	0.0280	-0.0981
Mean lake depth ^a	-1.4422 \pm 0.6957	0.0382	-0.0884

To check whether there were significant differences between the two years of sampling, we offered the sampling year as an additional independent variable to the regression analysis. Although the year of sampling was included as an additional variable in the models for submerged and nymphaeid macrophytes, it contributed less to the explained variance than the variables already listed in Table 5, indicating that the results were not strongly biased by the year of sampling.

During logistic regression analysis, submerged vegetation dominance was not significantly related to nutrient concentrations in the water column of the lakes. Many lakes with total P concentrations higher than 0.1 mg L⁻¹ were still dominated by submerged macrophytes (Fig. 5).

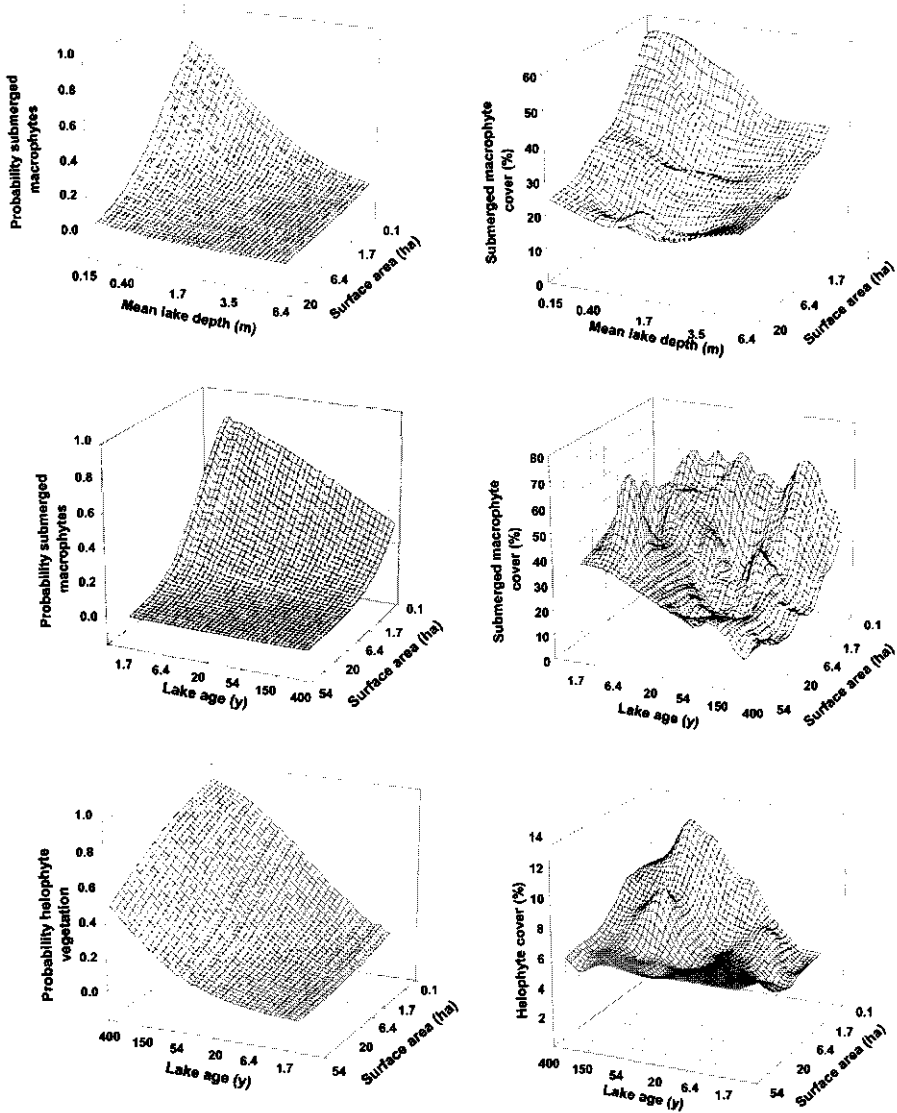


Figure 4. Modelled response of submerged macrophytes and helophytes in relation to age, surface area and mean lake depth as compared with a response surface computed from the raw coverage data by means of interpolation (inverse distance to a power; submerged macrophytes: smoothing factor 0.2; helophytes: smoothing factor 0.4)

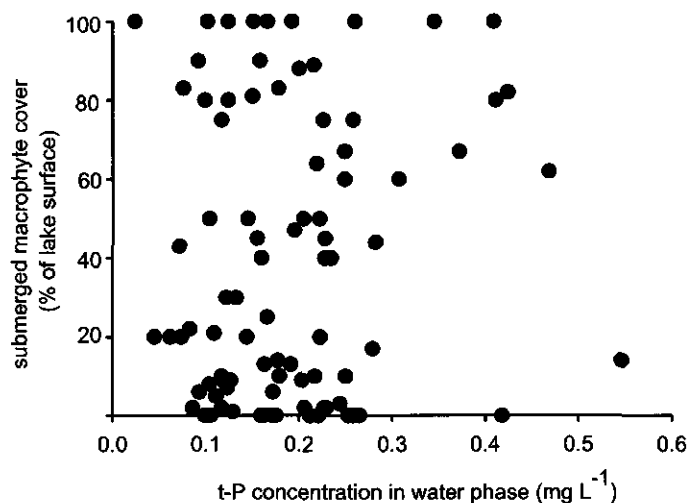


Figure 5. Relationship between total P concentration (mg L^{-1}) and submerged vegetation cover (% of surface area) in the lakes. Three outliers with total P values between $0.6 - 1.3 \text{ mg P L}^{-1}$ with submerged macrophyte cover $\leq 10\%$ have been removed.

Discussion

The results show that both extremes of vegetation cover can be found among lakes of the Lower Rhine floodplains. Water bodies completely covered by macrophytes and those without vegetation lie next to each other in floodplain areas, a phenomenon also described for the Danube delta (Coops *et al.*, 1999) and the Rhône (Bornette *et al.*, 1998). In our data set the frequency distribution of submerged macrophyte cover in lakes was bimodal indicating the tendency to be either abundant or almost absent (Fig. 2). Such bimodality could result from the existence of contrasting states under similar environmental conditions, which has been demonstrated to occur in shallow lakes outside floodplain areas (Scheffer, 1998; Jeppesen *et al.*, 1997), and has also been described more recently for lakes in regularly inundated floodplain areas along the Danube (Dokulil & Janauer, 2000) and the river Murray in Australia (Ogden, 2000).

Many studies show the large effect of water clarity on submerged macrophyte cover (e.g. Canfield *et al.*, 1985; Middelboe & Markager, 1997; Hudon, Lalonde & Gagnon, 2000). Accordingly, Secchi-depth was strongly correlated with submerged vegetation abundance in our lakes (Table 3). However, we did not consider turbidity as an independent variable in our analysis of vegetation abundance. The rationale is that causality is likely to be complicated. In shallow lakes submerged macrophyte cover strongly affects turbidity

(Jeppesen *et al.*, 1997), due to a suite of mechanisms including lower resuspension, increased zooplankton grazing pressure and competition for nutrients between macrophytes and algae (Scheffer, 1998). Since, in this study, the sampling period for turbidity occurred in the period when submerged macrophyte cover peaked, water clarity may largely be a result rather than a cause of submerged macrophyte cover.

Although we found relationships between vegetation structure and the relative impact of river hydrodynamics ('hydrological connectivity'), this aspect appeared less dominant than has been concluded in previous studies (Van den Brink *et al.*, 1991; Bornette *et al.*, 1998, Heiler *et al.*, 1995, Bornette *et al.*, 1998). In contrast, we found strong relationships between vegetation structure, morphometry and lake age, which have previously received little attention. Obviously, causality cannot be inferred from statistical relationships. In the sections below we discuss how our results, with respect to hydrological connectivity, land use, morphometry and lake age, may be interpreted in the light of previous work.

Hydrological connectivity

Inundation duration was negatively correlated with submerged macrophyte dominance, as found in earlier studies (Van den Brink *et al.*, 1991; Heiler *et al.*, 1995). Winter inundation is unlikely to have much direct impact on the vegetation, as in these temperate lakes plants overwinter largely as dormant underground structures. The negative correlation between inundation duration and macrophyte dominance found by Van den Brink *et al.* (1991) could be due to the fact that winter inundation duration is related to (1) the occurrence of summer inundations within the study period, which have deleterious effects on macrophyte growth in floodplain lakes (Brock, Van der Velde & Van de Steeg, 1987); (2) higher nutrient load in the recent past, which is in agreement with the positive correlation between total-P concentration and inundation duration (Roozen *et al.*, 2003); (3) higher salinity (Van den Brink *et al.*, 1992), which can reduce growth of submerged macrophytes (Van den Brink & Van der Velde, 1993).

By contrast, no correlations between percentage drawdown area and the abundance of submerged macrophytes, nymphaeids or helophytes were found in the regression analysis (Table 5). This does not imply that drawdown is an unimportant process for these growth forms. Note that the number of lakes in the data set with a considerable drawdown area in the study period is very low (Fig. 2), which makes the effects of drawdown hard to detect.

Land use

The negative correlation between the occurrence of helophytes and the presence of trees may be explained by competition for light and altered sediment characteristics. Trees (mainly *Salix* species) often grow in the shallow littoral, thereby occupying space which otherwise could be dominated by helophytes. Cattle grazing can obviously eliminate helophytes through a direct reduction in above ground biomass (Hroudová *et al.*, 1996)

and by the destruction of rhizomes by trampling. The cause of the negative relationship between the use of manure and helophyte occurrence is obscure. Eutrophication seems an unlikely candidate, since submerged macrophytes are more sensitive yet show no relationship with manure use (Table 4, 5). Perhaps the relationship with observed manure use is caused by the fact that manured fields had been used for cattle grazing in the years before the survey. Indeed, cattle grazing and manure use are highly correlated in our data-set (Table 3).

Nutrient content

It is often observed that submerged macrophyte abundance decreases with total-P content of the water, probably due to light limitation caused by algal growth (Jeppesen *et al.*, 1990; Scheffer, 1998). Surprisingly, logistic regression analysis showed that neither total-P nor total-N were significantly related to dominance by submerged macrophytes. Many floodplain lakes in our data-set were still dominated by submerged macrophytes at a total-P concentration up to 0.4 mg L^{-1} (Fig. 5). This value is much higher than found in a large study of Danish lakes outside floodplain areas (i.e. $0.08\text{--}0.15 \text{ mg L}^{-1}$, Jeppesen *et al.*, 1990). This discrepancy may be related to the fact that our data-set contains many very small lakes which have a higher chance of being dominated by submerged vegetation. Also Mjelde & Faafeng (1997) reported dense submerged macrophyte cover over a wide range of total P concentration ($0.03\text{--}0.70 \text{ mg P L}^{-1}$) in relatively small shallow lakes, although the surface area range in their dataset (6–112 ha) is larger than in ours (0.01–45 ha). The effect of lake morphometry on submerged macrophyte dominance is discussed below.

Morphometry

Small shallow lakes with a high relative shoreline length supported the highest abundance of submerged macrophytes in our data-set (Table 3, Figs. 1 & 4). It has often been shown that the abundance of submerged macrophytes decreases with water depth, largely due to light limitation (Canfield *et al.*, 1985; Chambers & Kalff, 1985a; Skubinna *et al.*, 1995). On the contrary, the pronounced negative relationship between lake surface area and submerged macrophyte dominance is novel. The effects of surface area on plant abundance have received hardly any attention in literature. Ogden (2000) reported a similar pattern for floodplain lakes along the Murray and Ovens River in Australia, but did not separate the effects of water depth and surface area. Further, in lakes outside floodplains lake area effects have hitherto been explained largely as a result of a positive correlation between lake size and depth (Duarte, Kalff & Peters, 1986b; Gasith & Hoyer, 1997). In our dataset surface area and depth had separate effects on submerged macrophyte cover. Several mechanisms can be hypothesised to explain a negative effect of lake size on submerged plant dominance.

1. Fish-kills may occur more frequently in small lakes, because there is a higher risk of oxygen depletion (Jeppesen *et al.*, 1990). In the wake of such events, submerged macrophytes may develop.
2. Smaller lakes tend to have a higher ratio of shoreline to surface area. Because shorelines act as a refuge for zooplankton (Lauridsen & Lodge, 1996; Nurminen, Horppila & Tallberg, 2001), this may favour transparency and hence growth of submerged macrophytes (Jeppesen *et al.*, 1990).
3. A large relative shoreline length may also favour recruitment and survival of pike (*Esox lucius* L.), a piscivore able to reduce recruitment of planktivorous fish (Berg, Jeppesen & Søndergaard, 1997; Søndergaard, Jeppesen & Berg, 1997; Jacobsen *et al.*, 1997), leading to clear water through a trophic cascade, stimulating plant growth.
4. Submerged macrophytes tend to remain present throughout the winter period in sheltered, small water bodies (Van Wijk, 1988), giving them an advantage in spring.
5. Colonisation, starting from the shallow 'hot spots' along the shoreline, may take several years to complete in large lakes (Van den Berg, 1999). Because the colonisation with submerged macrophytes is a sensitive phase (Scheffer, Bakema & Wortelboer, 1993), the chance for a switch from vegetation-poor to a vegetation-rich lake during a period of favourable conditions for submerged macrophyte growth could be lower in large lakes.
6. Macrophyte growth in large lakes can be hampered by wind-stress (Hudon *et al.*, 2000; Spence, 1982).
7. Turbidity due to wind-induced resuspension is less in small lakes (Jeppesen *et al.*, 1990; Strand & Weisner, 1996).

Testing these hypotheses requires further research, but some indications can be derived from our data. According to Roozen *et al.* (2003), wind is unlikely to be responsible for most of the resuspension related turbidity in our lakes (mechanism 7), because of small lake size and low exposure. Also, the effect of wind-stress on macrophytes (mechanism 6) seems unlikely to be important in these lakes. Indeed, in much larger shallow eutrophic lakes in the Netherlands, submerged plants have been observed to occur preferentially at exposed, rather than sheltered sites (Scheffer, De Redelijkheid & Noppert, 1992). By contrast, the pike hypothesis (mechanism 3) is supported by the observation that the fish community in small floodplain lakes with high cover of submerged macrophytes and helophytes is often dominated by pike, whereas larger lakes without vegetation are almost exclusively dominated by benthivorous bream (*Abramis brama* L.) (Grift *et al.*, 2001b). Fish-kills during periods of low water (mechanism 1) are also frequently observed in the studied floodplains (Scheffer pers. obs.), and Grift *et al.* (2001a) reported high mortality rates of bream in floodplain lakes during periods of low water level. In conclusion, the first five mechanisms remain likely candidates for the floodplain lakes studied.

In our data-set, nymphaeid abundance was not related to lake size, but showed a distinct optimum with respect to mean lake depth (Table 5b, Fig. 3). This depth zonation pattern is in accordance with observations by Van der Voo & Westhoff (1961), who reported also for Dutch floodplain lakes a depth range for nymphaeid occurrence from 0–3 m with an optimum in abundance between 0.8 and 1.2 m.

Lake age

The decline of submerged macrophytes and the increase of nymphaeids and helophytes with age are in line with the 'classical' sequence of aquatic vegetation succession (Pearsall, 1920; Hutchinson, 1975). Submerged macrophytes may accelerate the succession by altering net sedimentation, nutrient cycling and accumulation of organic matter, leading to a gradual enrichment of the sediment (Carpenter, 1981). In floodplain lakes these processes are accompanied by additional accumulation of fine materials (silt, clay) deposited during floods. The fine materials gradually decrease the porosity of the bottom, leading to a considerable reduction in groundwater exchange between river and lakes (Wood & Armitage, 1997). As a consequence, the amplitude of water-level fluctuations and the associated risk of desiccation of macrophyte seeds and seedlings decreases with lake age. At the same time, a low oxygen concentration resulting from organic matter accumulation stimulates germination of some late successional macrophyte species, such as *Nuphar lutea* (Smits, 1994), whereas low redox potential in the increasingly organic sediments could hamper growth of submerged macrophytes (Barko & Smart, 1986). Also, increased internal phosphorus loading from the gradually enriched sediments may stimulate phytoplankton, resulting in light limitation for submerged (but not for floating) plants. Eventually, a decrease in lake depth can further promote the transition to helophyte vegetation. Unlike in many other floodplains, such as those along the Rhône (Amoros & Bornette, 1999), the process of reduced hydrological connectivity in floodplain lakes along the Lower Rhine caused by accumulation of fine materials and organic matter is hardly reversed by bed erosion resulting from scouring overflows.

Combined effects of morphology, river dynamics and ageing

The results consistently show that the different environmental factors that affect vegetation abundance should not be viewed separately as 'limiting factors'. Rather the sensitivity to one factor always depends on the values of other factors. This is an implicit assumption of the logistic model but the figures of the raw data (Fig. 4) confirm this pattern. This implies, for instance, that small lakes tend to remain dominated by submerged macrophytes up to a greater depth than large lakes, and helophytes colonise smaller lakes faster.

Perhaps the most remarkable result from our analysis is that, independently of depth, lake surface area and age are such important factors determining vegetation structure. Nutrient loading is unlikely to differ substantially among our lakes, because they are all inundated

almost every year. The relatively minor role of river dynamics may largely be due to the fact that, unlike in other floodplain systems (Bornette *et al.*, 1998; Heiler *et al.*, 1995), our lakes are rarely inundated during the growing season and experience only moderate currents during inundation periods. Nonetheless Van den Brink *et al.* (1991), who investigated floodplain lakes along the Lower Rhine, found much stronger correlations to connectivity. This may be due in part to the fact that they also included in their survey permanently connected and never inundated lakes behind the major embankments in the hinterland. In addition, in their dataset lake morphometry was strongly correlated to connectivity, leading to potentially spurious results.

Our results have important practical implications for future management of the Lower Rhine floodplains. New water bodies will be excavated in the floodplains over the coming years in a campaign aimed at enhancing the water storage, discharge capacity and conservation value of the floodplain. Size, depth and connectivity to the river of these prospected lakes can in part be designed (Coops *et al.*, 2000). Our results suggest that the chance of new lakes becoming rich in vegetation is higher if many small lakes, rather than fewer large ones, are created. Also, the clear succession in vegetation structure patterns with age implies that, in these floodplains where natural erosion by scouring water is virtually absent, regular re-excavation of lakes may be essential if the aim is to promote biodiversity of the river – floodplain system.

Acknowledgements

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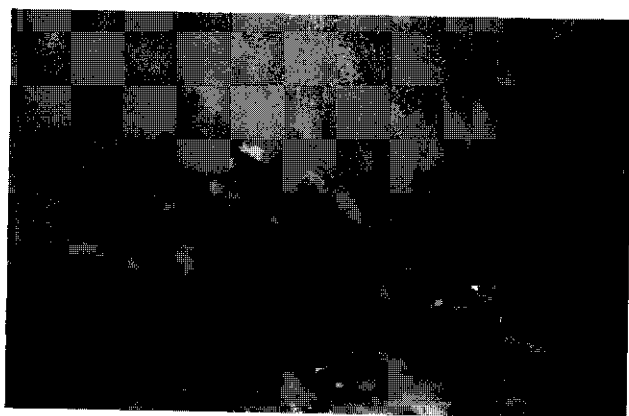
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Older lakes are often dominated by *Nuphar lutea*, here together with *Hippuris vulgaris*; Picture: Hugo Coops (RIZA)



Young, submerged leaves of *Nuphar lutea* are sensitive to desiccation. Picture: John van Schie (RIZA)

Chapter 4

Succession of aquatic vegetation driven by reduced water level fluctuations in floodplain lakes

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Abstract

In recent years, interest has grown in restoring floodplain function of regulated rivers. Successful rehabilitation of riparian systems requires knowledge of how regulation of river flow affects biodiversity and ecosystem function. The effects of changes in the river's low water level regime on aquatic ecosystems in floodplains have received little attention so far. In this study, we analyzed the aquatic vegetation of 215 floodplain lakes along the Lower Rhine (The Netherlands) in relation to lake characteristics and lake water level fluctuations in 1999-2000. Vegetation composition was related to lake morphology and age, cattle access to the shoreline, the amount of time the river was in flood, and lake sediment area exposed at low water level (drawdown). Surprisingly, vegetation composition was correlated more strongly to lake age and occurrence of drawdown than the amount of time the river was in flood. In older lakes, water level fluctuations are reduced due to an accumulation of clay and silt which 'seals' sediment, preventing drawdown during periods of low river levels. Our results suggest that this clay sealing process is a major driving force for aquatic vegetation succession in floodplain lakes along the Lower Rhine, as succession drives from desiccation-tolerant species (e.g. *Chara* spp.) in young lakes to desiccation-sensitive species (e.g. *Nuphar lutea*) in old lakes. Water levels were stable in lakes along a river branch that is impounded below mean flow only. There, the original low water level regime has been replaced by an artificial regime with higher water levels than would be expected naturally. Consequently, in these lakes drawdown was rare or absent, and the aquatic macrophyte vegetation was characterized by low species richness and frequent dominance by the invasive species *Elodea nuttallii*. Our results show that stabilization of river water levels during low flow may negatively affect vegetation composition and succession in floodplain lakes adjacent to these rivers. A management scheme including incidental temporary lowering of the river water level which results in drawdown of floodplain lakes, would enhance the ecological status of those rivers with stabilized water levels during low flow.

Introduction

Dams regulate the flow regime in the majority of the world's large river systems. More than 840 000 dams obstruct approximately two-thirds of the fresh water flowing to the oceans (Petts 1984; Dynesius & Nilsson 1994; McCully 1996). In recent years, interest has grown in restoring floodplain function by reconnecting the floodplain with the main channel of regulated rivers. To provide guidelines for the rehabilitation of these riparian systems, knowledge is needed on the way in which regulation of the river flow affects biodiversity and ecosystem function of large rivers. Several studies have focused on the effects of changes in the flooding regime on ecosystem composition and succession of riparian ecosystems (Bravard, Amoros & Pautou 1986; Jansson *et al.* 2000; Dynesius *et al.* 2004). However, comparatively little is known about the effects of changes in the river's low water level regime on aquatic ecosystems in floodplains along regulated rivers.

In floodplains along large lowland rivers, lake systems represent an important component of riparian wetlands. Along unregulated rivers, lakes originate from past geomorphological change, such as meander cut-off (Bravard *et al.* 1986). In addition to natural lakes, human interference has created many artificial water bodies along regulated rivers through the extraction of gravel, sand and clay. Young lakes in river floodplains may be colonized rapidly by submerged vegetation, followed by a succession of nymphaeids and helophytes (Van Donselaar 1961). River flooding through surface connection with the main channel may be an important determinant of vegetation composition in floodplain lakes (Bornette, Amoros & Chessel 1994; Van der Voo & Westhoff 1961; Sparks & Spink 1998; Van den Brink *et al.* 1991). In contrast, the impact of fluctuating lake water levels during isolated stages is largely unknown (Amoros & Bornette 1999). Input of seepage water may affect the vegetation by increasing or decreasing nutrient concentrations in lake water (Bornette *et al.* 1994; Bornette, Guerlesquin & Henry 1996; Tockner *et al.* 1999). Additionally, fluctuating river levels may influence the amplitude of water level fluctuations in floodplain lakes by groundwater flow. When the water level is low in the main channel, infiltration of lake water into the alluvial aquifer may result in a lowering of lake water levels, which - depending on the morphometry of the lake - may result in lake-bottom exposure (drawdown) (Van Geest *et al.*, in press). Drawdown has been shown to have strong effects on the composition and abundance of aquatic vegetation (Wilcox & Meeker 1991; Wagner & Falter 2002).

River flooding through surface connection with the main channel (Brock, Van der Velde & Van de Steeg 1987; Henry, Bornette & Amoros 1994), river seepage and infiltration induced water level fluctuations affect all aquatic vegetation development in floodplain lakes. Their relative importance may depend on what is referred to as 'hydrological connectivity' (Tockner, Malard & Ward 2000; Amoros & Bornette 2002), i.e. the degree

of hydrological contact between the river and a particular lake in the floodplain. The hydrological connectivity of a floodplain lake under non-flooded conditions may be expressed by the degree to which the lake follows water level fluctuations of the river. When lakes become older, water level fluctuations will decrease as the result of decreased hydraulic conductivity of the lake bottom, caused by accumulation of organic matter, silt and clay in the sediment (Wood & Armitage 1997). As a result, sediment exposure will occur less frequently with increasing lake age (Van Geest *et al.*, in press). We hypothesize that a shift in the vegetation composition with lake ageing occurs: desiccation-tolerant macrophyte species dominate in young lakes, whereas desiccation-sensitive species are favoured in later successional stages.

In this paper we evaluate the relative importance of drawdown (by infiltration) and flooding (by surface connection) on vegetation composition in 215 lakes situated in the remaining active floodplain of the Lower Rhine in The Netherlands. Further, we analyze vegetation succession in the floodplain lakes by synchronic analysis of differently aged lakes. In addition, the presence in the Lower Rhine of two unimpounded branches and one impounded branch enabled us to evaluate the potential consequences of hydrological regulation measures on aquatic vegetation composition and succession.

Study area

The Rhine, from its source in Switzerland to the outflow to the North Sea, is 1320 km long and has a catchment area of 185 000 km² (Lelek 1989), of which 25 000 km² is situated in The Netherlands. Where the Rhine enters The Netherlands, the flow varies roughly between 800 and 12 000 m³ s⁻¹, resulting in a difference between the minimum and maximum water level of up to 8 metres (Middelkoop 1997). Typically, the highest river flows occur in winter and the lowest in late summer and early autumn (Buijse *et al.* 2002). During the growing season of the vegetation (May – October), periods of extreme low water levels may occur.

After crossing the border of The Netherlands, the Lower Rhine splits into three branches, the Waal, the IJssel, and Neder-Rijn. No weirs are present along the Waal and IJssel, whereas the lower water levels of the Neder-Rijn have become regulated by the construction of three weirs in the 1960s. All weirs are closed when the mean river flow of the Rhine falls below 2 200 m³ s⁻¹. Hence, in the Neder-Rijn the construction of weirs did not result in changes in the flooding regime, whereas the natural water level regime with occasional low river water levels has been replaced by an artificial distribution with higher minimum water levels than would be expected naturally (Figure 1). Consequently, water levels rarely fall below a fixed level in the Neder-Rijn and the floodplain lakes alike. Indeed, lake drawdown was strongly reduced along the impounded Neder-Rijn,

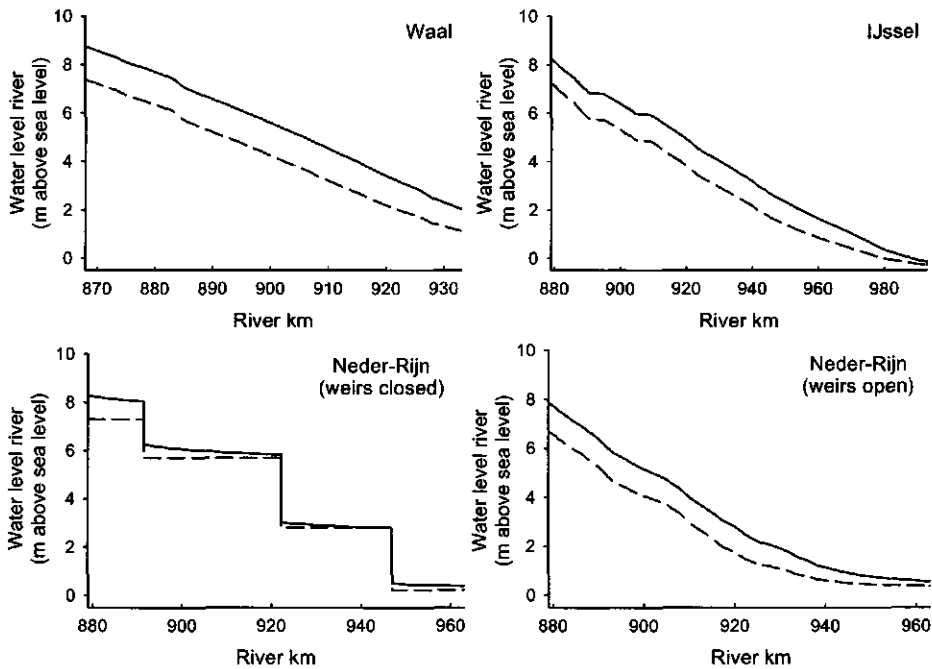


Figure 1. The mean and minimum water level (m above sea-level) in the three branches of the Lower Rhine (Waal, IJssel and Neder-Rijn, respectively) in the period May – October 1990 – 1999. For the Neder-Rijn, also the mean and minimum river water level (m above sea-level) are also shown at times when the weirs would be open (calculations based on the water quantity model SOBEK, RIZA, the Netherlands). For each branch, the indicated river km represents the upper and lower limits of the locations of the lakes.

whereas drawdown occurred in lakes along the unpounded Waal and IJssel, especially in young lakes (Van Geest *et al.*, in press). For lakes along the Waal and IJssel in 1999, the mean drawdown area (\pm S.E.) was $29\% \pm 7$ for lakes of 1 – 29 years old, $18\% \pm 5$ for lakes of 30 – 99 years old, and $10\% \pm 3$ for lakes ≥ 100 years old. For lakes along the Neder-Rijn, these values were 2 ± 1 , 2 ± 2 and 8 ± 2 , respectively.

Methods

In this study, we confined our research to lakes that are shallow (mean depth < 2 meter) and disconnected from the main channel during summer. In 1999, submerged and floating-leaved macrophytes were sampled in 100 floodplain lakes along the Lower Rhine. In 2000, an additional 115 lakes was sampled.

Sampling and classification of plots

In July – early August 1999, aquatic vegetation was sampled in 917 plots distributed over 100 floodplain lakes along the Lower Rhine. The number of plots per lake varied (4-31), depending on lake size and apparent complexity of the vegetation structure. Plots were selected to represent the range of vegetation types present in the lake. Plot size varied from 1 m² (submerged vegetation) to 4 m² (nymphaeid vegetation). All plots were sampled from a boat. In each plot, species composition and cover were determined by combining visual estimates and collection. Species cover in each plot was expressed in one of seven classes (1, < 1%; 2, 1-5%; 3, 6-15%; 4, 16-25%; 5, 26-50%; 6, 51-75%; 7, 76-100%), and total percentage cover of submerged plants, floating plants, helophytes and of filamentous algae were estimated in the same way. Two-way indicator species analysis (TWINSPAN; Hill 1979) was used to assign plots to vegetation types. Classes of plant cover were used as pseudo-species cut levels. Eleven vegetation types were distinguished based on differences in species dominance. The vegetation types were named according to their dominant species. In addition, plots with total vegetation cover < 15% were classified as a separate 'vegetation-poor' type. Based on the classification of the plots, the area covered by each vegetation type proportional to the total lake surface area was determined for each lake sampled in 1999. In 2000, for an additional 115 lakes the cover of vegetation types was estimated visually using the same classification system. In both years, a vegetation type was regarded as a characteristic type if it occupied at least 5 – 10% of the total lake surface area.

Sampling of species richness

Preliminary research indicated that calculation of species richness of aquatic macrophytes on the basis of data from the plots alone would result in an underestimation of species richness in the lakes. Therefore, for the 100 lakes sampled in 1999, species composition and abundance of submerged and floating-leaved macrophyte vegetation of the whole lake area were surveyed by boat until no new species were found. The time spent per lake varied from approximately 30 minutes for very small lakes (< 0.10 ha) to several hours for lakes with a large surface area or a complex vegetation structure. Species abundances were recorded using the Tansley-scale (rare, occasional, frequent, abundant, dominant), and were converted to an ordinal scale ranging from 1 to 5 for statistical analysis. For the 115 additional lakes sampled in 2000, no equivalent data were obtained for species richness.

Abiotic variables

The abiotic variables were selected to represent potentially important factors for macrophyte growth, such as inundation duration by overland flooding, occurrence of drawdown, water depth, and water clarity.

For all 215 lakes, estimates of the average amount of time the area was flooded annually by the river, the surface area, and the shoreline length were obtained from GIS-maps (RIZA, The Netherlands). Water depth in July was established at several locations per lake. The proportion of the surface area of the lake bottom that became exposed between July and October ('drawdown area') was determined by visual estimation. The approximate age of lakes was derived from historic topographical maps. Reliable estimates of the age of the lakes could be made up to 300 years; lakes older than this were classified as being 300 years old. The uncertainty of the lake age estimation was approximately one year for lakes originating from 1980 onwards, 3 - 7 years for lakes originating during the period 1910 - 1980, and 10 - 25 years for lakes originating before 1910. During fieldwork, the prevailing land use in the adjacent floodplain was recorded (presence of intensive agriculture, presence of adjoining trees, and cattle access to shoreline).

In addition, several abiotic variables were determined for lakes sampled in 1999. For all 917 plots in these lakes, we measured water clarity with a small black and white disk called a Secchi disk. The Secchi-depth is the vertical distance from the water surface where the Secchi disk disappears from view when it is dropped in the water. Secchi-depth was measured once during the period of maximum seasonal development of macrophytes (July and early August). Based on these data, the proportion of the lake bottom within the euphotic depth ('euphotic zone') was calculated as the percentage of the lake surface area where the water depth was equal or less than 1.7 times the Secchi-depth (Reynolds 1984). Furthermore, the seasonal water level trend between July and October 1999 was measured from a marked rod placed in each lake. Because of sampling difficulties, complete abiotic data were available for 94 of the 100 lakes sampled in 1999.

The resulting dataset of 215 lakes represents the range of values along the three Rhine branches of potentially important factors for macrophyte growth such as average inundation duration ($1 - 258 \text{ days yr}^{-1}$), lake surface area ($0.01 - 44.6 \text{ ha}$), shoreline length ($40 - 6535 \text{ m}$), lake age ($1 - > 300 \text{ yr}$) and distance to the main channel ($10 - 1400 \text{ m}$). For the subset of 100 lakes sampled in 1999, 36 lakes were of natural origin (e.g. cut-off meanders), and 64 lakes were of artificial origin (e.g. clay pits). Along the Waal, there were 10 natural and 30 artificial lakes, while along the IJssel and Neder-Rijn, the numbers were 14 and 12, and 12 and 22, respectively. Overall, artificially created lakes (mean lake age 47 years, $n = 64$ lakes) were younger than natural lakes (mean lake 247 year; $n = 36$ lakes) (Mann-Whitney U Test; $U = 18.00$; $P < 0.001$). However, between these two categories of lakes there were no significant differences in surface area and mean depth ($U = 1005.0$ and 1037.5 , $P = 0.29$ and 0.41 , respectively).

Table 1. Independent variables used for canonical correspondence analysis (CCA) and multiple logistic regression. ^a = ln-transformed; ^b = ln(x + 1)-transformed

Variable	unit	comments
Mean lake depth ^a	m	calculated from 4 – 31 water depth measurements in July 1999 in each lake
Lake surface area ^a	ha	surface area of lake at start of growing season
Drawdown area ^b	%	% of lake surface area in October that has been exposed compared to the surface area in July
Lake age ^a	yr	for accuracy: see Mat. & Methods
Inundation duration ^a	d.yr ⁻¹	long year average 1900 – 1995
Presence of intensive agriculture	categories	see Material and Methods
Presence of trees	categories	see Material and Methods
Access of cattle to shoreline	categories	see Material and Methods

Data analyses

Of the 215 lakes, 165 were vegetated (vegetation cover at least 5-10% of lake area; see above). The relationship between the lake area covered by the different vegetation types and abiotic lake characteristics (Table 1) was analysed using canonical correspondence analysis (CCA) (Canoco version 4; ter Braak 1998). For each lake, the percentage cover of the eleven classified vegetation types was used as a characteristic of the lake's vegetation. Default parameters were used in the analysis. The approximate significance level for the correlation between each abiotic variable and vegetation composition was computed by a Monte Carlo permutation test (ter Braak 1998). The number of random permutations was 9 999. A significant ordination indicated a significant correlation between the ordination of the lakes according to their abiotic characteristics and the ordination of the lakes based on their floristic composition.

Subsequently, a more detailed analysis was carried on the 100 lakes sampled in 1999. In this analysis, the probability of presence of each vegetation type was related to abiotic lake characteristics by means of multiple logistic regression analysis (Jongman, ter Braak & Van Tongeren 1995). In addition to the abiotic lake characteristics given in Table 1, the variable 'euphotic zone' was included in this analysis. The parameters were estimated by means of the maximum-likelihood principle. The abiotic variables inundation duration, lake age, mean lake depth, and lake surface area were ln(x) transformed; the proportion of drawdown area was ln(x+1) transformed. For each analysis both forward and backward multiple logistic regressions were carried out; only the results of the backward regression are presented because the two produced comparable results.

To determine the effect of stabilization of the river water level on the aquatic macrophyte composition of the lakes, we calculated the occurrence of characteristic vegetation types for each river branch, calculated as the number of lakes where the vegetation types occurred divided by the total number of lakes along each branch. Furthermore, we calculated the species richness (sum of submerged and rooted floating-leaved species) for each lake. Because species richness can be influenced strongly by the number of species that occur in low abundance (Nillson & Nillson, 1983), we checked if the same relationships were found when the species with low abundance (the category 'rare' according to the Tansley-scale) were excluded from the analyses.

Results

Relationships between vegetation types and abiotic lake characteristics

Canonical correspondence analysis (CCA) results indicate that vegetation composition in the sampled floodplain lakes was significantly related to the water level regime of the river (inundation duration, drawdown area), lake age, morphometry (depth, surface area), and cattle access to the shoreline (Figure 2). Dominance of benthic filamentous macroalgae, *Persicaria amphibia* (L.) Gray, *Chara vulgaris* (L.) and *Nymphoides peltata* (S.G. Gmel.) Kuntze were positively related to the proportion of drawdown area in the lakes (Figure 2, Table 2). Remarkably, inundation through surface flooding had no relationship with characteristic vegetation types in our study (Table 2). The submerged vegetation types dominated by *Potamogeton pusillus* (L.)/*P. trichoides* Cham.& Schldl., *C. vulgaris*, and *Elodea nuttallii* (Planch.) St. John predominated in younger lakes (Table 2, 3). In contrast, *Ceratophyllum demersum* L. (Table 3) and *Potamogeton lucens* L. (Table 2, 3) showed the opposite pattern, with maximum occurrence in lakes older than 100 years, and the highest occurrence of *P. pectinatus* L. occurred in intermediately aged lakes (30 – 99 years, see Table 3). The vegetation types *Nuphar lutea* (L.) Sm. and *N. peltata* were common in lakes that were 30 – 40 years and older, although *N. peltata* also occurred in 8% of the lakes aged 1 – 30 years. Relatively large (> 5 ha) lakes were usually dominated by nymphaeids or were almost without vegetation, whereas relatively small and shallow lakes were usually dominated by submerged vegetation (Figure 2). *P. lucens* and *N. lutea* were positively related to mean lake depth, whereas *P. pusillus*/*trichoides* was negatively related to mean lake depth (Table 2). Furthermore, *C. vulgaris*, *P. lucens*, and *P. pectinatus* were characteristic of lakes with a large proportion of the bottom within euphotic depth (Table 2).

Relationship between sediment exposure and macrophyte vegetation

The probability of the lake bottom becoming exposed was not directly dependent on water depth in July, because lakes showed strongly different degrees of water level decrease during summer. Large areas of the plots containing *P. amphibia* (94%) and *C. vulgaris* (76%) were exposed in October 1999, whereas plots with *N. lutea* were not exposed

(Figure 3). *Potamogeton lucens*, *P. pectinatus*, *P. pusillus/trichoides*, and *N. peltata* occurred in plots with an intermediate incidence of sediment exposure (Figure 3). Most vegetation types had maximum presence at water depths of 0.5 – 1.0 m, and were almost absent in water deeper than two metres (Figure 3). Vegetation types of *P. amphibia*, *C. vulgaris*, and *P. pusillus/P. trichoides* showed maximum occurrence in shallow water (< 1 m), whereas optimal conditions for *P. lucens* was in relatively deep water (0.5 – 2.0 m) (Figure 3).

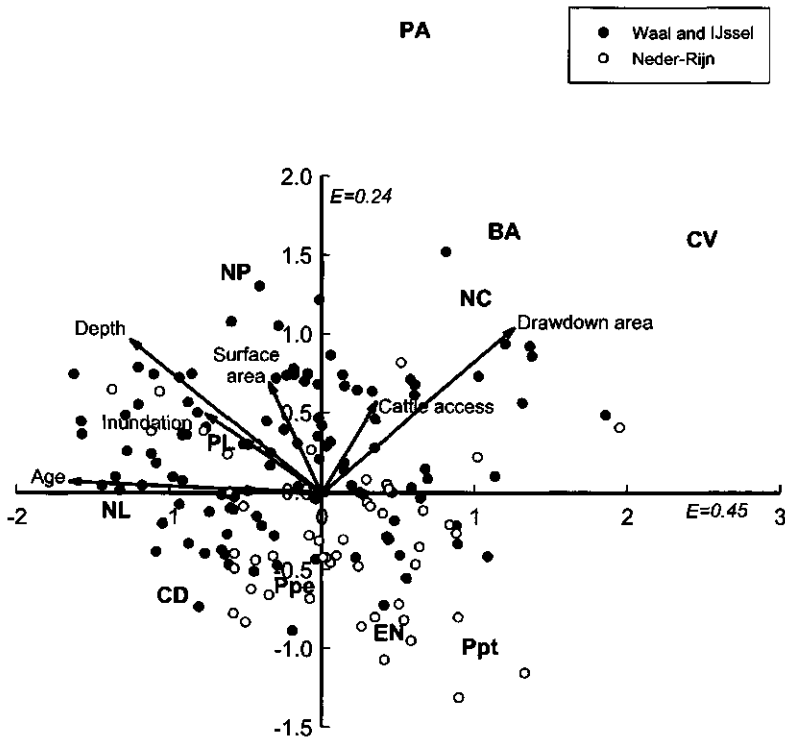


Figure 2. Distribution of vegetation types in 165 floodplain lakes along the Lower Rhine. Canonical correspondence analysis (CCA) ordination diagram with vegetation types, floodplain lakes and environmental variables. The abiotic variables explained 18% of the variation in vegetation composition. Abbreviations of the vegetation types: BA = benthic filamentous macroalgae; CD = *Ceratophyllum demersum*; CV = *Chara vulgaris*; EN = *Elodea nuttallii*; NC = *Nitella capillaris*; NL = *Nuphar lutea*; NP = *Nymphoides peltata*; PA = *Persicaria amphibia*; PL = *Potamogeton lucens*; Ppe = *Potamogeton pectinatus*; Ppt = *Potamogeton pusillus*/P. *trichoides*; E = eigenvalue

Table 2. Results of backward multiple logistic regression analysis in a set of 94 lakes for dominance of vegetation types of Benthic filamentous macro-algae (BA), *Chara vulgaris* (CV), *Elodea nuttallii* (EN), *Nuphar lutea* (NL), *Nymphaoides peltata* (NP), *Persicaria amphibia* (PA), *Potamogeton lucens* (PL), *Potamogeton pectinatus* (Ppe), and *Potamogeton pusillus/trichoides* (Ppt). Vegetation types that occurred in less than 10 lakes were excluded from the analysis. The abiotic variables inundation duration, presence of trees, and presence of intensive agriculture did not significantly explain vegetation type occurrence. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ^a = \ln -transformed; ^b = $\ln(x+1)$ -transformed

Vegetation type	N lakes	Surface area ^a (ha)	Mean lake depth ^a (m)	Drawdown area ^b (%)	Lake age ^a (yr)	Euphotic zone (%)	Cattle grazing	Constant
BA	12							-3.15
CV	10			0.58**	-0.34*	0.05*	2.88*	-10.8
EN	28	1.00**		1.28**	1.39***			
NL	27		0.98*		0.55**			-7.46
NP	29			0.35*				-3.78
PA	11			0.93**				-4.23
PL	24		1.40*		0.42*	0.04***		-5.57
Ppe	27				0.41*	0.026***		-4.33
Ppt	23		-1.15**					-1.29

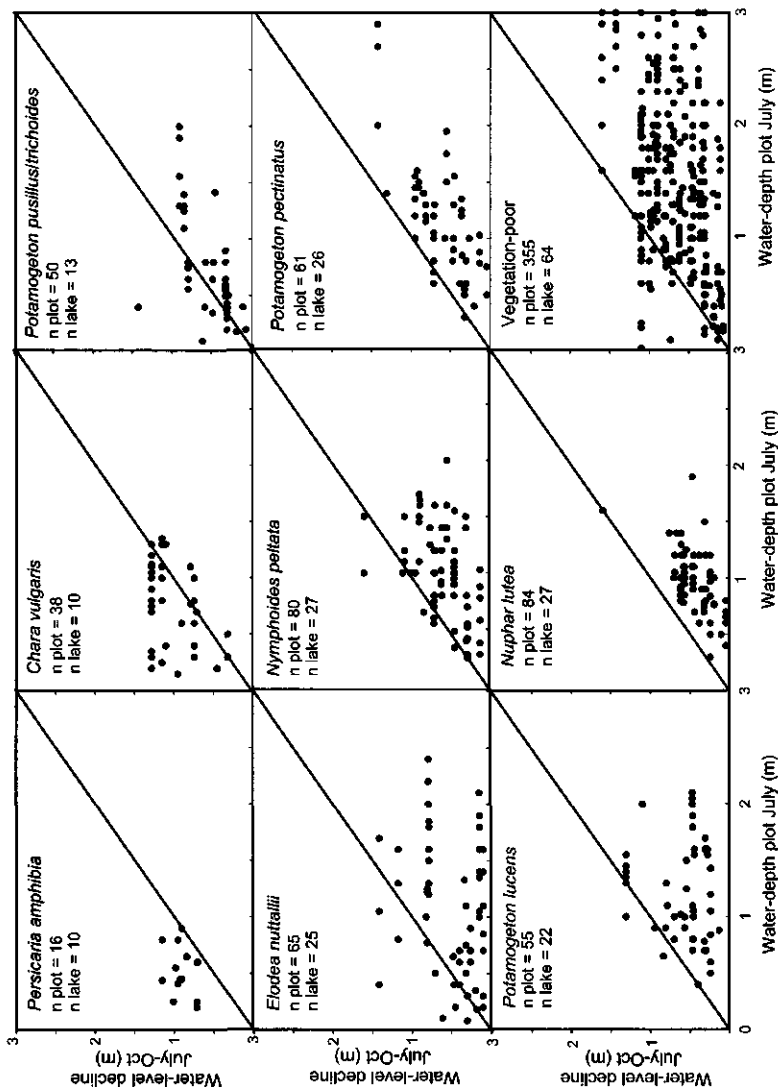


Figure 3. Occurrence of the main vegetation types in sample plots in relation to water-depth in July 1999 (m) and water-level decline July-October 1999 (m). Plots with vegetation types of benthic filamentous macro-algae, *Ceratophyllum demersum* or *Nitella capillaris* were excluded.

Differences between river branches

There were significant differences in the occurrence of vegetation types in lakes along the impounded Neder-Rijn, and unimpounded Waal and IJssel, respectively ($\chi^2 = 58.20$; $df = 20$, $P < 0.01$). The vegetation types characterized by *C. vulgaris*, *N. lutea*, *N. peltata*, *P. amphibia*, and *P. lucens* occurred in a lower number of lakes along the Neder-Rijn compared to lakes along the Waal and IJssel, in particular in lakes of 30 – 100 years old (Figure 2, Table 3). By contrast, the vegetation type *E. nuttallii* was more common in lakes along the Neder-Rijn than along the other two branches (Figure 2, Table 3). In lakes older than 100 years, *N. lutea* and *P. lucens* occurred equally along all three river branches (Table 3). The reduced occurrence of several vegetation types along the Neder-Rijn (see above) resulted in a lower species richness of submerged and rooted floating-leaved species in lakes along this impounded river branch compared to lakes along the free-flowing Waal and IJssel (Figure 4). Similar results were obtained when species that occurred in very low abundance in the lakes (code 'rare' according to Tansley-scale) were excluded from the analysis, indicating the robustness of this relationship.

Table 3. Percentage occurrence of vegetation types in lakes of different age-classes along the unimpounded Waal and IJssel (category 'U') and impounded Neder-Rijn (category 'I').

Age-class (years)	1–29		30–100		>100	
	U	I	U	I	U	I
River regulation						
N lakes	21	16	55	24	70	29
Benthic fil. macro-algae	24	6	0	0	9	0
<i>Ceratophyllum demersum</i>	0	0	5	4	13	7
<i>Chara vulgaris</i>	29	6	4	4	6	0
<i>Elodea nuttallii</i>	29	50	16	50	13	14
<i>Nitella capillaris</i>	5	0	2	8	1	0
<i>Nuphar lutea</i>	0	0	31	0	43	45
<i>Nymphoides peltata</i>	14	0	27	4	41	7
<i>Persicaria amphibia</i>	19	0	7	0	7	0
<i>Potamogeton lucens</i>	14	6	24	4	23	21
<i>P. pectinatus</i>	14	6	20	21	11	14
<i>P. pusillus/trichoides</i>	38	31	16	17	11	21

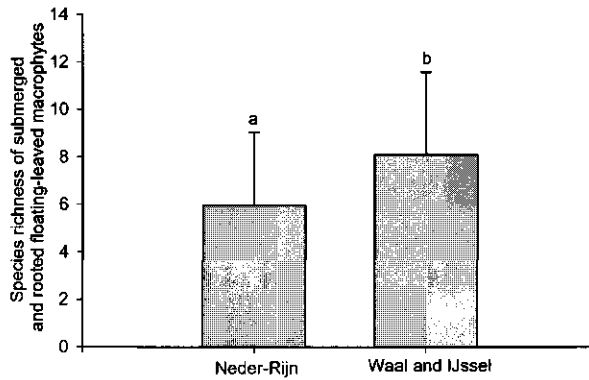


Figure 4. Mean (\pm s.d.) of the species number of submerged and rooted floating-leaved macrophyte species in lakes along the impounded Neder-Rijn (n lakes = 34), and unimpounded Waal (n = 40) and IJssel (n = 26) in 1999. Different letters indicate groups that differ in species number with a significance of $P < 0.01$ (t-test).

Discussion

Our results indicate that the variation in aquatic macrophyte vegetation between lakes in these floodplains is largely determined by differences in lake morphometry, water transparency, water level fluctuations and lake age, while within-lake macrophyte distribution depends on depth and the probability of sediment exposure (drawdown) in summer. Surprisingly, macrophyte composition was correlated more strongly to lake age and occurrence of drawdown than to the duration of overland flooding.

Ageing of lakes tends to coincide with a reduction in water level fluctuations due to sedimentation of fine organic and mineral particles (Rostan, Amoros & Juget 1987; Schwarz, Malanson & Weirich 1996; Middelkoop 1997). The accumulated layer of clay sediments induces a reduced porosity of the lake bottom, thereby reducing the exchange of groundwater between the river and the lake (Wood & Armitage 1997). Indeed, in the set of 100 floodplain lakes sampled in 1999, young lakes had a significantly higher occurrence of sandy sediments and exhibited larger water level fluctuations compared to older lakes, in which clay sediments prevailed (Van Geest *et al.*, in press). In lakes along other rivers, floods may have a scouring effect by removing the accumulated sediment layer (Henry *et al.* 1994; Bornette *et al.* 1994). However, due to a lack of erosive currents during flooding of lakes along the Lower Rhine, there is probably a systematic decrease in the amplitude of water level fluctuations with increasing age.

The decreasing amplitude of water level fluctuations with lake age may have a strong impact on macrophyte succession. Young lakes tended to be dominated by desiccation-

tolerant species like *C. vulgaris*, and old lakes by desiccation-sensitive species such as *N. lutea*. Amphibious species, such as *P. amphibia*, show a clear association with alternating exposed and reflooded sites (Partridge 2001), while the abundance of *Chara* spp. seems positively related to previous drawdown. In addition, the prevalence of *N. peltata* was positively related to the probability of sediment exposure. According to Smits, Van Ruremonde & Van der Velde (1989), germination of seeds of *N. peltata* requires oxygen, while seeds and seedlings of this species show some resistance to the effects of desiccation. In contrast, *Elodea* spp. were reported to be susceptible to desiccation (Martin *et al.* 1995). In addition, *N. lutea* was negatively related with the probability of sediment exposure, and germination of *N. lutea* is stimulated by anoxic conditions in sediments, whereas the seeds and especially juvenile submerged plants of this species are highly susceptible to desiccation (Smits *et al.* 1989).

Our evidence for the importance of reduced amplitude of water level fluctuations with lake age is indirect, because it is based upon a comparison of differently aged lakes. Nevertheless, we observed a clear characterization of species dominating certain age groups of lakes fitting the 'reduced water level fluctuation hypothesis'. However, macrophyte succession during lake ageing may be driven by other factors at the same time. For instance, organic matter accumulates in lake sediments over the course of time, thereby changing sediment properties and the nutrient status. Furthermore, macrophyte succession may be influenced by differences in dispersal characteristics of species. In general, early successional species have easily dispersed propagules, such as oospores, plant fragments and turions in *C. vulgaris* and *P. pusillus* (Wade 1990; Haag 1983). In contrast, late-successional species such as *N. lutea* (Smits *et al.* 1989) often possess heavy or large propagules that are transported over relatively short distances (Silvertown 1982), making them poor colonizers. Overall, it can be concluded that the succession of macrophytes shifts from being externally driven in young floodplain lakes (allogenic succession) to internally driven in old lakes (autogenic succession).

Surprisingly, surface flooding had no relationship with species dominance in our study (Table 2), although the total cover of submerged macrophytes declined in lakes with higher duration of surface flooding (Van Geest *et al.* 2003). Apparently, water level fluctuations and associated drawdown events overrule the effects of flooding by the river on macrophyte species dominance in these lakes. In contrast, other studies have emphasized the importance of the erosive power of the water current and timing and duration of flooding for macrophyte composition and succession in floodplains (Bornette, Amoros & Lamoroux 1998; Henry *et al.* 1994; Janauer & Kum 1996; Tyser *et al.* 2001). The discrepancy between these studies and our results might be caused by differences in the timing and intensity of flooding. In our temperate regions, floods occur predominantly during winter when vegetation largely remains underground as dormant structures and the

temperature is low. This reduces the ecological effects of floods compared to summer flooding (Brock *et al.* 1987). In addition, in lakes along the Lower Rhine the erosive force of floods in lakes is relatively weak, which may explain the minor impact of floods compared to other studies.

The impoundment in the 1960s of the Neder-Rijn, one of the three branches of the Lower Rhine, has resulted in strongly stabilized water levels in the main channel and adjacent floodplain lakes (Figure 1). Hence, the amplitude of water level fluctuations and occurrence of drawdown are strongly reduced in lakes along the Neder-Rijn compared to the unimpounded Waal and IJssel. Our results suggest a reduced species richness of the lakes along the Neder-Rijn, caused by stabilization of the water level in this river branch. Species richness of macrophytes in lakes along the three branches of the Lower Rhine tended to peak at intermediate amplitude of water level fluctuations (Van Geest *et al.*, in press). In lakes with small water level fluctuations, the absence of drawdown events may result in reduced species richness. Disturbances caused by drawdown may prevent competitive exclusion by desiccation-sensitive species, or may stimulate germination of species like *Chara* (Bonis & Grillas 2002), thereby increasing species richness (Hill, Keddy & Wisheu 1998). This may explain the rare occurrence of desiccation-tolerant species such as *C. vulgaris*, *N. peltata*, and *P. amphibia* in lakes along the Neder-Rijn (Table 3). The rarity of late-successional species like *P. lucens* and *N. lutea* in 30 – 100 years old lakes along the Neder-Rijn (Table 3) is more difficult to explain, but might be due to competition with the desiccation-sensitive *E. nuttallii*. The latter species, which is a rapid colonizer in riverine habitats (Barrat-Segretain, Henry & Bornette 1999; Barrat-Segretain 2001), tended to dominate the vegetation of lakes with stable water levels.

The rarity of characteristic riverine species is in line with patterns found in similar studies along rivers with strong regulation of the water level regime (Nilsson *et al.* 1991; Jansson *et al.* 2000; Robertson, Bacon & Heagney 2001; Johansson & Nilsson 2002). This pattern is often thought to result from changes in the flooding regime (Ward & Stanford 1995). However, along the Neder-Rijn the construction of the weirs did not result in changes in flooding regime, because the weirs are closed below mean river flows only. Thus, our results show that a reduced occurrence of drawdown because of water level stabilization in the main channel during low river flow can also affect the establishment and growth of characteristic riverine species in floodplain lakes, a factor that has received little attention so far.

The water level regime has been strongly regulated in the majority of large temperate rivers during the past few centuries. In North America, Europe, and the former Soviet Union, 71% of the large rivers have been affected by dams and reservoirs, water diversion and abstraction (Dynesius & Nilsson 1994). In many river systems, the natural low river

water levels has been replaced by an artificial distribution with higher water levels than would be expected naturally (McMahon & Finlayson 2003). Our results indicate that for macrophyte composition and succession of aquatic habitats along regulated rivers, changes in the water level regime during low river flow may be as important as changes in the flooding regime. Consequently, restoration of aquatic habitats in floodplains along river stretches with stabilized water levels during low discharges may be difficult to achieve. Where possible, the natural water level regime in the river should be restored to conserve the full successional range of floodplain water bodies including those with the highest biodiversity. Along most regulated rivers, reinstatement of the natural water level regime may not be achievable. However, it might be possible to allow low river levels in certain years to promote incidental drawdowns of lakes. Along the unregulated branches of the Lower Rhine, the number of lakes with drawdown varies strongly from one year to another, because of large inter-annual variation in the minimum water levels of the river. In years with prolonged periods of very low water levels (such as 1959, 1976, 1978, and 1991), 25 to 60% of the lakes dried out, whereas in other years the proportion of dried-out lakes was small (Coops & Van Geest, in press). Although difficult in practice, incidental temporary lowering of the river water level might be considered a suitable management to enhance the ecological status of the Neder-Rijn river branch as well as other regulated rivers.

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Picture by Gerben van Geest

In years with extreme low water-levels, lake sediments may become exposed (picture above). Under these conditions, bi-annual species (such as *Oenanthe aquatica*) may germinate and become a dominant aspect of the vegetation in subsequent year (picture below), together with *Nymphoides peltata* and submerged macrophytes.



Picture by Hugo Coops (RIZA)

Chapter 5

Low water levels stimulate macrophyte abundance in eutrophic shallow floodplain lakes

Van Geest, G.J., H. Coops & M. Scheffer

Abstract

We monitored the macrophyte composition and cover in 70 lakes in the floodplains of the regulated river Rhine in The Netherlands from 1999 to 2003. There were large interannual differences in submerged vegetation cover, whereas for nymphaeids and helophytes the differences were relatively small. The interannual variation in submerged vegetation cover was strongly related to probability of lake drawdown and lake surface area. Remarkably, we found no effects of nutrient level, and submerged vegetation occurred abundantly in small lakes with high nutrient levels. We suggest that this pattern may be explained from occasional drawdown events in lakes along the Lower Rhine, triggering shifts towards dominance by submerged vegetation. Without drawdown, these lakes will gradually return into the unvegetated state, although this may take several years. Therefore, if drawdown occurs frequently, the majority of the lakes will be in a transient vegetated state most of the time. This implies that hydrological regulation may be an important factor aggravating the permanent loss of submerged vegetation due to cultural eutrophication.

Introduction

Vegetation dynamics in shallow lakes can be rather erratic, and in many studied cases, the driving forces have not been clearly identified. Changes in macrophyte cover and composition in shallow lakes are often explained as a result of varying nutrients loads (Toivonen & Baeck, 1989; Hough *et al.*, 1989; Tracy *et al.*, 2003). Increased nutrient levels may result in a reduced cover and a lower species richness of aquatic macrophytes, due to a decreased transparency resulting from enhanced algal growth or higher concentrations of suspended sediments (Jeppesen *et al.*, 1997; Scheffer, 1998). In addition, water-level fluctuations may cause shifts in macrophyte cover and composition (Blindow *et al.*, 1993; Scheffer, 1998; Havens *et al.*, 2004). However, many well-studied lakes have artificially stabilized water levels, and therefore lack the influence of fluctuating water levels. Thus, water-level fluctuations have received far less attention compared to the effects of nutrients in explaining aquatic vegetation patterns.

In floodplains, most lakes are subject to large water-level fluctuations. Flooding through overland inflow from the river is often regarded as a major driving force for changes in vegetation composition and structure (Chapter 3 and 4; Brock *et al.*, 1987; Van den Brink *et al.*, 1991). Importantly, floodplain lakes may also be subject to extreme low water levels. Infiltration of lake water into the alluvial aquifer may result in a decline of lake water-levels during low river water-levels. Depending on lake morphometry, this may result in exposure of the lake bottom (drawdown) (Chapter 2), which may have a strong impact on the composition and abundance of aquatic vegetation (Chapter 4; Wilcox & Meeker, 1991; Wagner & Falter, 2002).

In this study, we analyzed interannual changes in aquatic macrophyte cover for a set of 70 floodplain lakes along the river Lower Rhine in relation to water-level fluctuations, lake morphometry, and lake age. Subsequently, we evaluated the impact of water-level fluctuations on macrophyte cover in these lakes.

Study area

The Lower Rhine in the Netherlands consists of three branches, the Waal, IJssel, and Neder-Rijn, along which 70 lakes were selected for annual monitoring of macrophyte composition and cover. At the location where the Rhine enters the Netherlands, the discharge varies annually between c. 800 and 12,000 m³ s⁻¹, resulting in water-level fluctuations of up to 8 metres. Typically, the maximum annual river discharge occurs in winter and the minimum in autumn, though high and low discharges may occur at any moment throughout the year (Buijse *et al.*, 2002). In some years, prolonged periods of extremely low water levels occur at the end of the growing season. Because water levels in floodplain lakes are strongly linked to the water level in the river through groundwater flow (Chapter 2), periods of low water level in the river may result in partial or complete drawdown of the lakes as well. In the period 1999 – 2002, no prolonged periods of low

river water level occurred (Figure 1). Consequently, almost none of the investigated lakes were drawn down during these years. By contrast, river water levels became extremely low during 2003, and the lowest river water-level measured ever since the start of the monitoring in 1824 occurred in early October 2003. As a result, many floodplain lakes along the Lower Rhine dried out in late 2003.

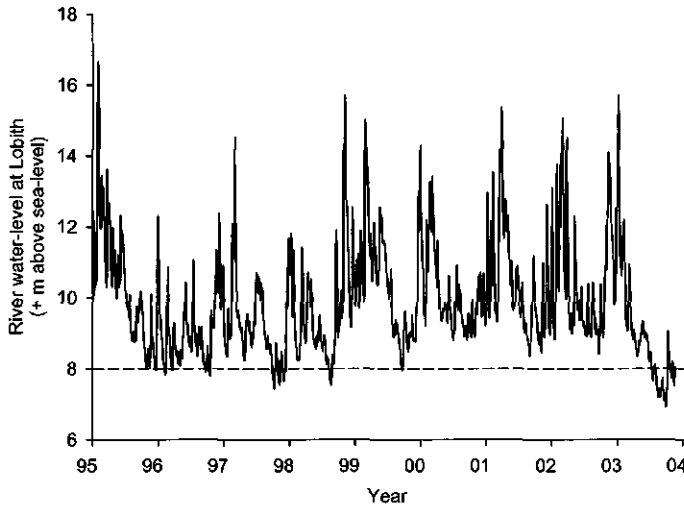


Figure 1. River water-level in the Lower Rhine at Lobith (m + sea-level) during 1995 – 2003. Note that prolonged periods with water level < 8.00 m at Lobith are associated with extreme low water levels in many floodplain lakes along the Lower Rhine.

Besides the effects of drawdown, macrophyte cover may also be strongly influenced by the water level in spring. During 1999 – 2003, there were large interannual differences in mean water-level in spring in the Lower Rhine. In 1999 and 2001, spring water levels were relatively high, whereas in 2000, 2002 and 2003, they were lower (Figure 2). Although water levels were not routinely monitored in individual lakes during spring 1999 – 2003, it can be assumed that interannual differences in water levels of the lakes mirror those of the river water-level (Chapter 2). During each winter in the years 1999 – 2003, all lakes were inundated by the river through surface overflow; yet none of the lakes was permanently connected to the main channel.

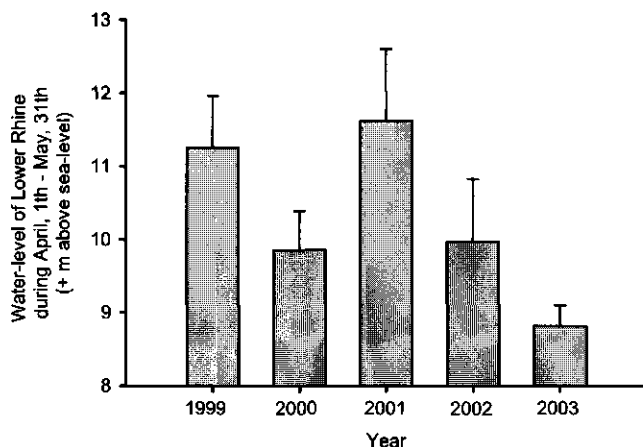


Figure 2. Water level of the Lower Rhine at Lobith in the period April – May 1999 – 2003

Methods

In 70 lakes in the floodplains of the Rhine branches (Waal, IJssel, and Neder-Rijn: 33, 20, and 17 lakes, respectively), vegetation composition and - cover were monitored annually once per year (July – August) during 1999 – 2003. In each lake, the proportion of the total surface covered by vegetation types (as described in Chapter 4) was estimated visually. For each lake, estimates of inundation duration, surface area, and shoreline length were obtained from GIS-maps (RIZA, The Netherlands), and the approximate age was derived from historic topographical maps. Reliable estimates of lake age could be made up to 300 years; older lakes were regarded as 300 years old. The uncertainty of the lake age estimation was about one year for lakes that were newly dug after 1980, 3 - 7 years for lakes originating from the period 1910 - 1980, and 10 - 25 years for lakes prior to 1910.

In July and October 1999, water depths were measured at several locations in each lake using a marked rod to assess the seasonal water-level change (WL_{J-O}). Based on these data, mean lake depth (D_{meanJ}), maximum lake depth (D_{maxJ}), and the proportion of the surface area of the lake bottom which became exposed between July and October 1999 ('drawdown area') was calculated. In addition, the ratios $(WL_{J-O} / D_{meanJ})_{1999}$ and $(WL_{J-O} / D_{maxJ})_{1999}$ were calculated as indicators of the probability of drawdown of a lake. The ratio $(WL_{J-O} / D_{meanJ})_{1999}$ indicates the probability for partial lake drawdown, as field observations indicate that for this ratio, a value of one equals approximately 50% drawdown area of a lake surface area (Figure 3). By contrast, the ratio $(WL_{J-O} / D_{maxJ})_{1999}$ is defined as an indicator for complete lake drawdown, as a value of one equals 100% lake

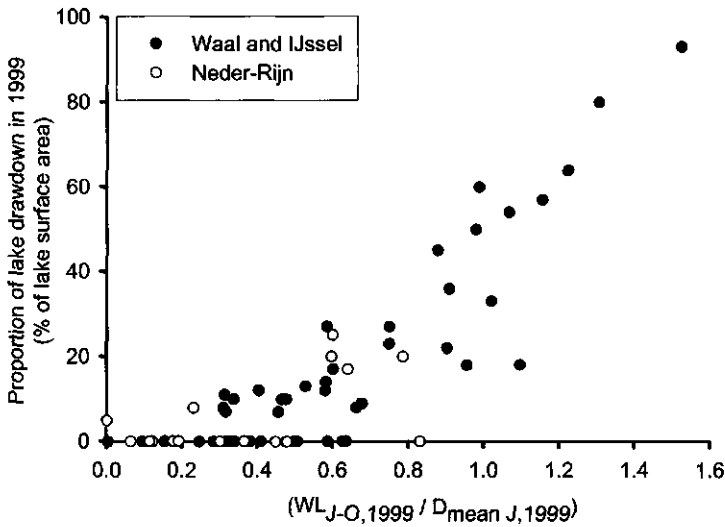


Figure 3. Relationship between the ratio of seasonal water-level trend between July and October (WL_{J-O}) and mean lake depth (D_{meanJ})₁₉₉₉ in 1999

drawdown. In 1999, there was a clear relationship between $(WL_{J-O} / D_{meanJ})_{1999}$ and the measured proportion of drawdown area in the lakes (Figure 3). To check if $(WL_{J-O} / D_{meanJ})_{1999}$ may also be used as a reliable indicator for lake drawdown in other years, for each lake the proportion of drawdown area was estimated visually during October 2003, which coincided with the end of a prolonged period of extremely low water levels in the main channel. Overall, the indicator for partial and complete lake drawdown were highly correlated to percentage lake drawdown in 2003 for lakes along the Waal and IJssel (Spearman $R = 0.73$ and 0.72 respectively, $p < 0.000001$), indicating that both indicators give reliable estimates of the probability for lake drawdown. However, for lakes along the Neder-Rijn the correlation between the indicator for partial and complete lake drawdown and percentage drawdown lake area in 2003 was less strong (Spearman $R = 0.48$ and 0.52 , respectively, $p < 0.05$), which can be explained by active regulation of the water-level in the main channel during low river discharges. Therefore, we excluded lakes along the Neder-Rijn from the statistical analysis. Furthermore, we only used lakes older than 5 years to exclude the effects of disturbances of recent excavation. As a result, the statistical analyses were carried out with a data set of 42 lakes along the Waal and IJssel.

Data analysis

To visualize interannual changes in cover of submerged vegetation, nymphaeids, and helophytes, we plotted for each lake the cover value in one year (C_Y) against the cover value in the subsequent year (C_{Y+1}), and computed absolute year-to-year change ($C_{Y+1} -$

C_Y) for each lake and each pair of successive years. For submerged vegetation, we made a distinction between 'collapsing' and 'recovering' lakes (with a 'decline' or 'increase' of submerged vegetation cover in each pair of successive years, respectively). We used multiple linear regression (Jongman *et al.*, 1995) to evaluate the relationship between five environmental variables (Table 1) and collapsing or recovering lakes ($C_{Y+1} - C_Y \leq 0$ or $C_{Y+1} - C_Y \geq 0$, respectively). All interannual changes in vegetation cover were normally distributed after angular transformation.

Table 1. Five independent environmental variables used in multiple linear regression analysis to predict interannual changes in submerged vegetation cover in the lakes during 1999 – 2003; ^a = $\ln(x)$ -transformed

Variable	unit	comments
Lake age ^a	yr	for accuracy: see Material & Methods
Lake surface area ^a	ha	surface area of lake at start of growing season
Mean lake depth ^a	m	calculated from 5 – 31 water depth measurements in July 1999 in each lake
Inundation duration ^a	d.yr ⁻¹	long year average 1990–1995
Probability for complete lake drawdown	-	index for probability of lake drawdown (for calculation: see Material & Methods)

To summarize the observed annual changes in cover and composition of submerged vegetation, we constructed a Markov chain-model as proposed by Horn (1975). To calculate the transition probability matrix for our data set, each lake was categorised according to its dominant submerged vegetation type (inclusive the category vegetation-poor). Subsequently, for all lakes dominated by a certain submerged vegetation type in one year (Y_t), the probability was calculated to remain the same vegetation type or to be taken over by other vegetation types in the next year (Y_{t+1}). The overall transition matrix of the period 1999 – 2002 was calculated on the total of inter-annual changes in vegetation composition in the years 1999/2000, 2000/2001, and 2001/2002.

Results

There were large interannual differences in cover of submerged vegetation, whereas there was little variation in cover for nymphaeids, in particular *Nuphar lutea* vegetation, and helophytes (Figure 4). For submerged vegetation, in each pair of years there was a group of lakes with decreasing and a group of increasing cover values (Table 2). Overall, the number of lakes rich in submerged vegetation dropped from 60 to approximately 30% between 1999 and 2003 (Figure 5). Over this time period, the largest decrease in the number of vegetation-rich lakes occurred between 1999 and 2000 (Figure 5). In addition,

there were large changes in the dominant submerged vegetation types in the lakes (Table 3). Few lakes dominated by *Elodea nuttallii*, *Potamogeton lucens*, *P. pectinatus*, *P. pusillus*, or *Chara vulgaris*, were dominated by the same vegetation type in the next year, and about 30% of the lakes dominated by these vegetation types turned into the vegetation-poor state in the subsequent year.

The interannual decline in submerged vegetation cover over 1999-2000 and 2000-2001 was positively related to probability for complete lake drawdown ($R^2_{\text{adjusted}} = 0.39$ and 0.27 , respectively). In addition, for 2000-2001 and 2001-2002 a decline in submerged vegetation cover was negatively related to lake surface area (Table 4). When the probability for complete lake drawdown ($WL_{J-O} / D_{\text{max}J}$)₁₉₉₉ was substituted with the probability for partial lake drawdown ($WL_{J-O} / D_{\text{mean}J}$)₁₉₉₉, the latter variable contributed only marginally significant for the decline in submerged vegetation cover over 1999 – 2000 ($p < 0.1$; $R^2_{\text{adjusted}} = 0.25$).

Table 2. Percentage of interannual shifts between vegetation-rich (submerged vegetation cover $\geq 20\%$) and vegetation-poor lakes ($< 20\%$) during 1999 – 2003. For each pair of years, the comparison is based on 70 lakes, except for 2002-2003, as in 2003 six lakes were already dried out during the sampling period of the aquatic vegetation.

Year _n – Year _{n+1} State Year _n – Year _{n+1}	1999-2000	2000-2001	2001-2002	2002-2003
Rich – Poor	27	7	16	12
Poor – Rich	7	7	6	6
Rich – Rich	36	36	27	22
Poor – Poor	30	50	51	60

Over the period 1999-2003, a significant relationship between *increasing* submerged vegetation cover was only obtained for 2001-2002. Over this pair of years, an increase in submerged vegetation cover was positively related to probability of lake drawdown, although the predictive power was rather weak ($R^2_{\text{adjusted}} = 0.10$). For 2002-2003, the interannual decline or increase of submerged vegetation cover was not significantly related to any environmental variables listed in Table 1. Similarly, no significant relationships were found between interannual changes in cover of nymphaeid species or helophytes and environmental variables during 1999 – 2003.

Using the water level in the main channel as a surrogate for lake water levels, it was shown that spring water levels were not related to the number of vegetation-rich lakes (Figure 2 and 5).

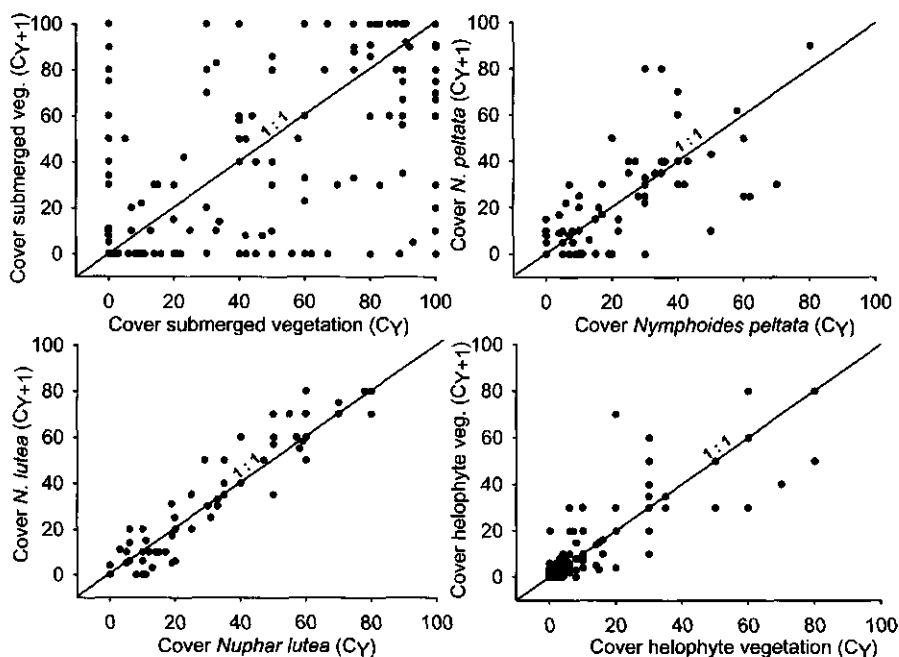


Figure 4. The percentage cover in lakes of respectively submerged vegetation, *Nymphaeoides peltata*, *Nuphar lutea* and helophyte vegetation in one year (C_Y) relative to the cover of these vegetation types in the next year (C_{Y+1}) during 1999 – 2003

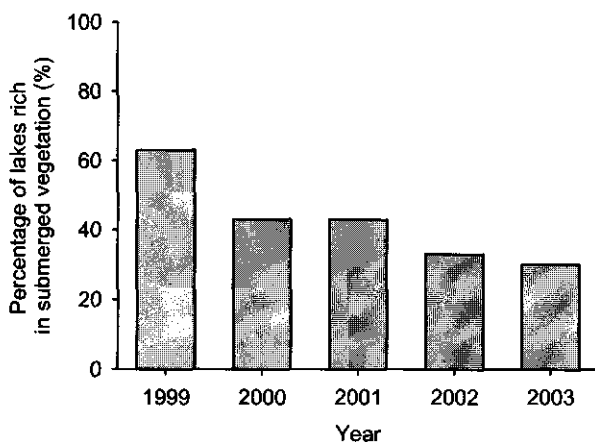


Figure 5. Percentage of vegetation-rich (submerged vegetation cover $\geq 20\%$) and vegetation-poor lakes ($< 20\%$) during 1999 – 2003

Table 3. The transition matrix (Markov chain) for changes in vegetation composition in the lakes for the period 1999 – 2002. The change for the vegetation types in the subsequent year is represented in proportions. CS = *Callitriche spec.*; CD = *Ceratophyllum demersum*, CV = *Chara vulgaris*, EN = *Elodea nuttallii*, PL = *Potamogeton lucens*, Ppe = *Potamogeton pectinatus*, Ppu = *Potamogeton pusillus*, PT = *Potamogeton trichoides*, UV = *Utricularia vulgaris*; ZP = *Zannichellia palustris*; VP = Vegetation-poor (submerged vegetation cover < 20%)

	N lakes											
	1999	CS	CD	CV	EN	PL	Ppe	Ppu	PT	UV	ZP	VP
CS	1	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
CD	2	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.67
CV	4	0.00	0.00	0.29	0.00	0.00	0.00	0.29	0.00	0.00	0.00	0.43
EN	7	0.00	0.06	0.00	0.39	0.06	0.00	0.00	0.11	0.00	0.00	0.11
PL	6	0.00	0.00	0.00	0.08	0.42	0.08	0.00	0.00	0.00	0.00	0.42
Ppe	12	0.00	0.00	0.00	0.09	0.00	0.26	0.04	0.22	0.00	0.00	0.39
Ppu	5	0.00	0.00	0.09	0.00	0.18	0.09	0.09	0.18	0.00	0.09	0.27
PT	3	0.00	0.00	0.00	0.21	0.00	0.14	0.07	0.50	0.00	0.00	0.07
UV	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
ZP	0	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.33	0.33
VP	29	0.00	0.00	0.00	0.02	0.00	0.04	0.02	0.00	0.00	0.03	0.89

Table 4. Results of multiple linear regression analysis for interannual decline in submerged vegetation cover during 1999 – 2003. No significant variables were obtained for interannual decline in submerged vegetation cover between 2002-2003. * = $\ln(x)$ -transformed; + = $p < 0.1$; * = $p < 0.05$; ** = $p < 0.01$

Pair of years	1999-2000	2000-2001	2001-2002
Probability complete drawdown	1.24**	0.53 ⁺	
Lake surface area ^a		-0.14**	-0.16**
R ² _{adjusted}	0.39	0.27	0.18

Discussion

Submerged vegetation cover fluctuated strongly between years, in contrast to relatively small between-year differences in other aquatic vegetation types, viz. nymphaeids and helophytes. The relative stability of the latter two groups may be related to the absence of floodplain inundations within the growing season during our study period. Brock *et al.* (1987) showed that summer inundations reduced strongly the cover of helophytes and *Nymphoides peltata*.

For submerged macrophytes, it is usually assumed that vegetation cover in shallow lakes is negatively related to nutrient level (Jeppesen *et al.*, 1990). However, we observed no

significant relationships between submerged vegetation cover total phosphorus or nitrogen levels, as many floodplain lakes along the Lower Rhine with total P concentrations up to 0.4 mg L^{-1} had a high cover of submerged vegetation (Chapter 3). By contrast, we found a strong relationship between submerged vegetation cover and water level in the lakes, a factor that has received little attention in literature so far. In the following sections, we first reflect briefly on the possible effects of water-level regime on submerged macrophyte abundance. Subsequently, we present a conceptual model to explain the effect of water-level fluctuations on submerged vegetation dynamics in our floodplain lakes.

Water-level fluctuations may have direct as well as indirect effects on submerged macrophytes. During extreme low water-levels, lake sediments may become exposed to the air (drawdown), thereby increasing sediment density by consolidation (James *et al.* 2001). An increased sediment density may stimulate conditions for submerged macrophyte growth, as highly fluid sediments impede establishment of propagules and anchorage of rooted macrophytes (Barko & Smart, 1986). Furthermore, the phosphorus exchange between water and sediment will be affected, due to changes in redox conditions, sorption mechanisms, microbial activity, and physical and biotic turbulence (Coops & Hosper, 2002). In addition, nitrogen loss occurs (De Groot & Van Wijck, 1993). Moreover, experimental drawdown of lake sediments stimulated germination of several submerged macrophyte species, i.e. *Chara* spp. (Chapter 7) and *Zannichellia palustris* (Bonis *et al.*, 1995), which is in line with increasing cover values of submerged vegetation after desiccation and subsequent resubmersion of lake sediments (Gibbs, 1973; Havens *et al.*, 2004). Also in the absence of drawdown, low water levels may result in an increased submerged vegetation cover, probably because of increased light availability in the water column at shallow water depths (Blindow *et al.*, 1993).

At the other extreme, inundation by river water results in an increased load of nutrients and suspended solids to floodplain lakes, which may increase turbidity and retard growth conditions for submerged macrophytes (Van den Brink *et al.*, 1991; Van den Brink *et al.*, 1992). In accordance, submerged vegetation cover was negatively related to inundation duration in a set of 215 lakes along the Lower Rhine (Chapter 3). Furthermore, inundation by the river may facilitate rapid recolonization of the lakes by large benthivorous bream (*Abramis brama* L.) (Grift *et al.*, 2001; Molls, 1999), a fish species which have shown to deteriorate growth conditions for submerged macrophytes (reviewed by Jeppesen *et al.*, 1997; Scheffer, 1998). Indeed, in many lakes along the lower Rhine, the fish community is dominated by bream (Grift, 2001; Molls, 1999), and in a set of 20 floodplain lakes along the Lower Rhine, the proportion of bream in the fish population is negatively related to submerged vegetation cover (Scheffer *et al.*, submitted).

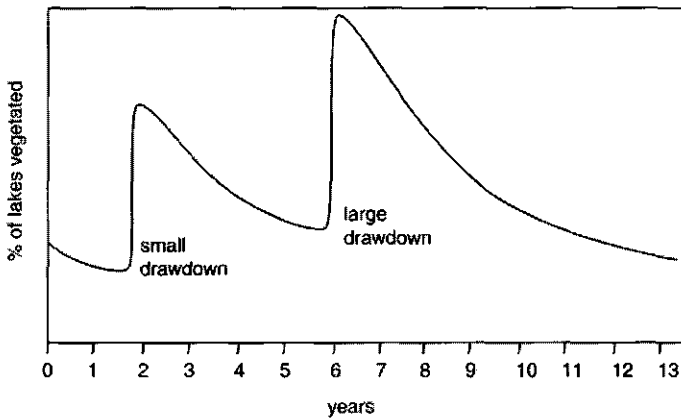


Figure 6. Conceptual model that explains submerged vegetation dynamics in shallow lakes. Drawdown will result in an increase in number of vegetation-rich lakes. However, when the shifting lakes do not experience extreme low water levels in subsequent years, and are regularly flooded by the river, these lakes gradually shift back towards the unvegetated state

A conceptual model of the dynamics of the number of vegetated lakes in relation to drawdown events is presented in Figure 6. Although there may be lakes which permanently harbour abundant vegetation, the overall high nutrient levels suggest that there will be an important group of lakes which would be unvegetated if the water level would remain stable. We hypothesize that many of these lakes occasionally experience low water levels, resulting in shifts towards the vegetated state triggered by the mechanisms discussed earlier. Subsequently, each of the lakes will switch back towards the unvegetated state after several to many years. Consequently, if drawdown occurs frequently, many lakes will be in a transient vegetated state most of the time.

The 5-year dynamics of submerged vegetation in our lakes fits with the disequilibrium model described above. Over the study period (1999 – 2003), there was a general tendency of vegetation loss in the lakes (Figure 5). We suggest that this tendency is explained by the absence of drawdown events in almost all lakes. By contrast, in the floodplain lakes along the lower Rhine prolonged periods with low water level occurred in the years prior to the study, 1997 and 1998. For a set of 121 lakes (partial overlapping with the lakes of this study), it was calculated that approximately 10-20% of these lakes showed drawdown in these years (Chapter 6). The low river water-level in 1997 and 1998 may have facilitated a relatively high number of lakes rich in submerged vegetation at the start of our study period in 1999. The idea that drawdown pushed many lakes to a transient vegetated state during these years, is in line with the observation that the probability of lakes to shift back to a vegetation-poor state during our study period was positively related to the probability to drawdown of these lakes. In addition to drawdown, low water levels in 1997 and 1998 may also have facilitated submerged vegetation growth

in subsequent years, by increasing light availability at shallow water depths. However, changes in submerged vegetation cover were much stronger related to the probability of complete lake drawdown than to the probability of partial lake drawdown, indicating that drawdown may have a stronger effect on vegetation cover than low water levels only.

Furthermore, our results indicate that – in the absence of low water levels – the effects of drawdown on submerged vegetation cover will last for only a few years. This may be caused by yearly inundation by river water of our lakes during 1999 – 2003. These inundations facilitated the input of nutrients and suspended solids, and immigration of fish, thereby impoverishing growth conditions for submerged macrophytes. The positive effect of drawdown on submerged vegetation cover in subsequent years might have lasted longer if the lakes would not have been yearly flooded by river water during 1999 – 2003.

In addition to the effect of water-level fluctuations, large interannual changes in submerged vegetation cover were restricted to lakes with a small surface area. This can be explained by the fact that along the Lower Rhine, submerged vegetation was either dominant or almost absent in small lakes, while in larger lakes submerged vegetation was usually absent (Chapter 3). Therefore, large changes in submerged vegetation cover were restricted to small lakes, thereby explaining the negative relationship between interannual decline in submerged vegetation cover and lake surface area in our data set.

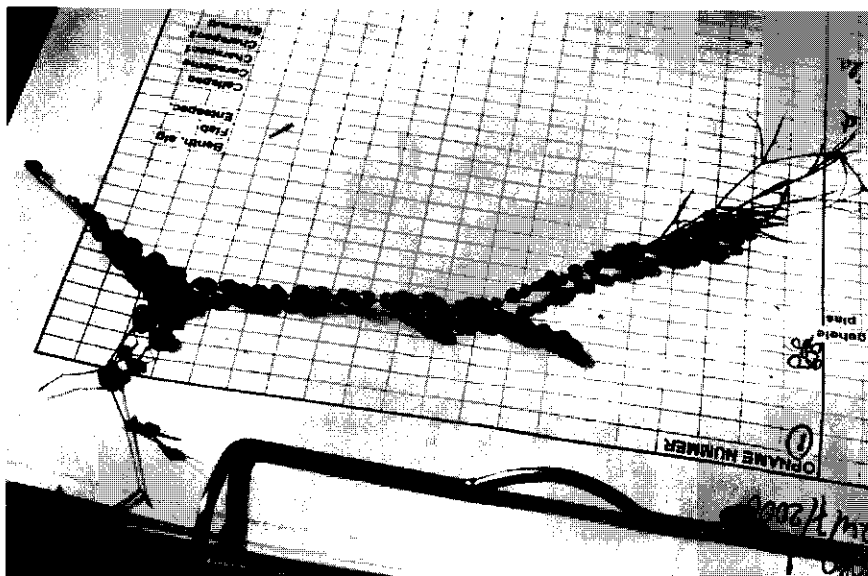
Submerged macrophyte cover may be strongly influenced by interannual variation in lake water-level during spring, as a result of increased irradiance at low water levels. In our data set however, spring water level and submerged vegetation cover were not related, and some years with high spring-water levels (such as in 1999) coincided with a high number of macrophyte-rich lakes. Apparently, the effects of previous drawdown events seem to overrule the effect of high spring water-levels in subsequent years.

Our results suggest that especially those water-level fluctuations that result in sediment exposure may play a dominant role in driving submerged vegetation dynamics in shallow lakes in addition to the classical relationship between nutrient levels and submerged vegetation. In particular, we hypothesize that occasional drawdown events in lakes may result in recolonization of submerged vegetation after resubmersion of lake sediments. However, our conclusions are derived in an indirect way; viz. the proportion of lakes that became vegetation-poor was positively related to the probability of lake drawdown. The ultimate test of this hypothesis would be to verify if drawdown of a large number of lakes would result in a strong increase in number of vegetation-rich lakes in subsequent growing season. The extreme low water-levels of the Lower Rhine in 2003, resulting in drawdown of many floodplain lakes for at least several weeks, may provide us the opportunity to test this hypothesis.

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In eutrophic floodplain lakes, macrophytes may become heavily infested by periphyton during the growing season, as is shown in this rather extreme example. Photo: John van Schie (RIZA)

Chapter 6

Extreme water-level fluctuations determine aquatic vegetation in modified large-river floodplains

H. Coops & G.J. Van Geest

Archiv für Hydrobiologie, supplement Large Rivers (in press)

Abstract

Water bodies in large-river floodplains are typically dominated by aquatic vegetation. The proportion of macrophyte-dominated lakes varies between years, depending on annually different water-level fluctuations within the lakes. We reanalysed aquatic-vegetation inventories made over five decades in floodplain lakes along the Lower Rhine, and related them to summer inundation and drawdown events. We observed a lower probability of submerged macrophyte dominance (lake cover > 20%) after inundation in summer, with contrasting responses for different species. Lake-bottom exposure during prolonged low water stages had an opposite effect, resulting in an increased probability of dominance by submerged vegetation and a decrease of nymphaeid vegetation. Our results indicate that under the current, hydromorphologically modified, conditions a small proportion of water bodies in the floodplains has abundant aquatic vegetation, unless new sites are repeatedly created which provide opportunities for colonisation. The results are important for management as they help in defining the ecological status of floodplain lakes.

Introduction

Large-river floodplains generally harbour a high diversity of plants and animals, linked to the multi-scale transitions between aquatic and terrestrial ecotopes (Tockner *et al.* 2000). Water bodies in floodplains are often characterised by extensive submersed and floating vegetation. These macrophyte-dominated, clear-water lakes may have a great conservation value compared to macrophyte-poor, algal-dominated lakes.

Hydrological disturbance may trigger shifts in shallow lakes between the macrophyte-dominated and the macrophyte-poor state (Scheffer 1998). In floodplains along large rivers, disturbance may come from both high- (floodplain inundation) and low-water periods (sediment exposure). Deep and long-lasting inundations of the growing vegetation may result in macrophyte declines (Spence 1982, Brock *et al.* 1987). On the other hand, flood scouring and drawdown may remove existing vegetation stands, and stimulate subsequent recolonization by pioneer species (Combroux *et al.* 2001).

Several studies have highlighted the impact of river flooding on aquatic communities in floodplain lakes (Henry *et al.* 1994, Van den Brink 1994, Bornette & Amoros 1996), while the impact of drawdowns induced by low flows has recently gained attention (McMahon & Finlayson 2003). Water bodies may be placed along a "hydrological connectivity gradient", representing the relative influence of river-level dynamics on the ecosystem. With increasing flood levels, floodplain lakes along the lower Rhine become inundated when levee heights are exceeded; the average annual inundation duration has been used by Van den Brink *et al.* (1991) as an indicator of the position of floodplain lakes in the connectivity gradient. They showed a strong effect of inundation duration on aquatic vegetation richness and abundance. However, in a recent study on the lower Rhine, average inundation duration was found to be only weakly correlated with macrophyte abundance (Van Geest *et al.* 2003). The explanation for this discrepancy may be that the studies by Van den Brink (1994) were made at the end of a decade with frequent summer inundations, whereas such inundations had been absent during more than ten years preceding the study of Van Geest *et al.* (2003).

We hypothesise that the recent history of extreme hydrological events in individual floodplain lakes, such as long-lasting inundation and drawdown, is a major factor determining aquatic vegetation abundance in floodplain lakes. To study this hypothesis, we used hydrological monitoring data of the lower Rhine and collected several floodplain macrophyte surveys in the period 1954 - 2001. The results have high significance for managing these ecosystems since large-scale floodplain modification and rehabilitation are planned that will highly impact the hydrological connectivity within the floodplains.

Study area

The floodplains along the lower Rhine branches were dyked many centuries ago and the forelands have been used traditionally for agriculture. Usually, artificial levees ('summer-dykes') prevent inundation of the forelands during minor floods (Van Urk & Smit 1989, Jongman 1992). Many water bodies of different types are situated in the forelands, mostly disconnected from the main channel during low stages. After high floods, water sometimes is discharged from water bodies through pumps or sluices. While many lakes have a natural origin, being cut-off branches (oxbows), the majority of water bodies results from human activities, such as clay-, sand-, and gravel extraction. The water bodies vary in size (0.01 - 45 ha), depth (0.1 - 5 m) and age (6 - > 300 years old). Flooding intensity and drawdown characteristics of the water bodies are highly variable; hardly any scouring occurs during floods, since flow over the forelands is very limited.

The high ecological value of floodplain lakes has been recognized, and deterioration of the river water quality in the 1960's and 1970's has been a matter of concern. Presently, most floodplains are still in agricultural use, though presently nature areas are being reshaped, often in combination with flood protection measures (Buijse *et al.* 2002).

Methods

Inundation of floodplain lakes

Floodplains along the Rhine branches have been classified according to their average annual inundation duration (class 1: 0-2 days, class 2: 2-20 days, class 3: 20-50 days, class 4: 50-150 days); for each lake, we used the class-middle inundation duration (1, 11, 35, and 100 days/year, respectively). Inundations were related to exceedance of water levels at Lobith (the location where the Rhine enters the Netherlands, 862 km from its source) using water-level dependency relationships (class 1: 14.50 m NAP, class 2: 12.00 m NAP, class 3: 11.00 m NAP, class 4: 9.50 m NAP). Using the daily water levels recorded at Lobith over the period 1940-2002, the number of days of inundation during June-September was determined for each inundation class.

Drawdown of floodplain lakes

Data on seasonal water-level decline and depth were available from measurements made in floodplain lakes in early July and late September / October 1999 (Van Geest *et al.* 2003). To express the rate of water-level decline, we distinguished four classes (class 0: 0-0.2 cm d⁻¹, class 1: 0.2-0.55 cm d⁻¹, class 2: 0.55-0.85 cm d⁻¹, class 3: > 0.85 cm d⁻¹), each represented by its median value (0.0, 0.4, 0.7 and 1.0 cm d⁻¹, respectively).

On 1 July 1999, water level at Lobith was 10.37 m +NAP, gradually decreasing to 7.94 m +NAP in the end of September 1999. Ignoring rainfall and evaporation during that period, the water level of each lake was assumed to continuously decline. In our model of water-

level decline, lakes are only refilled during inundation contact, getting isolated when river water levels fall below inundation height, after which the lake level starts to decline at a rate according to its class-average water-level decline. Decline of the water level proceeds until the river water level increases above the current lake level. Assuming a more or less flat lake bottom, drawdown was defined as decline of the water level below the average bottom depth.

Using water levels of the Rhine at Lobith, relative inundation heights of the floodplain and water-level decline, the incidence of drawdown was determined for each lake in the period 1940 – 2001. In the calculation of last summer inundation and lake drawdown, respectively, lakes aged less than 50 years were accounted for.

Vegetation data

Aquatic vegetation data from individual floodplain water bodies situated within the forelands of the Waal and IJssel river branches of the Lower Rhine were obtained from several sources. Table 1 lists the inventories made over the past 50 years by different researchers and with different goals and methods. The resulting dataset can therefore not be treated as giving a representative cross-section of lakes through time. The most extensive data assembled were on abundant presence of submerged and/or nymphaeid vegetation in each individual water body, using the criterium of 20% cover of the open-water surface, or matching descriptions in the different datasets. Lake data from which this could not be established were excluded from the analysis. To avoid bias from the high number of 1998 – 2001 data, we randomly selected one of these years in case more than one was available for a lake within that period. In total, 275 observations were obtained from 121 lakes.

Table 1. Sources of data from surveys made in floodplain lakes along the Lower Rhine

Years	Description	Number of lake years	References
1954-1956	Survey of old river branches (oxbow lakes) along the rivers Rhine and Meuse in the Netherlands (RIVON)	15	Van der Voo & Westhoff 1961; Van Donselaar 1961; Van Donselaar, unpublished data
1974-1991	Monitoring data of floodplain research project (University of Nijmegen)	27	Brock <i>et al.</i> 1987; Van de Steeg, unpublished inventory Rijswaard 1992, Van den Brink, 1994; unpublished data University of Nijmegen
1977-1995	Provincial inventories of Floodplain vegetation (Province of Gelderland) and RIN (Dorschkamp, Wageningen)	101	Bieleman <i>et al.</i> , 1977, Vos <i>et al.</i> , 1978, Jongman & Leemans, 1982; unpublished quadrat data, Province of Gelderland
1992/1993	Monitoring of macrophytes along the Dutch River Rhine (NIOO and RIZA)	8	Creemers, 1994; unpublished data RIZA
1998-2001	Survey of floodplain lakes (University of Wageningen and RIZA)	124	Coops <i>et al.</i> , 2000; Buijse <i>et al.</i> 2002; Van Geest <i>et al.</i> 2003

Results

Vegetation dominance and composition

Of the lake-years in the dataset, abundant submerged vegetation was present in 99 (57%) cases and 172 (63%) cases had abundant nymphaeid vegetation,. The proportion of lakes dominated by either submerged or nymphaeid vegetation fluctuated considerably over time (Figure 1), in particular for submerged vegetation. In the 1950's the proportion of lakes covered by submerged or nymphaeid vegetation was high, in contrast to a low proportion of submerged vegetation-covered lakes in the 1980's. The most commonly occurring species over the entire period were the submerged *Potamogeton lucens* and *P. pectinatus* and the nymphaeid species *Nymphoides peltata* and *Nuphar lutea*.

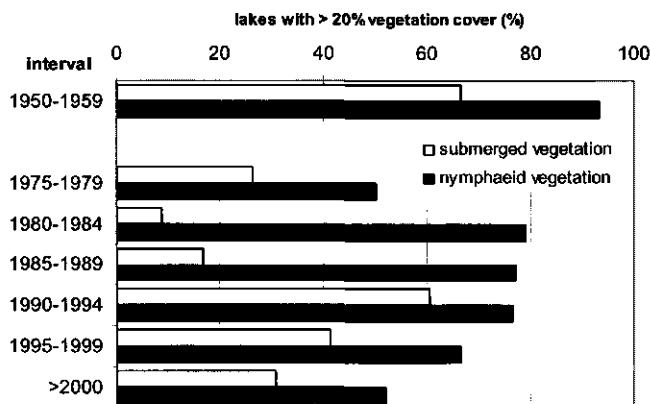


Figure 1. Proportion of lakes with > 20% cover by submerged- and nymphaeid vegetation, resp. in different survey periods.

Occurrence of inundation and drawdown

The number of inundation days for each summer season (1 June – 1 Sept) 1940 - 2001 is presented in Figure 2, based on classes of inundation duration. As most lakes were in inundation class 2 (79%), it is evident that between-year variation in inundation duration is large. Drawdown of floodplain lakes is determined not only by the river water-level and levee height, but also by characteristics of individual lakes: the rate of water-level decline after isolation, and bottom depth. Most lakes (55%) were in the class of water-level decline of 5-8 mm day⁻¹. Drawdowns occur almost every year in some lakes, and never in others, owing to the large variability of the annual water-level course. In the four most extreme years (1959, 1976, 1978, and 1991), 25 to 60% of the lakes dried up due to long-lasting low water levels. The opposite extreme was 1940, when the water levels remained high and none of the lakes dried up (Figure 3).

Impact of inundation and drawdown on macrophytes

Macrophyte occurrence was strongly related to summer flooding. The proportion of submerged macrophyte-covered lakes was affected by the duration of summer inundation in the previous year (Figure 4). When summer inundation was 20 days or more, the proportion of lakes that was macrophyte-covered in the next year was smaller than of lakes with no previous inundation (24% vs. 43%). In addition, submersed macrophyte dominance was lower in the years following summer inundation: $\pm 25\%$ of the lakes inundated maximally 4 years before had extensive submerged vegetation cover, in contrast to approximately 70% of the lakes that had not been inundated for at least 15 years (Table 2). Submerged species abundances tended to decline in the years following

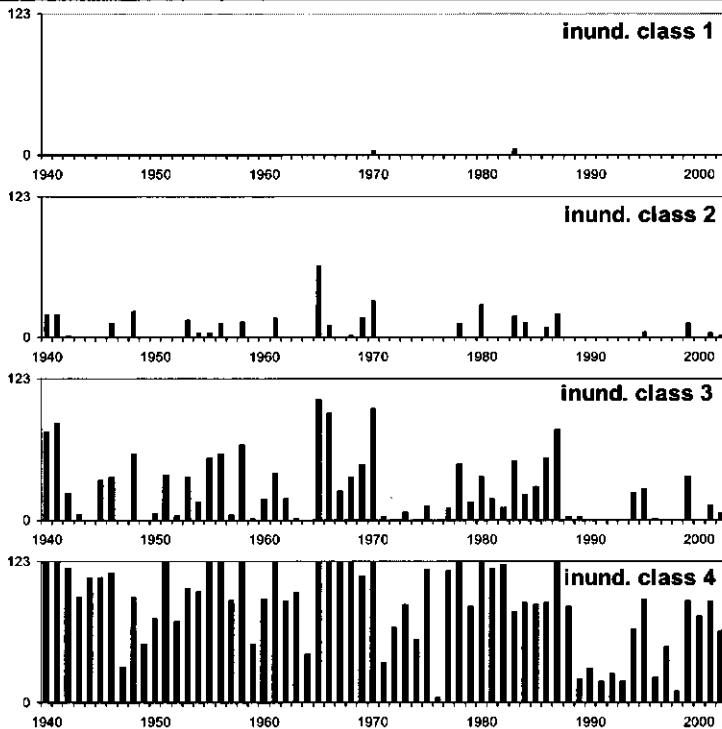


Figure 2. Summer inundations (1940-2001) of floodplains in four inundation duration classes (nr of days between 1 June and 1 October), based on class-middle average inundation durations (class 1: 1 d y^{-1} , class 2: 11 d y^{-1} , class 3: 35 d y^{-1} , class 4: 100 d y^{-1}).

summer inundation, whereas the two most dominant nymphaeid species differed with respect to inundation: the occurrence of *Nymphoides peltata* was higher in the first 15 years after summer inundation, whereas for *Nuphar lutea* there was no clear trend.

The effects of drawdown on submerged and nymphaeid occurrence showed a pattern opposite to the inundation response. The first years after a drawdown, the probability of abundant submerged macrophyte presence was observed to be more than 10% higher than afterwards (Table 2). Species' responses tended to be contrasting; e.g. *Chara* sp. had maximum occurrence in the years following drawdown, whereas *Nuphar lutea* and *Nymphoides peltata* had a lower occurrence in the first years after drawdown. The response of *Potamogeton lucens* to inundation resembled that of *Chara* sp., but it did not appear to rapidly recolonise lakes after drawdown. Remarkably, the ratio between macrophyte-rich and macrophyte-poor lakes was much higher in lakes that did not have any drawdown event compared to those that had, irrespective of the time since that event.

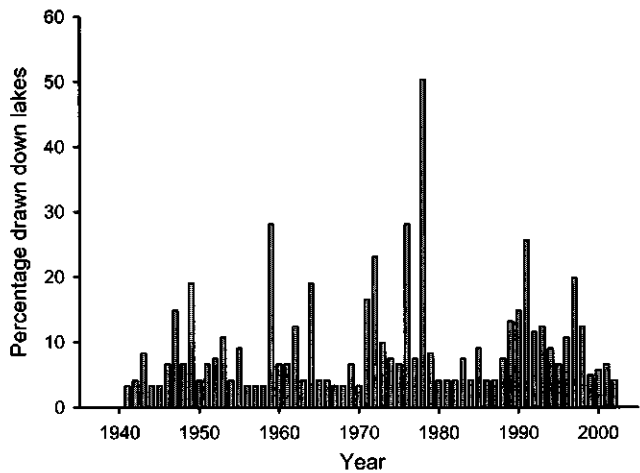


Figure 3. Percentage of floodplain lakes drawdown for each year 1940-2002

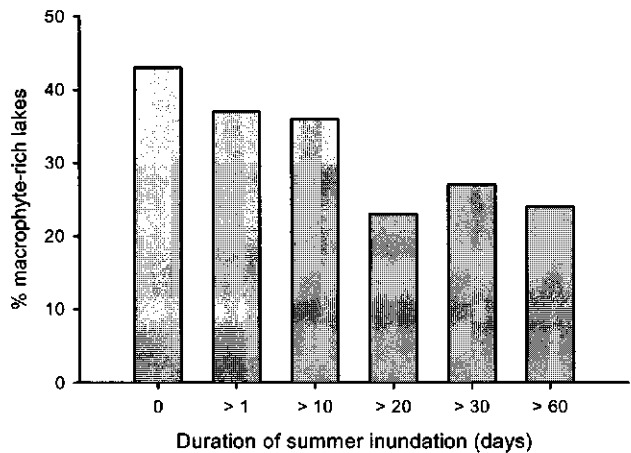


Figure 4. Proportion of floodplain lakes dominated by submerged macrophytes following a year without inundation, and following years with minimum inundation duration of 1, 10, 20 and 60 days, respectively

Table 2. Proportions of water bodies with abundant presence (> 20% lake cover) of submerged and floating-leaved species depending on the number of years since the last summer inundation, resp. drawdown.

<i>Nr. of years since summer inundation</i>	< 5	5-14	> 14
N lakes	86	179	13
Submerged macrophyte dominance	26.7	39.7	69.2
Floating-leaved macrophyte dominance	69.4	61.1	53.8
<i>Nr. of years since drawdown</i>	< 5	5-14	> 14
N lakes	80	35	163
Submerged macrophyte dominance	50.0	31.4	37.4
Floating-leaved macrophyte dominance	48.6	70.3	69.3

Discussion

Assessment of trends in macrophyte abundance was impeded by the available monitoring data that strongly differed in methods, goals and type of data. Standardisation of the data was necessary which reduced the degree of detail. Our approach was to use macrophyte dominance as a proxy of the ecosystem state of individual lakes in separate years, using a large number of observations. However, greater detail, e.g. on species, was limited due to the merging of different datasets, and some bias from the differences between the historical datasets could not be avoided.

Hydrological impact is difficult to assess in retrospect since hydrology acts along several direct and indirect pathways that are subject to change. Water levels of individual lakes are not routinely monitored in floodplain lakes. Hence our only sources of information were the classification of floodplain inundation levels, the lake water-level declines measured in 1999, and the daily water levels of the Rhine itself. Therefore our model was very simple and provided merely a rough estimate of inundation duration and drawdown incidence, respectively. Inaccuracies could arise from uncertainty about inundation classes, elevation levels of lakes within floodplains, and actual declines of the water level (especially when active drainage was applied). The use of class-middle inundation levels produced a strong bias as is obvious from Figure 2. Lakes in the highest inundation class seem to be often inundated throughout summer, which is not the case. Also, the active discharge from these embanked floodplains is not taken into account. Still, we believe that the data represent good relative inundation and drawdown intensities.

The relative degree of contact between floodplain lakes and the river channel, often referred to with the term hydrological connectivity, is crucial for the ecological development of the river and its backwaters (Squires *et al.* 2002). Various effects of inundation of floodplain lakes along the lower Rhine have been described, such as die-back of aquatic vegetation (Van de Steeg 1984, Brock *et al.* 1987) and altered nutrient

concentrations (Roozen *et al.*, submitted). The effect of summer inundations on macrophyte vegetation may be particularly strong in frequently inundated water bodies. In our dataset, approximately 25% of the lakes that had been inundated less than 5 years before were dominated by submerged macrophytes, in contrast to circa 70% of the lakes that had not been inundated for more than 15 years. Recovery may take many years, or may not take place at all, because a suitable propagule bank is lacking and re-establishment of vegetation may be prevented by poor underwater light conditions.

To explain changes in submerged and nymphaeid dominance patterns, trends of the respective species should be evaluated. For example *Nymphoides peltata* seemed to lack a response to summer inundation contradicting Brock *et al.*, (1987), who reported a strong decline of this species in an old oxbow subject intensive and long-lasting flooding in summer. We suggest *Nymphoides peltata* will only be wiped out after extremely intense flooding in summer.

On the other hand, floods import propagules (Cellot *et al.* 1998), while scouring of the lake bottom removes accumulated layers of silt and organic matter and allows buried propagules to germinate (Combroux *et al.* 2001). However, such impacts are less likely in floodplain lakes along the lower Rhine because minor levees reduce horizontal movement of water, especially during the filling and emptying stages of the floodplain.

Temporary lake drawdown creates a window of opportunity for establishment of species that produce large numbers of propagules, such as *Chara* sp. (Bonis & Grillas 2002, Riis & Biggs 2003). Furthermore, *Nymphoides peltata* recolonises shallow water rapidly after a site is reflooded, whereas *Nuphar lutea* is more resistant to inundation but unable to overcome drawdown events (Smits *et al.* 1989, Barrat-Segretain & Amoros 1995). Additionally, drawdown reduces turbidity under reflooded conditions, as a result of sediment consolidation (James *et al.*, 2001). Alternatively, reflooding could lead to nutrient release due to die-off of terrestrial vegetation established during exposure of the lake bottom (Baldwin & Mitchell 2000).

Despite the relatively small effect of drawdown (but see Figure 3, General Discussion, page 119), it was suggested that inundation and drawdown oppositely affect the probability of submerged macrophyte dominance. Like inundation, the impact of a drawdown event would vary depending on the actual area of exposed sediment, the type of sediment and the degree of desiccation. The first few years after a drawdown, the probability of macrophyte dominance was observed to be approximately 10% higher than afterwards.

The regime of inundation and drawdown of floodplain lakes may strongly affect vegetation succession. With increasing lake age and accumulation of organic matter and silt, the vegetation composition gradually shifts from submersed towards nymphaeid and helophyte vegetation. Disturbance due to extreme low water-levels may lead to a 'reset' of succession ('rejuvenation', Amoros *et al.* 1987), i.e. an increase in the cover of submerged vegetation. At the same time, lake water-level fluctuations tend to be reduced with time (Van Geest *et al.*, submitted), owing to reduced groundwater contact as the result of silt and organic matter accumulation. In combination with an elevated bottom level owing to sediment deposition, later succession stages may become more prominent in aged lakes.

As prospected for shallow lakes in general, climate change may affect future inundation and drawdown regimes (Coops *et al.*, 2003). Predictions of climate change in the Rhine catchment basin indicate substantially reduced average summer discharges of the river (up to -10% in 2050, Van Deursen, 2000) and drier spells. Although it is difficult to translate average discharge conditions into the probability of years with long-lasting low water-levels, the trend would be towards an increased probability of drawdown. The resulting effect would be an increased proportion of macrophyte-dominated lakes, although at the same time terrestrialsation of existing floodplain lakes speeds up. However, this trend shall potentially be overridden by the impact of current plans to increase the discharge capacity of the river and its floodplains to cope with increased risks of hinterland flooding, due to increased peak discharges which are expected as well. The anticipated floodplain modifications include an increased number of shallow, highly connective water bodies and withdrawal of levees. For floodplain lakes this essentially means a higher probability of drawdown as the result of lowered average water levels in the floodplain, as well as increased frequencies of minor inundations. Clearly the implications for successful river rehabilitation should be considered carefully.

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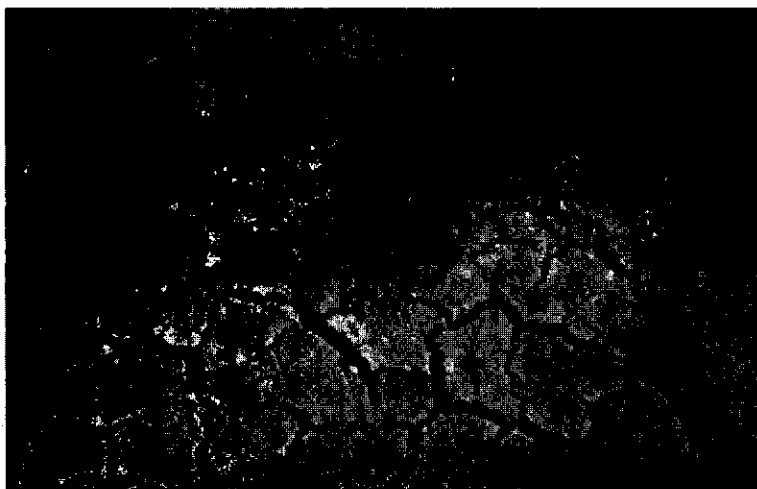
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In years with prolonged periods of low river water-levels, lake sediments may become exposed. This may stimulate germination of *Chara* oospores in the propagule bank after reflooding of the sediment. Picture: John van Schie (RIZA)



In young lakes with exposed soils, *Eleocharis acicularis* may become a dominant species. Photo: John van Schie (RIZA)

Chapter 7

The importance of sediment drawdown for *Chara* emergence in floodplain lakes

G.J. Van Geest & H. Coops

Abstract

In this study, we tested the hypothesis that sediment exposure may stimulate germination of *Chara* from seed banks in floodplain lakes along the Lower Rhine. Therefore, we examined the composition of the propagule bank in a *Chara*-dominated lake, and tested the effect of sediment exposure on sporeling emergence of *Chara* after reflooding of the sediment. Exposure of lake sediments resulted in a 12 fold increase in *Chara* sporeling density compared to cores which remained permanently inundated. The stimulatory effect of sediment exposure on *Chara* germination may explain the increased abundance of *Chara* in floodplain lakes along the Lower Rhine in years subsequent to drawdown events.

Introduction

Among submerged macrophytes, Charophytes are known as rapid colonisers in temporary habitats or after large disturbances. This may be the result of the production of many oospores, which can be easily dispersed over long distances and remain viable for more than one year (Bonis & Grillas, 2002). Buried oospores may undergo dormancy, resulting in high propagule densities of Charophytes in the sediment, sometimes representing more than 70% of all propagules of submerged macrophytes (Bonis & Grillas, 2002). In general, oospore germination percentage from intact propagule banks is low. Therefore, environmental variables that increase the proportion of germinated *Chara* oospores may also stimulate establishment of *Chara* spp. in shallow lakes.

Along the Lower Rhine in The Netherlands, dense vegetations of *Chara vulgaris* are restricted to floodplain lakes which experience regular sediment exposure (drawdown) as a result of low water levels (Chapter 4). Especially in years following drawdown, the occurrence of *Chara* spp. is increased in lakes along the Lower Rhine (Figure 3 in General Discussion). Various mechanisms may stimulate macrophyte growth after resubmersion of exposed sediments, i.e. reduction of the organic matter content and consolidation of the sediment (James *et al.*, 2001), or an increased P-adsorption capacity (De Groot & Fabre, 1993). In addition to these factors, successful establishment of *Chara* may also be explained by an increased proportion of germinated oospores from the propagule bank, caused by exposure of the sediment in the previous year.

In this paper, we tested the hypothesis that successful establishment of dense vegetations of *Chara* in spring depends on the occurrence of drawdown in the preceding year. Therefore, we examined the composition of the propagule bank in a *Chara*-dominated lake, and tested the effect of sediment exposure on sporeling emergence of *Chara* after reflooding of the sediment.

Material and Methods

Study site

The lake is situated near Ochten along the Waal in The Netherlands, and is excavated in the year 1990. In years after drawdown events in this lake, the macrophyte vegetation is dominated by *Chara vulgaris*. The slopes along the shores are steep ($> 45^\circ$), and the substratum of the lake consists of clay and silt. The lake water level is strongly influenced by seepage and infiltration between the lake and the river, thereby determining water depth and surface area of the lake. During high water level of the river in spring, maximum lake depth and surface area equal 2.5 m and 2.6 ha, whereas during low water level of the river, the lake may completely disappear due to drawdown.

Sampling of vegetation composition and propagule bank

During August 1998, bathymetry and vegetation composition of the lake was mapped in detail. To study the depth distribution of the number of seeds in the soil, two sediment samples were taken with perspex cylindrical tubes ($\varnothing = 6$ cm, $h = 10$ cm) in September 1998: one in a deep and one in a shallow lake part. Due to handling, the sediment consolidated in the highest burial depth of the cores, resulting in 8 sections of 1 centimetre. To study the spatial distribution of seed bank density and composition in the lake, a transect was set up along an elevation gradient in September 1998. The transect length was 170 metres and ran from one edge of the lake to the other. We sampled only the upper 5 cm of the sediment, because 95% of the total number of propagules were concentrated in this layer (Figure 1). Along the transect, the lake sediment was sampled every ten metres with a sediment corer ($\varnothing = 20$ cm, $h = 5$ cm), resulting in 18 sampling sites. After sieving the sediment (0.2 mm sieve), the number of propagules was determined and identified by direct count, carried out under a binocular microscope. Subsamples were used when the total numbers of propagules exceeded 200 per sample. Seeds were identified using Beijerinck (1947) and Van der Meijden (1996); oospores of *Chara* spp. were not identified to species level.

The sampled sites were categorized into three elevation zones. The difference in height between the sampled sites is expressed relative to the average height of the highest elevation. High elevation = $0 \text{ cm} \pm 28 \text{ cm}$ ($n = 2$); middle elevation = $-42 \text{ cm} \pm 10 \text{ cm}$ ($n = 10$); and low elevation = $-68 \text{ cm} \pm 5 \text{ cm}$ ($n = 6$).

Effect of drawdown on seedling emergence

To test the effect of drawdown on seedling emergence, a greenhouse experiment was carried out with lake sediment and its propagule bank which was collected in the field. In August 2001, samples of about the upper five cm of the sediment were taken at the same location with an Eckmann grab at a transect sampling site with high oospore density and abundant *Chara* growth in 1998 and 1999. The sediment was immersed in tap water and stored at 18°C and prevailing day-night rhythm. No germination was observed during the storage period.

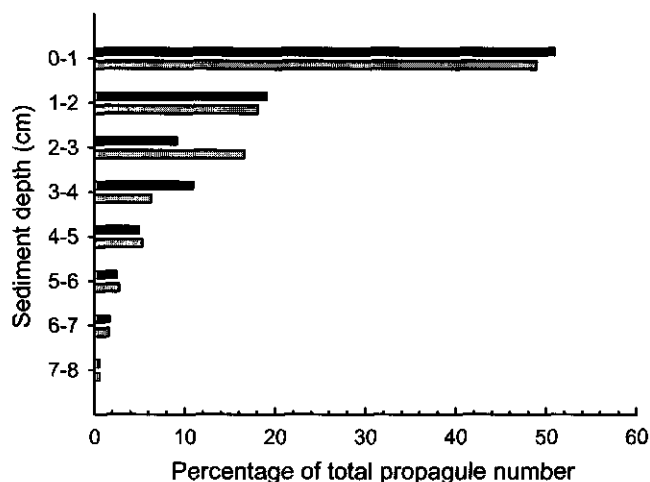


Figure 1. Vertical distribution of seeds and oospores in the sediment. Total number of propagules was $617,770 \text{ m}^{-2}$ for shallow lake part (black) and $627,862 \text{ m}^{-2}$ for deep lake part (grey)

From December 12th 2001 until January 16th 2002 (duration 35 days), a drawdown treatment was carried out in a greenhouse with an air temperature of approximately 20°C . The sediment was intensively homogenised and put into cores ($\varnothing = 9.5 \text{ cm}$, $h = 10 \text{ cm}$). Subsequently, the cores were each put each separately in 5L plastic buckets. Cores for the drawdown treatment were placed in dry buckets, whereas the control cores were immersed in tap water resulting in 3 cm water depth at the sediment surface. Four replicates were used for each treatment. The bottom of the cores was closed with 0.5 mm gauze, which retained the sediment but allowed drainage of pore water. Drainage water from the drawdown treatment cores was removed daily from the buckets. The decrease in weight of the cores was monitored by almost daily weighting. During the drawdown treatment, all cores decreased equally in weight, and at the last day of the drawdown treatment, the mean decrease ($\pm \text{s.d.}$) relative to their initial weight was $30.3\% \pm 6.4$. The water level in the control buckets was kept constant by regular replenishment with demineralised water. At the end of the experiment, all cores for the germination experiment were immersed in tap water and stored in the dark at 4°C .

The seedling emergence experiment lasted 53 days (June 10th – August 2nd 2002) and was carried out in a greenhouse, with prevailing light conditions and an air temperature of $20 - 29^{\circ}\text{C}$. All cores were placed separately in plastic buckets filled with tap water up to 3 cm above the sediment surface. The water level in the buckets was kept constant by regular replenishment with demineralised water. During this period the seedlings were identified and counted once or twice per week. Seedlings were removed carefully after identification.

Results

Vegetation composition

In 1998, the sampling sites at high elevation were already exposed from the start of the growing season. The macrophyte vegetation in this zone consisted of the amphibic species *Eleocharis acicularis*, in addition to many terrestrial species. The sampling sites at intermediate elevation were exposed from the beginning of June. In this zone, *E. acicularis* was accompanied by *Limosella aquatica* and *Alisma gramineum*. In the deepest lake parts which ran dry at early August, a dense mat of desiccated *Chara cf. vulgaris* covered the lake bottom (Figure 2b).

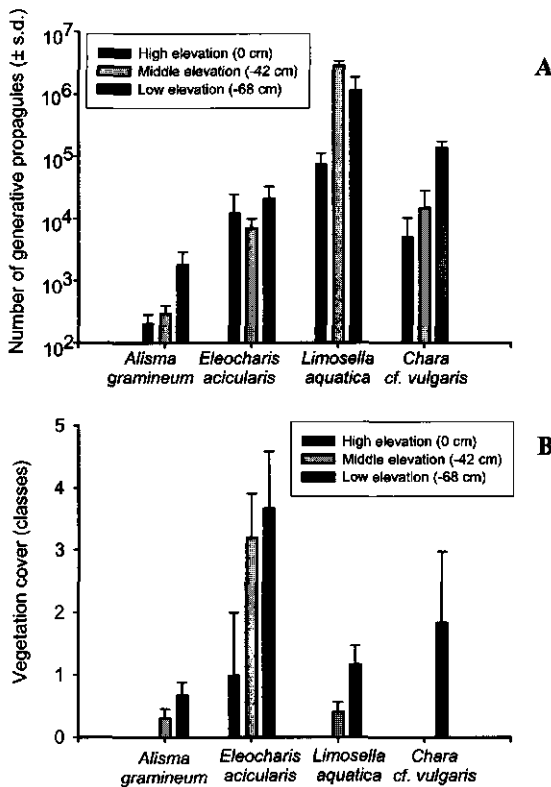


Figure 2. Propagule density in the seed bank ($n\ m^{-2}$) and vegetation cover of the most common macrophytes in 1998. Species cover was expressed in one of seven classes (1, < 1%; 2, 1-5%; 3, 6-15%; 4, 16-25%; 5, 26-50%; 6, 51-75%; 7, 76-100%). The sampled sites were categorized into three elevation zones. The difference in height between the sampled sites is expressed relative to the average height of the highest elevation. High elevation = $0\ cm \pm 28\ cm$ ($n = 2$); middle elevation = $-42\ cm \pm 10$ ($n = 10$); and low elevation = $-68\ cm \pm 5$ ($n = 6$)

Seed bank structure

Seed density declined exponentially with sediment depth, with 95% of the total seed number concentrated in the upper 5 cm (Figure 1). The seed bank reached extreme high densities up to $6.4 \cdot 10^6 \text{ m}^{-2}$, and was dominated by sexual propagules of *Chara* spp. and three species of exposed soil (*E. acicularis*, *A. gramineum* and *L. aquatica*) (Figure 2). High propagule numbers of *Chara* spec. and *A. gramineum* were present at the low part of the elevation gradient, whereas seed number of *L. aquatica* was highest at both middle and low elevation (Figure 2). The cover of species in the vegetation often reflected propagule densities in the seed bank, although at middle and/or high elevation, some species that were present in the seed bank were absent in the vegetation (i.e. *Chara* spp., *A. gramineum*) (Figure 2).

Seedling emergence experiment

During the seedling emergence experiment, propagules of *C. vulgaris*, *Juncus bufonius*, and *A. gramineum* germinated from the cores. Only sporelings of *C. vulgaris* germinated in sufficient numbers for statistical analysis. For *Chara* spp., vegetative propagules were not present in the sediment, and it was regularly observed that emerging sporelings originated from oospores. Desiccation resulted in a 12-fold increase in the number of emerged *Chara* sporelings compared to permanently inundated cores (Mann-Whitney U test; $U = 0.00$; $n = 4$ for each treatment; $p < 0.05$; Figure 3).

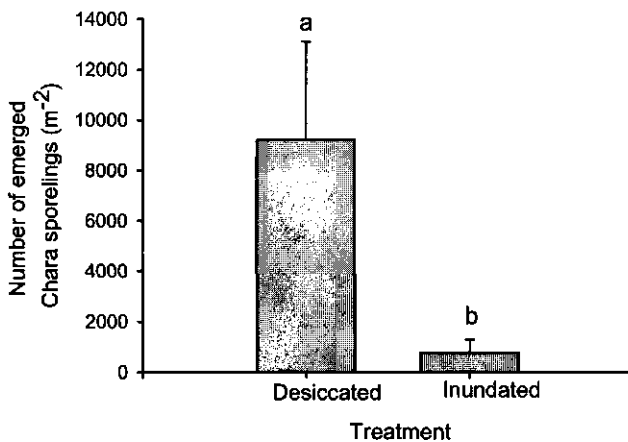


Figure 3. Number of emerged *Chara* sporelings ($n \text{ m}^{-2}$) in the desiccated and permanently inundated cores.

Discussion

Shallow lakes in floodplains along the Lower Rhine are characterised by unpredictable drawdown events, thereby strongly affecting vegetation composition and succession, as was shown in the studied lake. The differences in vegetation composition may be facilitated by enhanced recruitment from the seed bank, as indicated by high propagule densities of both 'drawdown' and submersed species in the lake sediment. Drawdown has a strong effect on germination patterns from the propagule bank, as germination of *C. vulgaris* was strongly stimulated by sediment exposure in the previous year. Several studies have found high propagule densities in seed banks at sites with regular drawdown (Bonis & Grillas, 2002; Combroux *et al.*, 2001). A high propagule density in the sediment creates a storage effect (Warner & Chesson, 1985), which enable pioneer species to recolonise rapidly when environmental conditions for growth are suitable (Bonis & Lepart, 1994; Bonis *et al.*, 1995).

Sediment exposure resulted in a 12 fold increase in *Chara* sporeling density, indicating that some aspect of desiccation stimulated germination of *Chara* oospores. In the field however, the magnitude of this increase may be different, because propagule germination strongly depends on other variables, such as water temperature and irradiance levels (Baskin & Baskin, 1998). Increased emergence of *Chara* sporelings from propagule banks as a result of drawdown has also been found in subtropical regions (Casanova & Brock, 1996; Brock & Rogers, 1998; Havens *et al.*, 2004). This study shows that drawdown may also stimulate emergence of *Chara* sporelings in lakes situated in temperate regions.

The increased emergence of *Chara* as a result of drawdown may partly explain the cyclic pattern of *Chara* abundance in floodplains along the Lower Rhine (see Figure 3 in General Discussion). Van den Berg *et al.* (2001) proposed that a closed canopy of *Chara* would only develop once sporeling density exceeds a certain threshold. Our results suggest that in floodplain lakes along the Lower Rhine, this threshold is exceeded only in lakes which have been drawn down in the preceding year. In lakes without drawdown in the previous year, the sporeling density may be too low for successful establishment of dense *Chara* vegetations. Van Wijck & De Groot (1993) found also that a summer drawdown in a marsh of the delta of the Rhône led to a considerable increase in the cover of *Chara* spp. in the following spring.

Overall, it can be concluded that the composition of the seed bank plays an important role for the cyclic pattern of *Chara* abundance in floodplains along the Lower Rhine, and that sediment exposure stimulates sporeling emergence of *Chara* in the subsequent growing season.

Acknowledgements

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Chapter 8

General Discussion

G.J. Van Geest

The results presented in this thesis can be summarized in five main conclusions:

1. In the absence of river flooding, fluctuations in lake water-level are largely driven by variations in river water-level through groundwater flow.
2. Over time, the amplitude of water-level fluctuations within individual lakes becomes reduced due to accumulation of clay and silt, preventing sediment exposure (drawdown) during periods of low river levels.
3. The reduced incidence of sediment exposure with lake age is of major importance for aquatic vegetation succession in floodplain lakes along the Lower Rhine, as macrophyte composition shifts from dominance by desiccation-tolerant species in young lakes to desiccation-sensitive species in old lakes.
4. High abundance of submerged macrophytes is strongly stimulated by drawdown events in the previous year. As a result of inter-annual variation in river water-levels, the number of drawn down lakes varies strongly from one year to another. Consequently, the number of lakes with abundant submerged vegetation shows also strong inter-annual variation.
5. Newly created lakes may sustain a high value for the macrophyte community, under the condition that they are small (< 1 ha) and shallow (< 1.5 m), and have frequently exposed sediments.

In this chapter, I first put the most important findings of this study in perspective of previous studies. Then, a description is given of various programs and measures concerning the management of the Lower Rhine and their potential consequences for the status of macrophytes. Finally, suggestions are given for how the results of this study can be used to rehabilitate conditions for macrophytes in floodplains along the Lower Rhine.

8.1. Contribution to theory

In floodplain macrophyte studies, river hydrology is often discerned as the major driving force for the vegetation. Firstly, the hydrological relationship between the main channel and adjacent floodplain lakes is described in more detail. Subsequently, the results of this study will be put in the perspective of previous studies. Other factors, such as nutrient levels, will also be examined, and the stability of macrophyte vegetation in this regularly disturbed environment will be discussed in the context of what is known of alternative stable states in shallow lakes.

8.1.1. Hydrological relationship between the main channel and floodplain lakes

The characteristic ecology of floodplain lakes is in part due to their relatively strong water-level fluctuations. In floodplain lakes, such water-level fluctuations are largely the result of natural fluctuations in river discharge. For floodplain lakes along the Lower Rhine, Van den Brink (1994) distinguished five hydrological stages (Figure 1). Depending on river water-level and height of minor embankments and natural levees, the river may inundate the floodplain through surface overflow (the 'connection stage', Figure 1). When the water level in the river recedes, the water level in the floodplain behind the minor embankments may remain high ('drainage stage'). However, in the floodplains along the Lower Rhine, this stage lasts relative short, as the outflow of water from the floodplain is generally stimulated for agricultural practices. During the subsequent isolated stage, groundwater flow between the main channel and the lake may influence the amplitude of fluctuations in lake-water levels. When the water level is low in the main channel, infiltration of lake water into the alluvial aquifer may result in a decline of lake-water levels. Under these conditions, the impact of the river's water-level regime on lake water-levels depends on the conductivity of the soil to groundwater flow, called 'hydraulic conductivity' (Brunke & Gonser, 1997). During prolonged periods of low river-water levels, infiltration of lake water into the alluvial aquifer may result in exposure of lake sediments ('desiccation stage'; Chapter 2). When lakes become older, the amplitude of water-level fluctuations will decrease as the result of reduced hydraulic conductivity of the lake bottom, which is caused by accumulation of organic matter, silt and clay in the sediment (Chapter 2, Wood & Armitage, 1997). As a result, sediment exposure will occur less frequently with progressing lake age (Figure 2). In the Neder-Rijn and Lek however, the construction of weirs has resulted in a water-level regime with higher minimum water levels than would be expected naturally (Chapter 4). Consequently, water levels rarely fall below a fixed level in the Neder-Rijn and the floodplain lakes alike, and the occurrence of (partial) lake drawdown is strongly reduced, especially in young lakes (Figure 2).

Flooding through river overflow (Brock *et al.*, 1987; Henry *et al.*, 1994) and seepage- and infiltration-induced water-level fluctuations affect aquatic vegetation development in floodplain lakes. Additionally, input of seepage water from hill slope aquifers from moraines, such as Utrechtse Heuvelrug or Veluwe, may affect macrophyte vegetation by decreasing nutrient concentrations in lake water (Bornette *et al.*, 1994; Bornette *et al.*, 1996). In the next paragraphs, the effects of river floods and seepage- and infiltration-induced water-level fluctuations on macrophyte composition and succession will be discussed in more detail.

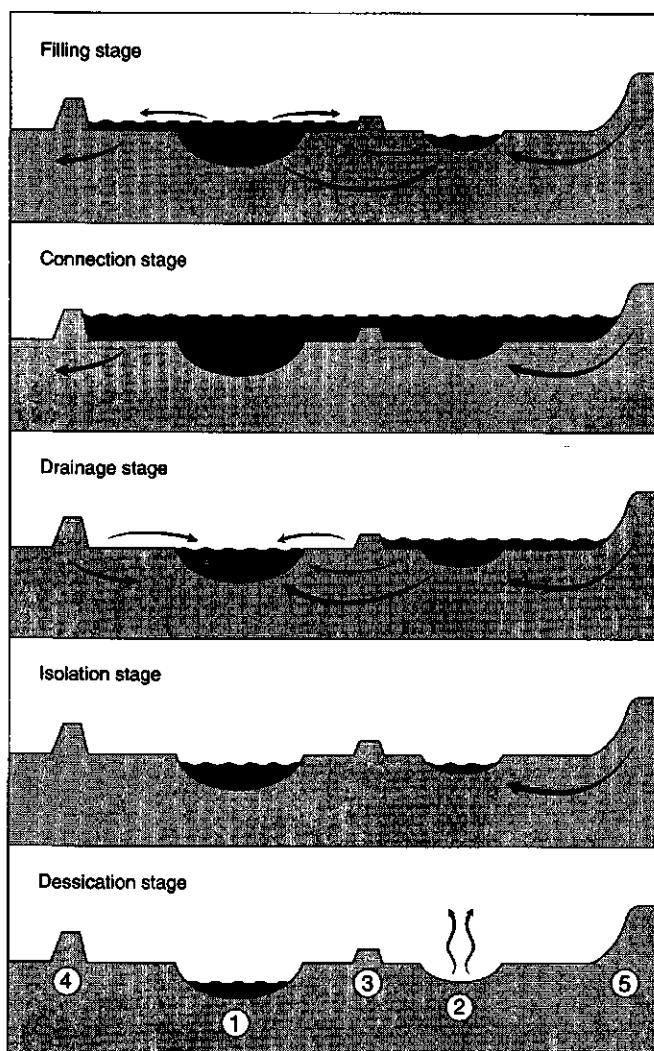


Figure 1. Hydrological stages of a floodplain lake during a flood pulse (after Van den Brink, 1994). Arrows indicate directions of (ground)water flow. 1 = main channel; 2 = floodplain lake; 3 = minor embankment; 4 = major embankment; 5 = moraine hill

8.1.2. The effect of river floods on macrophyte succession

Generally, disturbance due to flooding by the river is regarded as a driving force for macrophyte succession in floodplain lakes (Van der Voo & Westhoff, 1961; Van den Brink *et al.*, 1991; Henry *et al.*, 1994; Tremolieres *et al.*, 1994; Sparks & Spink, 1998). In accordance with the results of Van den Brink *et al.* (1991), who also investigated floodplain lakes along the Lower Rhine, submerged macrophyte cover in floodplain lakes was negatively related to inundation duration of individual lakes (Chapter 3). However, Van den Brink *et al.* (1991) found a much stronger effect of inundation duration on macrophyte composition than in this study. This may be partly due to the fact that, contrary to the present study, Van den Brink *et al.* (1991) included permanently connected and never inundated lakes behind the major embankments in the hinterland in their survey. Furthermore, the relatively weak relationship in the present study may be related to different flood intensities in the years prior to the research periods of the respective studies. In temperate rivers in Western Europe, such as the Lower Rhine, floods predominantly occur during winter when vegetation largely lays dormant underground, reducing the ecological effects of floods compared to summer flooding (Junk, 1999). In the years prior to the research of Van den Brink *et al.* (1991), several summer floods occurred, which had a strong negative impact on macrophyte vegetation in lakes along the Lower Rhine (Brock *et al.*, 1987; Van den Brink *et al.*, 1991; Van de Steeg & Blom, 1999). Furthermore, in that time anthropogenically increased nutrient concentrations and salinity of the Lower Rhine had resulted in lake eutrophication and deteriorated growth conditions for macrophytes (Van den Brink *et al.*, 1992; Van den Brink & Van der Velde, 1993). However, over the last decade water quality has improved strongly (Nienhuis *et al.*, 2002), and severe summer floods did not occur in the years after 1987 (Chapter 6). As a result, the macrophyte vegetation in all lakes may have been equally little affected by summer floods, explaining the relatively weak relationship between inundation duration and macrophyte composition in the present study.

8.1.3. Effects of low river water-levels on macrophyte succession

In contrast to river flooding, fluctuating lake water-levels during the isolated stage has been much less studied (Amoros & Bornette, 2002). In lakes outside floodplain areas, strong effects of drawdown on the composition and abundance of aquatic vegetation have been shown (Wilcox & Meeker, 1991; Wagner & Falter, 2002).

Over time, the amplitude of water-level fluctuations in lakes decreases with age because of accumulation of clay and silt which 'seal' the sediment, preventing seepage and infiltration of groundwater. As a result, the probability of lake drawdown during periods of low river levels decreases with lake age (Figure 2), even though silting up results in a shallower water body. My results suggest that this clay sealing process is accompanied by a dominance shift from desiccation-tolerant species (e.g. *Chara vulgaris*) in young lakes to desiccation-sensitive species (*Nuphar lutea*) in old lakes (Chapter 4).

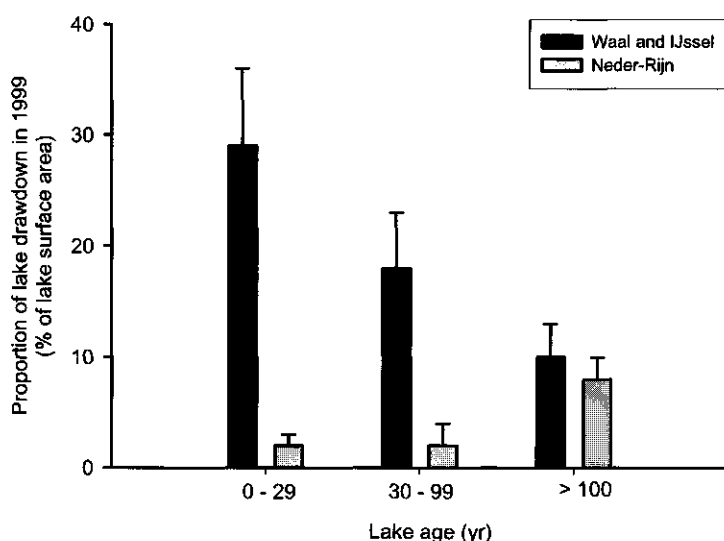


Figure 2. The proportion of lake drawdown in lakes along unimpounded Waal and IJssel, and impounded Neder-Rijn/Lek in relation to age of the lakes. The proportion of drawdown area decreased with lake age along the unimpounded Waal and IJssel, whereas drawdown was strongly reduced along the impounded Neder-Rijn, and not related to lake age.

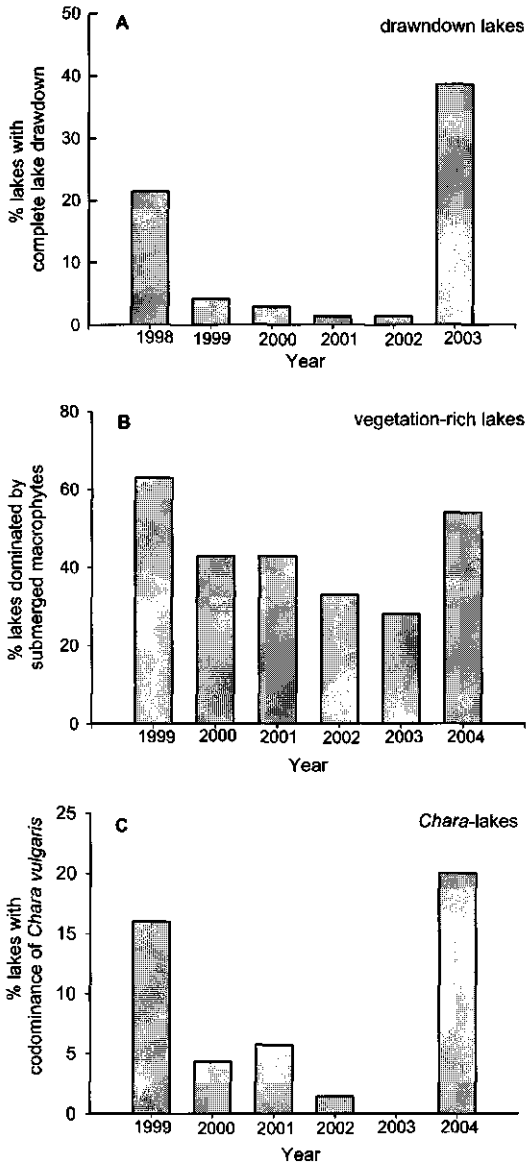


Figure 3. (a).Percentage lakes with drawdown during 1998 – 2003.
(Data of 1998: estimate based on field observations + data Chapter 6; 1999 – 2003: field observations)
(b).Percentage lakes dominated by submerged macrophyte vegetation during 1999 - 2004 (cover \geq 20% of lake area)
(c).Percentage lakes (co-)dominated by *Chara vulgaris* during 1999 – 2004

N.B. Note the differences in x-axes between Figure 3a and 3b,c

In addition, macrophyte composition in lakes is influenced by annually varying river water-levels. Because the pattern of fluctuating water-levels in the Lower Rhine varies considerably from one year to another, no lakes may dry out at all in some years, while along the free flowing Waal and IJssel approximately 50% of the lakes were drawn down temporarily in extremely dry years such as 1978 (Chapter 6) and 2003. The responses of the aquatic macrophyte vegetation to these droughts strongly depend on the macrophyte growth forms and species that make up the vegetation. The hypothesis that submerged macrophyte cover in lakes is stimulated by temporary drawdown events in the preceding year (Chapter 5) was confirmed in 2004 (Figure 3). However, it can be anticipated that many lakes covered by submerged macrophytes in 2004 will lose this vegetation within 1-2 years when drawdown remains absent.

The long-term decline of submerged vegetation cover in lakes can be explained by the reduced occurrence of drawdown with lake age. In addition, macrophyte succession may be driven by other factors than hydrology at the same time. Due to organic matter accumulation, redox potential in the sediment will be reduced, potentially hampering submerged macrophyte growth (Barko & Smart, 1986), or causing a shift towards dominance of non-rooted species such as *Ceratophyllum demersum*. Furthermore, increased cover of floating-leaved nymphaeids in lakes may result in reduced irradiance and hence retarded growth of submerged macrophytes (Hutchinson, 1975).

Macrophyte succession

There has been a long history on research of macrophyte succession in lakes and wetlands (Pearsall, 1920; Hutchinson, 1975). Early views emphasized the importance of accumulation of organic matter and increased shading by canopy, resulting in a unidirectional temporal sequence from submerged macrophytes, towards nymphaeids and helophytes. An alternative view regards macrophyte succession as a cyclic pattern of vegetation dominance induced by different hydrological stages and disturbances (Van der Valk, 1981). Exceptionally high or low water-levels may eradicate or push back existing vegetation stands, especially when such disturbances occur during the growing season, allowing for a temporary dominance of rapidly colonizing species. According to this view, macrophyte composition in lakes is the result of short-term responses to fluctuating water levels rather than a long-term sequence of successive phases.

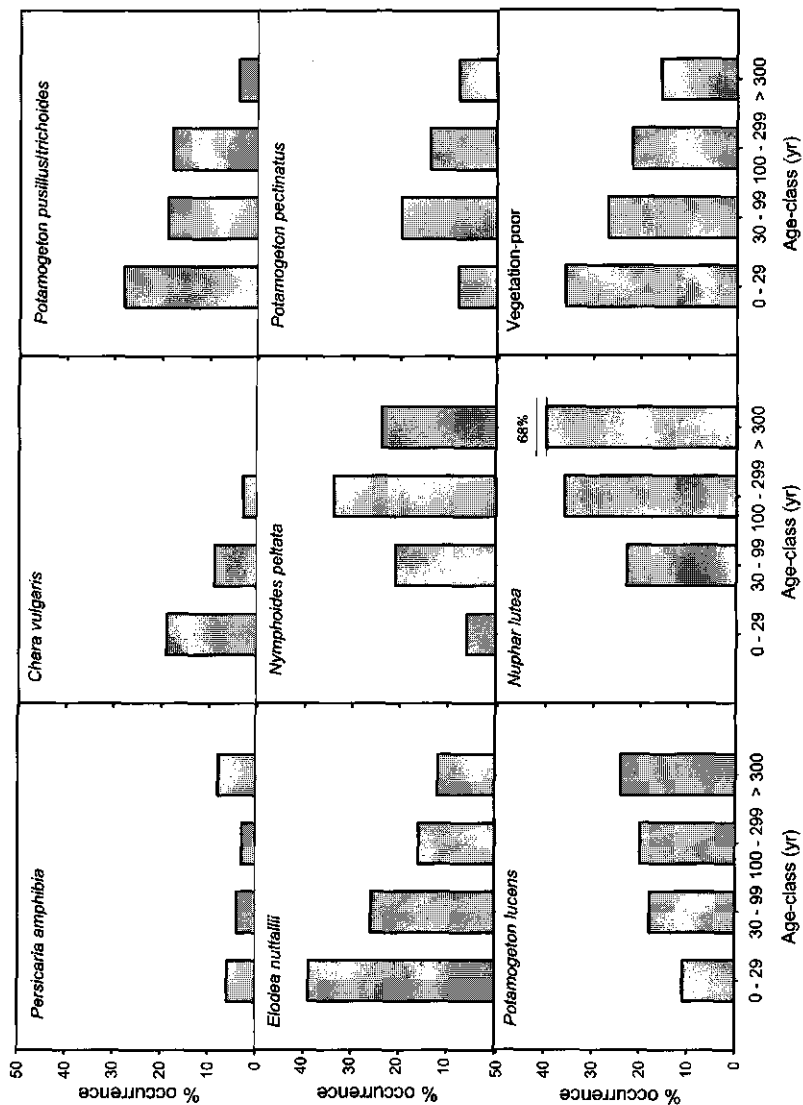


Figure 4. Vegetation type occurrence in relation to lake age, based on a dataset of 215 lakes along the Lower Rhine sampled in 1999 and 2000

For floodplain lakes along the Lower Rhine, the predominant aspect of succession depends on the temporal scale. Although macrophyte succession proceeds according to the classical sequence, rate and direction of succession varies considerably from one place to another. Several factors may explain the large variation in vegetation composition between lakes.

Firstly, macrophyte community in lakes is strongly influenced by short-term changes in cover and composition, which are related to the occurrence of extreme water levels (Chapter 5, 6). Especially cover and composition of submerged vegetation showed large inter-annual shifts during the years 1999 – 2002. In this period, only 10 – 40% of the lakes were dominated by the same submerged vegetation type as in the previous year (Chapter 5). By contrast, the cover of *Nuphar lutea* and helophytes showed little inter-annual variation in this period (Chapter 5). Apparently, the cover of these species was not affected by the water-level regime of the lakes during 1999 - 2002. Nevertheless, the abundance of certain helophyte species (such as *Typha angustifolia* and *Schoenoplectus lacustris*) can be strongly reduced by the occurrence of extreme summer floods, such as in 1980 (Brock *et al.*, 1987; Van de Steeg & Blom, 1999).

Secondly, the rate of macrophyte succession in the lakes is strongly affected by the drawdown frequency. Lakes which are situated close to the main channel or along river stretches with highly fluctuating water levels, will maintain larger amplitudes of water-level fluctuations during lake ageing compared to lakes which are more remote or situated along river stretches with relatively stable water levels. Consequently, in the lakes with large water-level fluctuations macrophyte succession will precede with a slower rate compared to lakes with reduced water-level fluctuations, because macrophyte succession at times is reversed by the occurrence of extreme water levels.

Thirdly, the composition of the macrophyte community is strongly influenced by water depth during the growing season (Spence, 1982). In floodplains along the Lower Rhine, dominance of *Potamogeton lucens* and *Nuphar lutea* is most likely in relatively deep water lakes, whereas vegetation types of *P. pusillus/trichoides* are characteristic for shallow water bodies (Chapter 4). Because the depth profile varies between lakes, this will result in additional variation in macrophyte composition.

Based on a survey of a large number of oxbow lakes along the Lower Rhine, Van Donselaar (1961) regarded differences in erosive water currents during river flooding as the driving force for rate, direction and endpoints of macrophyte succession. However, ecological effects of strong water currents are less likely along the Lower Rhine, because the erosive force of water flow during river flooding is relatively weak (Middelkoop, 1997). By contrast, my results suggest that macrophyte succession is strongly affected by

the occurrence of low water levels (Chapter 4, 5). Nevertheless, additional effects of river flooding cannot be ruled out. During flooding, fine sediments (clay, silt) are deposited, whereas loose organic materials may be exported from the system, resulting in a negative relation between inundation duration and occurrence of organic, reductive sediments as reported by Van den Brink *et al.* (1995).

The gradual decline of submerged macrophytes and increase in nymphaeids and helophytes with lake age (Chapter 3, Figure 4) is in line with the classical sequence of successional terrestrialization (Pearsall, 1920; Hutchinson, 1975). However, in these studies the occurrence of a vegetation-poor, turbid state is not included. My results indicate that the occurrence of such states does not influence the direction and endpoints of macrophyte succession, because helophytes and juvenile (submerged) plants of *Nuphar lutea* were also found in turbid lakes. Consequently, macrophyte succession will converge to dominance by nymphaeids and helophytes, regardless of the presence of either a turbid or vegetation-rich state in early stages of succession.

Overall, macrophyte development in lakes along the Lower Rhine follows a pattern which is in line with the classical sequence, but this pattern is certainly not fixed and unidirectional, as macrophyte succession is regularly 'reversed' by the occurrence of extreme water levels.

Shifts between low and high submerged macrophyte cover: alternative stable states or transient dynamics?

Over the past decade, there has been a growing interest in the shifts between 'alternative stable states' of ecosystems (Scheffer *et al.*, 1993; Scheffer *et al.*, 2001). One of the best described examples of such patterns is that of shallow lakes, that tend to be either in a state of clear, relatively nutrient-poor water with dominance of submerged vegetation or in a state of turbid, relatively nutrient-rich water and domination of phytoplankton and benthivorous fish (reviewed by Jeppesen *et al.*, 1997; Scheffer, 1998). Either state is stabilized by various feedback mechanisms and a shift from one state to the other requires loss of stabilizing mechanisms of one state, and establishment of stabilizing mechanisms of the other state. Submerged macrophytes play a key role in stabilizing the clear-water state, by preventing resuspension of sediment, providing refuge to zooplankton and piscivorous fish, etc. Summer floods may result in a shift towards the vegetation-poor, turbid state, which is subsequently stabilized by benthivorous fish (Roozen *et al.*, 2003), or wind-generated sediment suspension.

The observation that lakes are either rich or poor in submerged macrophytes (Chapter 3), and exhibit large shifts in submerged macrophyte cover from one year to the other (Chapter 5), suggests that alternative states with- *versus* without macrophytes also occur

in floodplain lakes along the Lower Rhine. Indeed, submerged macrophyte abundance is positively related to water clarity (Roozen *et al.*, 2003; Figure 5). However, in contrast to prediction, neither P- nor N-content of the lake water is significantly related to submerged macrophyte abundance, and many floodplain lakes are dominated by submerged macrophytes while total-P concentrations are up to 0.4 mg L^{-1} (Chapter 3). These maximum values are far higher than those reported for a large set of Danish lakes, in which submerged macrophyte abundance decreases at total P values higher than $0.08 - 0.15 \text{ mg L}^{-1}$ (Jeppesen *et al.*, 1990). The difference between the results of Jeppesen *et al.* (1990) and this study may be the water-level regime of the lakes. In lakes with stabilized water levels, submerged macrophyte abundance is usually low when the nutrient levels are high, whereas in eutrophic floodplain lakes along the Lower Rhine, drawdown events caused by low water-levels stimulate submerged macrophyte growth in the subsequent year. This implies that frequent drawdowns will result in a transient vegetation-rich state of these lakes for most of the time.

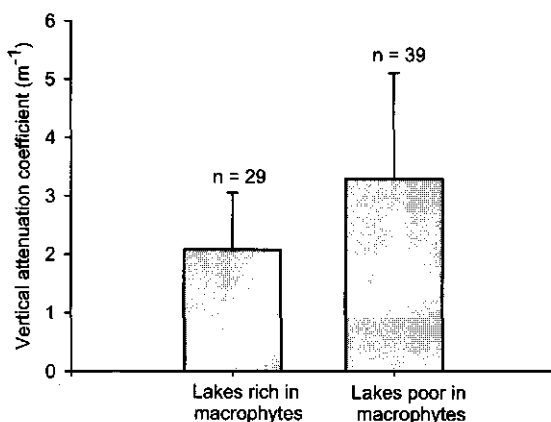


Figure 5. Vertical attenuation coefficient (m^{-1}) \pm s.d. in lakes in July 1999 which were either rich (≥ 20 % of lake surface area) or poor ($< 20\%$) in submerged macrophytes (significant difference with $p < 0.01$; Mann-Whitney U test; $U = 326$)

Over the last century, submerged macrophyte cover in many shallow lakes in Western Europe has decreased strongly, which is often explained as the result of increased nutrient loading. However, coinciding with the increased nutrient loading, the water-level regime of these lakes has been strongly regulated, which may also have caused deteriorated growth conditions for submerged macrophytes. Consequently, hydrological regulation of shallow lakes may be an important factor aggravating the permanent loss of submerged vegetation due to cultural eutrophication.

Despite the absence of drawdown, some lakes remained rich in submerged macrophytes during the research period. This discrepancy can be explained by the small surface area of the lakes (< 1 ha), which may potentially benefit conditions for submerged macrophyte growth through a variety of mechanisms as discussed in Chapter 3. Contrastingly, in the case of the Danube delta, many large lakes (> 100 ha) were dominated by submerged macrophytes at high nutrient levels (Oosterberg *et al.*, 2000), despite the absence of drawdown in these lakes. The cause of the high submerged macrophyte cover in the lakes in the Danube delta is probably related to the occurrence of a clear water phase during spring, which coincides with the timing of river floods in this area.

8.2. River management

Current policy documents in the Netherlands aim at integrated hydrological, ecological and economic functioning of rivers on a catchment-scale basis. This means that management of the Lower Rhine combines measures for safe passage of floods (increasing the retention capacity upstream and discharge capacity downstream in the catchment), for transport infrastructure (enhancing the main navigation routes), and ecological rehabilitation (nature development in the floodplains). For the coming decades, the floodplain landscape along the Lower Rhine will change drastically as a result of the measures proposed in the policy document "Ruimte voor de rivier" (Ministry of Transport and Water, 2000), resulting in the programme 'Room for Rhine branches'. Bypass-channels will be dug and large parts of the floodplain area will be transformed into extensively grazed wetland areas (Smits *et al.*, 2000), especially as the result of large-scale excavation (1 – 2 m) of floodplains. Several already implemented projects in individual floodplains have demonstrated great benefits to natural habitats such as floodplain forest, species-rich grasslands and shallow side channels (Nienhuis *et al.*, 2002; Van der Molen & Buijse, in press).

Ecological objectives are also set by European directives, notably the EU Water Framework Directive. This directive requires for each water body within its area that the Good Ecological State is defined, and that measures are taken and monitoring is conducted to reach that state within a limited timeframe. In the following sections, the background of these developments and their potential impact on macrophyte growth in the future will be discussed.

8.2.1. Changes in river hydrology

For the coming decades, it is expected that the discharge regime of the Lower Rhine will be altered as a result of climate changes in the catchment area (Middelkoop 2000). Although the overall yearly discharge will remain rather constant, it has been calculated that extremely high and low flows will occur more often. Over the 21st century, winter rainfall totals and intensities will increase by 10-40% (lower and upper estimate for

KNMI climate scenarios), resulting in an increased occurrence of peak flows (Middelkoop, 2000). Furthermore, the input of melt water during summer will decrease over the next decades. Consequently, the discharge regime of the Rhine will shift from a 'rain-fed/melt water' river into a mainly 'rain-fed' river, resulting in more rapid discharge changes and more extreme low-water levels during summer (Pfister *et al.*, 2004).

Besides the effects of global change, the water level in lakes along the Lower Rhine will also change as a result of river bed incision combined with the continuous sedimentation of floodplains adjacent to the river. Along the Waal at Nijmegen, river incision has already caused a gradual decline in average water-levels during the growing season of about 1 – 1.5 m between 1800 and 1999 (Figure 6). As a result, the minimum water level of the river during the growing season in the year 1800 corresponds approximately to the current mean water-level. In addition, it is estimated that deposition of sediments during floods has resulted in an increase of the altitude of the floodplain by 1.7 – 3.6 meter compared to 200 years ago (Middelkoop, 1997). Both river incision and sedimentation have supported a decline of the groundwater table, resulting in decreased lake water-levels. It is expected that river incision will proceed with a rate of approximately 0.8 cm per year at Lobith, resulting in increasingly low river water-levels during low discharges. Consequently, long periods with low groundwater levels in the floodplain will become more common and lake drawdown will occur more often.

Without further management to anticipate the alteration of the river discharge regime, the changes in river discharge will have a strong effect on macrophyte growth in existing floodplain lakes along the Lower Rhine. Due to the expected increase in flooding frequency during winter and a decreased proportion of lakes with low inundation duration, macrophyte cover and species richness will be reduced (Chapter 3 and 6, Van den Brink *et al.*, 1991). Furthermore, both river incision and changed discharge regime will cause a higher incidence of extremely low river water levels, thereby increasing the occurrence of lake drawdown. Although this may result in an increased proportion of lakes present in the transient submerged macrophyte-rich state, it may as well accelerate terrestrialization rates of lakes, as low water levels and prolonged sediment exposure stimulate the establishment of helophytes and woody species (*Salix* spp.).

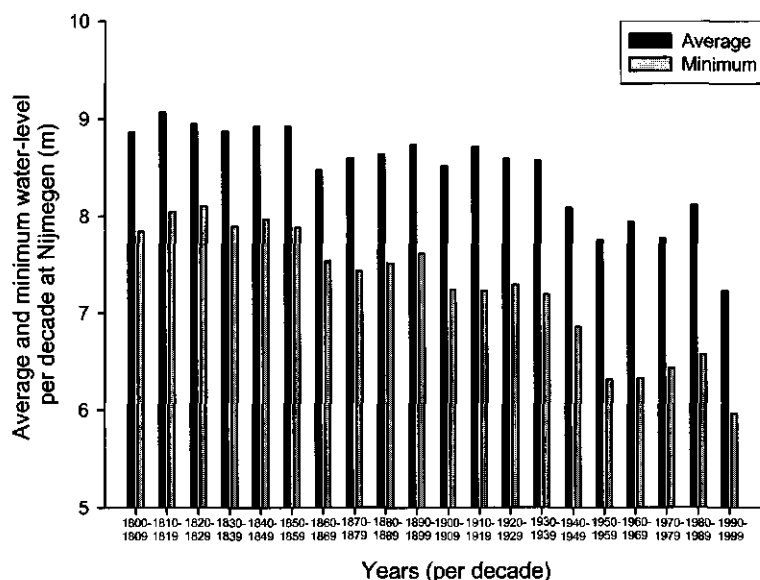


Figure 6. Average and minimum water level at Nijmegen (situated at river km 884 along the Waal) for each decade during 1800 – 1999

8.2.2. Measures to increase river discharge capacity

Several types of measures have been planned to achieve an increased river discharge capacity in the near future (Rijkswaterstaat, 1995, 1996). Some of the proposed measures in the floodplains are: 1) floodplain lowering, (the concept of 'cyclic floodplain rejuvenation' (Duel, Baptist & Penning, 2001) has been developed in which a combination of clay extraction and nature development was proposed), 2) floodplain widening by moving major embankments, and 3) removal of obstacles that reduce river discharge (such as brick factories, minor embankments, and bridges). According to the concept of cyclic floodplain rejuvenation, river discharge capacity during peak flows will be increased by large-scale lowering of floodplains and (re-)construction of secondary channels (Smits *et al.*, 2000). However, enhanced sedimentation and floodplain forest development will gradually reduce the discharge capacity of the lowered floodplains, and re-excavation after a number of decades would be necessary to sustain an unobstructed river discharge of the Lower Rhine.

Large-scale lowering of floodplains offers opportunities for creation of new lakes in floodplains along the Lower Rhine. Such new lakes may compensate for the loss of continuous formation of natural lakes along the Lower Rhine. In addition, lowering of floodplains will reduce the effects of a decreasing groundwater table due to river incision, resulting in a more natural water-level regime in these lakes. On the other hand, existing lakes will become (semi-)terrestrial areas in the lowered floodplains, potentially resulting in a loss of lakes with more advanced phases of macrophyte succession. This loss will not

be compensated by the creation of new lakes, since the time interval for cyclic rejuvenation is much shorter than the time necessary for the development of older successional phases. To meet safety criteria for peak flows, Baptist *et al.* (2004) calculated that the lowered floodplains have to be re-excavated every 25 – 35 years, whereas macrophyte succession occurs at time scales of several decades to centuries (Chapter 3, 4). Additionally, the newly created lakes will be exposed to high inundation duration, and will therefore generally have a low vegetation cover and a low species richness of macrophytes (Chapter 3 and 6; Van den Brink *et al.*, 1991). Therefore, when a 'cyclic rejuvenation' scheme covers all floodplains, many vegetation types which are characteristic for riverine areas will be virtually absent (Table 1).

8.2.3. The "Good Ecological Status" of floodplain lakes

In 2000, the EU Water Framework Directive was adopted by the member states of the EU. This directive requires the achievement of the 'Good Ecological Status' for all water bodies within the European Union by 2015. For so-called "heavily modified water bodies", past hydro-morphological adaptations should be taken into account when assessing their ecological status. Floodplain lakes along the Lower Rhine should be classified as heavily modified, because they have been irreversibly impacted by construction of major embankments, minor levees, and weirs. Considering these modifications, the Maximum Ecological Potential (MEP) must be derived from the natural reference. By analogy of the derivation of the Good Ecological Status from reference (entirely undisturbed) conditions, EU member states have the obligation for heavily modified water bodies of achieving the Good Ecological Potential (GEP), which only slightly deviates from the MEP.

Water bodies have to be monitored to assess their ecological status. This assessment will be based on the four quality elements of aquatic ecosystems: macrophytes, phytoplankton, macro-invertebrates, and fish. The abundance and composition of the macrophyte community in these lakes is an important component for the assessment, as macrophyte-dominated lakes are a characteristic component of natural river systems, and differences in macrophyte composition can clearly be related to human impact and successional age. The Good Ecological Potential of a river branch and its floodplains includes the view that all successional phases are well developed, and that the gradient from high to low inundation duration remains intact. Furthermore, during the assessment the effects of hydrological disturbances must be taken into account, because extreme water levels may result in large shifts in macrophyte composition and abundance. Based on data of the past 50 years, the effects of 'pressures' (particularly eutrophication) and 'impacts' (stabilization of water-level) on macrophyte composition along the branches of the Lower Rhine have been identified (Table 1).

Table 1 (next page). Proportion of lakes rich in submerged vegetation ($\geq 20\%$ cover of lake surface area) and the number of well developed vegetation types along the Rhine branches in relation to water-level stabilization, eutrophication, and cyclic floodplain rejuvenation. MEP = maximum ecological potential; RG = rompgemeenschap (according to Schaminee *et al.*, 1995); L = lakes with low inundation duration (≤ 20 days year⁻¹); H = lakes with high inundation duration (> 20 days year⁻¹). There is no category 'cyclic rejuvenation' in combination with 'low inundation duration', because cyclic rejuvenation will be applied only for floodplains with a high inundation duration.

Table 1. (for explanation, see previous page)

Association (according to Schaminée *et al.*, 1995)

		H	L	H	L	H	L	H	L	H
% lakes dominated by submerged macrophytes (cover > 20% of lake area)										
<i>Myriophyllum spicatum</i> (RG)	5RG Aarvederkruid (RG)	1	1	1	1	1	1	1	1	1
<i>Ceratophyllum demersum</i> (RG)	5RG Grof boomblad (RG)	1	1	1	1	1	1	1	1	1
<i>Potamogeton pectinatus</i> (RG)	5RG Schedefonteinkruid (RG)	1	1	1	1	1	1	1	1	1
<i>Typho-Phragmitetum</i>	8Bb4a Riet	1	1	1	1	1	1	1	1	1
<i>Sagittario-Sparganietum</i>	8Ab2 Egelskop / Pijlkruid	1	1	1	1	1	1	1	1	1
<i>Scirpetum lacustris</i>	8Bb1 Mattenbies		1		1		1		1	
<i>Alismato-Scirpetum maritimi</i>	8Bb3d Heen / Grote waterweegbree	1	1	1	1	1	1	1	1	1
<i>Lenno-Spirodelum polytrichae</i>	1Aa2 Veelwortelig kroos		1		1		1		1	
<i>Myriophyllo-Nupharetum</i>	5Ba3 Witte waterlelie / Gele plomp		1		1		1		1	
<i>Chara globularis</i> (RG)	4RG1 Brekbaar kranblad (RG)		1		1		1		1	
<i>Eleochar. acicularis</i> - <i>Limnoselletum</i>	29Aa4 Slijkgroen	1	1	1	1	1	1	1	1	1
<i>Ranunculetum circinatis</i>	5Bc3 Stijve wateranonkel	1	1	1	1	1	1	1	1	1
<i>Charietum vulgaris</i>	4Bb1 Gewoon kranblad	1	1	1	1	1	1	1	1	1
<i>Tolypelletum proliferae</i>	4Bb3 Groot boomglanswier	1	1	1	1	1	1	1	1	1
<i>Potamoeto-Nymphoidetum</i>	5Ba4 Watergentiaan	1	1	1	1	1	1	1	1	1
<i>Ran.fluitantis</i> - <i>Pot. perfoliati</i>	5Ba1 Doorgroeid fonteinkruid	1	1	1	1	1	1	1	1	1
<i>Rorippo-Oenanthetum aquaticae</i>	8Ab1 Watertorkruid	1	1	1	1	1	1	1	1	1
<i>Elodea nuttallii</i> (RG)	5RG Smalle waterpest (RG)		1		1		1		1	
<i>Potamoetum lucentis</i>	5Bb2 Glanzig fonteinkruid		1		1		1		1	
<i>Equisetum fluviale</i> (RG)	8RG6 Holpijp (RG)		1		1		1		1	
<i>Eleochar. palustris</i> - <i>Hippuridetum</i>	8Aa1 Lidsteng		1		1		1		1	
<i>Lenno-Nettelietum capillaris</i>	4Bb2 Kleinhoofdig glanswier		1		1		1		1	
<i>Najadetum. marinae</i>	5Aa3 Groot rimpkruid		1		1		1		1	
<i>Stratiotetum</i>	5Bb1 Krabbescheer		1		1		1		1	
<i>Utricularietum vulgaris</i>	5Bb2 Groot blaasjeskruid		1		1		1		1	
<i>Groenlandietum</i>	5Bc2 Paarbladig fonteinkruid		1		1		1		1	
<i>Ricciatum fluitantis</i>	1Ab1 Watervorkje		1		1		1		1	
<i>Potamoetum obtusifolii</i>	5Bc4 Slomp fonteinkruid		1		1		1		1	
<i>Callitriche-Hottonietum</i>	5Ca1 Watervoller / Sterrekroos		1		1		1		1	
<i>Cicuto-Caletum</i>	8Ba1 Slangewortel / Waterscheerling		1		1		1		1	
<i>Cicuto-Caricetum pseudocyperici</i>	8Ba2 Waterscheerling / Hoge cyperzegge		1		1		1		1	
Total number of associations		13	28	8	22	10	17	8	12	7

Water managers should develop measures to achieve the Good Ecological Potential. From Table 1 it may be clear that the objectives may be different depending on the future floodplain management strategy: if concepts like large-scale floodplain lowering and 'cyclic rejuvenation' are implemented in the present forelands, it is clear that the focus of assessment of the ecological state should be on the 'highly dynamic' elements. This would mean that there remains little or no room for the low-connective part of the gradient, including the high natural values of old floodplain lakes. However, the water manager should be alert for conservation obligations in such lakes, e.g. values protected under the EU Birds and Habitats directive.

8.3. Perspectives for floodplain lakes

At present, many lakes along the Lower Rhine have species-rich macrophyte communities which are characteristic for a wide range of successional phases. In the near future, however, conditions for macrophyte growth will change as a result of measures to increase river discharge. Depending on the location along the river these measures will vary, because of differences in hydrological and morphological characteristics of the Lower Rhine branches. Consequently, the impact of these measures for the status of macrophytes will also be different along these branches.

There are clear differences in discharge regime and floodplain characteristics between the branches of the Lower Rhine. During high river discharge, about two thirds of the flow enters the Waal, while the Neder-Rijn receives two-ninths, and the IJssel one-ninth. Because the main part of the river discharge is diverted to the Waal, safety measures along this branch will focus on large scale excavation and cyclic rejuvenation (Baptist *et al.*, 2004). For the Neder-Rijn, large scale floodplain excavation is not considered as an option, because this may decrease the stability of the major embankments. Instead, along this river branch obstacles will be removed and floodplains will be widened. In the upstream river stretches of the IJssel, most major embankments will also be safe at increased river discharge in the future, and floodplain excavation will only be carried out on a local scale. Along the middle and downstream parts of the river IJssel however, more extensive measures will be taken to sustain safe flood-levels on the long-term.

As a result of excavation, many floodplain lakes along the Waal will be exposed to higher river dynamics, and consequently more frequent inundations and drawdowns. In general, increased inundation duration will result in decreased species richness and cover of macrophytes (Chapter 3; Van den Brink *et al.*, 1991; Van de Steeg & Blom, 1999). Nevertheless, some vegetation types may benefit from creation of new lakes in excavated areas (Table 1), especially when these lakes are small (< 1 ha) and shallow (max. depth < 1.5 m), and have regularly exposed sediments. Already in the first years after excavation, these lakes may become dominated by Charophytes or narrow-leaved *Potamogeton*

species. In addition, internationally endangered Charophyte species such as *Tolypella intricata* and *T. prolifera* (Stewart & Church, 1992; Schmidt *et al.*, 1996; Utdrag ur Gårdenfors, 2000) may colonize these lakes. These pioneer species are characteristic for dynamic riverine habitats, and may recover quickly after disturbances such as summer floods.

However, in frequently flooded lakes the conditions for submerged macrophyte growth will be suboptimal compared to lakes with low inundation duration (Table 1). The regular occurrence of summer floods in lowered floodplains will result in a higher occurrence of the unvegetated state, although a further reduction of anthropogenic nutrient levels may improve conditions for macrophyte growth. In addition, when cyclic rejuvenation is applied with a 're-excavation cycle' of 25 – 35 years (Baptist *et al.*, 2004), vegetation types of more advanced successional phases will be virtually absent in these floodplains (Table 1).

Along the Neder-Rijn and IJssel, measures are not focused on large scale floodplain excavation, and will have a less dramatic impact on conditions for macrophyte growth. As a result, old lakes with advanced phases of succession may remain present, whereas the gradient from low to high connectivity has a higher potential to be maintained or restored. In lakes along these river branches, input of seepage water from the hill slope aquifer of the moraines Veluwe and Utrechtse Heuvelrug may decrease nutrient levels, thereby improving conditions for macrophyte growth. Furthermore, along the IJssel and – to a lesser extent – the Waal, the amplitude of water-level fluctuations becomes reduced in downstream direction (Figure 7). This implies that during river flooding, lakes in more upstream floodplains are exposed to far deeper and more prolonged submergence with turbid river water than in floodplains along downstream reaches. Similarly, extremely low water-levels will occur more often in upstream parts, resulting in a higher occurrence of lake drawdown. As a result, the impact of both river flooding and drawdown on macrophyte composition and succession will be more strongly in upstream than in downstream parts of the two river branches involved. Consequently, downstream reaches of the IJssel and Waal offer the highest potential for development of habitats characteristic for low-dynamic rivers. Likewise, conditions may be suitable for development of certain low-dynamic vegetation types along the Neder-Rijn/Lek (Table 1).

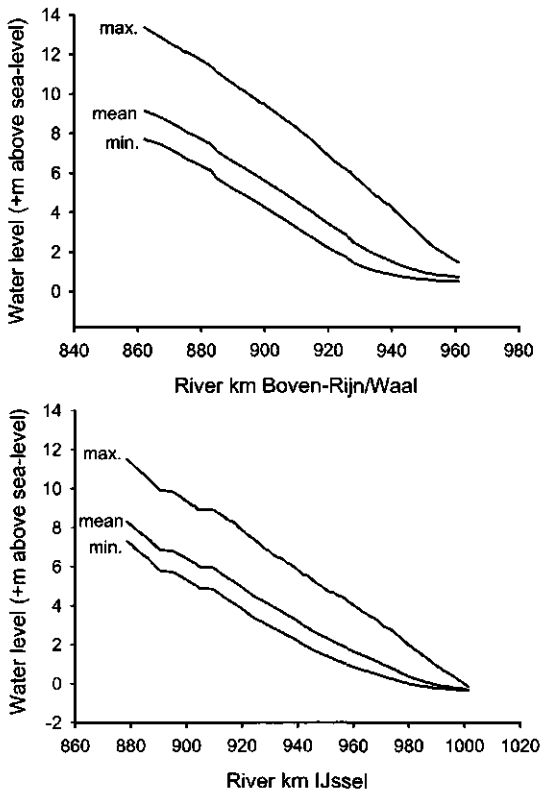


Figure 7. The maximum, mean and minimum water-level in the period May-October 1990 – 1999 in the Waal and IJssel

In lakes along the Neder-Rijn, macrophyte diversity is reduced due to stabilization of the water level during periods of low river discharge (Chapter 4). Because weirs in the Neder-Rijn play an important role for the distribution of river discharge among the branches of the Lower Rhine, reinstatement of the natural water-level regime in the Neder-Rijn is highly unlikely. Still, an option might be to allow low water levels in certain years and promote incidental drawdown of lakes. The potential to stimulate such drawdown events differs in longitudinal direction of the Neder-Rijn/Lek. Lakes which are situated near the downstream end of a weir section have the highest potential for a natural water-level regime with declining water-levels during the growing season. However, for lakes situated close to the weirs in upstream direction, a natural water-level regime cannot be realized, because closing of the weirs will always result in increased water levels (Figure 8).

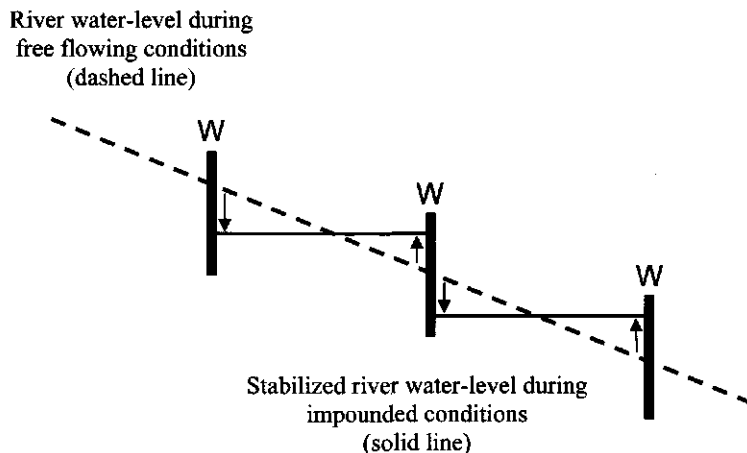


Figure 8. Water-levels in de Neder-Rijn/Lek during free-flowing (dashed line) and impounded conditions (solid line). W = weir. The arrows indicate the direction of water-level change due to closure of the weirs. Directly at the downstream river stretch of a weir, closure of the weirs results in declining water-levels, whereas directly at upstream stretches of weirs, closure results in increasing water-levels.

Therefore, along the Neder-Rijn/Lek, excavation of relatively shallow lakes (depth < 1 meter) situated nearby a downstream end of a weir and at short distance to the main channel, effectively results in the highest potential for species-rich macrophyte vegetation.

Along the Lower Rhine, the natural gradient in flooding frequency by the river has been strongly disrupted by the construction of major embankments long ago. Nowadays, the majority of the lakes in the active floodplain of the Lower Rhine are flooded annually. Characteristic vegetation types of rarely flooded habitats at intermediate nutrient levels (with species such as *Hottonia palustris*, *Myriophyllum verticillatum* and *Utricularia vulgaris*) are rare in the active floodplain of the Lower Rhine (data set of this thesis). By contrast, these vegetation types have their optimum occurrence in never inundated water bodies behind the major embankments in the adjacent hinterland (Weeda *et al.*, 2000). The distribution patterns and ecological characteristics of these species suggest that the regular occurrence of river floods may be responsible for the scarcity of these species in the active floodplain of the Lower Rhine. Similarly, Grift (2001) proposed that the low proportion of limnophilic fish species in floodplains along the Lower Rhine characteristic for the same habitat type may be caused by the absence of rarely flooded lakes along this river.

Whether rarely flooded habitats should be preserved or restored along the Lower Rhine, depends on the rehabilitation goal and how vegetation types characteristic for these habitats are valued relative to other, more dynamic habitats. When floodplain

rehabilitation aims at restoring habitats of the complete connectivity gradient, rarely flooded lakes should be preserved because of their additional value and because they were originally present (Grift, 2001). On the other hand, it can be argued that dynamic habitats can only be developed in riverine areas, whereas species that are characteristic for rarely flooded lakes also occur in habitats outside the riverine landscape (e.g. peat lakes). Ideally, floodplain management should focus on increasing the area for both high and low dynamic habitats, because this will result in the highest biodiversity on the river-scale. Probably, low dynamic habitats can be developed in areas behind major embankments, e.g. in proposed retention areas which will only be flooded once or twice every century during extreme river floods.



Lakes with dominance of *Utricularia vulgaris* are rare in the active floodplain of the Lower Rhine, probably as a result of the high frequency of inundation by the river. Photo: John van Schie (RIZA)

Finally, my results suggest that lake morphometry plays an important role for macrophyte composition and succession, because it contributes to the variation in vegetation density and composition as least as much as variables related to river dynamics. This implies that emphasis must be put on lake morphometry in the 'design' of new lakes in excavated areas. Conditions for submerged macrophyte growth are most suitable when lakes are small (< 1 ha), shallow (max. depth < 1.5 m at start of growth season), and have occasionally exposed sediments. Similarly, the water-level regime of new lakes can in part be designed, through choice of the location along the river, the distance between the lake and the river and depth profile of the lake. Specifically, lakes which are situated at a short distance from the main channel will show stronger water-level fluctuations compared to more remote lakes.

Overall, by concentrating the focus for restoration on ecosystems characteristic of highly dynamic habitats in the most connective parts of the river Waal, and by utilizing the differences in hydrological characteristics between the three Lower Rhine branches, many submerged macrophyte-rich floodplain lakes along the Lower Rhine can be maintained or restored.

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Macrophyte succession in floodplain lakes

Two questions are central to the work in this thesis:

1. What are the factors determining macrophyte composition in floodplain lakes along the Lower Rhine?
2. What advice can be given for design of future water bodies?

As water level fluctuations are a prominent feature of floodplain lakes, I first analyzed the factors determining water-level fluctuations in 100 lakes in the active floodplain (*Chapter 2*). Fluctuations in lake water level appeared largely driven by groundwater connection to the river. Hence, lake-level fluctuations are largest in lakes close to the main channel and along strongly fluctuating segments of the river. Also, lake-level fluctuations are usually smaller in older (> 30 years) lakes, due to accumulated clay and silt on the lake bottom reducing groundwater conductivity. Species richness of floating-leaved and emergent macrophytes in this set of lakes is highest at intermediate water-level fluctuations, whereas species richness of submerged macrophytes was highest in more fluctuating lakes. The incidence of drawdown was also positively correlated to species richness of submerged macrophytes.

In a next step (*Chapter 3*), I analyzed the factors governing vegetation structure in a set of 215 floodplain lakes. The frequency distribution of the cover of submerged macrophytes was distributed bimodally. Thus, submerged macrophytes in any one lake tended to be either very scarce or very abundant. Remarkably, clear water lakes with submerged macrophyte dominance occurred despite high total phosphorus concentrations (0.020 to 0.40 mg total P L⁻¹). Another novel finding was that the probability of dominance by submerged macrophytes is much larger in small lakes than in larger lakes of the same depth. Also, submerged macrophyte dominance decreased with lake age, water depth and the average duration of annual flooding. By contrast, nymphaeid cover showed an optimum with respect to mean lake depth, and the probability of occurrence of nymphaeids and helophytes increased with lake age. Helophyte vegetations were also less likely to be found in the presence of trees or cattle, and in larger and deeper lakes. In all cases the critical level of one factor (e.g. mean lake depth) depended on other factors (e.g. surface area or age of lake). For instance, small lakes tended to remain dominated by submerged macrophytes up to a greater depth than large lakes, and helophytes colonised smaller lakes in an earlier phase. Against our expectations, the effect of inundation by the river was small. This may be related to the fact that most of our lakes are rarely inundated during the growing season and experience only moderate current velocities while flooded.

In *Chapter 4*, the factors affecting the composition of aquatic vegetation in these 215 floodplain lakes is further explored. Vegetation composition appeared to be related to lake size and age, cattle access to the shoreline, the duration of the annual flood events, and the fraction of the lake sediment that becomes exposed at low water level (drawdown). Remarkably, vegetation composition was correlated more strongly to lake age and occurrence of drawdown than to the duration of the flood events. As discussed in *Chapter 1*, water-level fluctuations become reduced with lake age due to accumulation of clay and silt which 'seals' lake sediments, preventing drawdown during periods of low river levels. In view of our results we hypothesize that this clay sealing process is a major driving force for aquatic vegetation succession in floodplain lakes along the Lower Rhine, as succession drives from desiccation-tolerant species (e.g. *Chara* spp.) in young lakes to desiccation-sensitive species (e.g. *Nuphar lutea*) in old lakes. In one of our river branches, the water-level regime is regulated, resulting in relatively constant and high water levels in the river and the related floodplain lakes. The vegetation in these lakes was characterized by low species richness and a frequent dominance by the invasive species *Elodea nuttallii*, suggesting that stabilization of river water levels during low discharge may seriously affect the vegetation of floodplain lakes.

Because water-levels of the Lower Rhine vary considerably from one year to another, in some years no lakes may dry out at all while in other years up to 50% of the lakes are drawn down. To study the effect of this inter-annual variation, macrophyte composition and cover in 70 lakes in floodplains along the Lower Rhine was monitored from 1999 to 2003 (*Chapter 5*). We found large inter-annual differences in cover of submerged vegetation, whereas abundance of nymphaeids and helophytes varied much less between years. The inter-annual variation in submerged vegetation cover was most pronounced in lakes that were small and experienced drawdown events. As found also in the large set of lakes examined in *chapter 3*, submerged vegetation occurred abundantly in small lakes irrespective of the nutrient levels. We suggest that this pattern may be explained from occasional drawdown events in the lakes, triggering shifts towards dominance by submerged vegetation. Without drawdown, these lakes gradually return into the unvegetated state, but this may take several years. Therefore, if drawdown occurs frequently, the majority of the lakes will be in a transient vegetated state most of the time. A corollary is that hydrological regulation may be an important factor aggravating the permanent loss of submerged vegetation due to cultural eutrophication.

To get an image of the longer term vegetation dynamics in the area we reanalyzed aquatic-vegetation inventories made over five decades in the floodplain lakes (*Chapter 6*). This analysis revealed that the probability of submerged macrophyte dominance (lake cover $\geq 20\%$) was reduced after summer floods. Lake-bottom desiccation during

prolonged low water periods had an opposite effect, resulting in an increased probability of dominance by submerged vegetation and a decrease of nymphaeid vegetation.

As Charophyte abundance appears particularly associated to drawdown events we hypothesized that sediment exposure may stimulate germination of *Chara* from seed banks (*Chapter 7*). To test this hypothesis, we examined the composition of the propagule bank in a *Chara*-dominated lake, and experimentally analyzed the effect of sediment exposure on sporeling emergence of *Chara* after re-submersion of the sediment. Exposure of lake sediments resulted in a 12-fold increase in *Chara* sporeling density compared to cores which remained permanently inundated. Thus the stimulatory effect of sediment exposure on *Chara* germination may indeed explain the increased abundance of *Chara* subsequent to dry years.

We conclude (*Chapter 8*) that although macrophyte development in lakes along the Lower Rhine follows a pattern which is in line with the classical sequence, this development is not unidirectional, as macrophyte succession is regularly 'reversed' by the occurrence of extreme water levels. Our findings have some obvious management implications. As a result of large scale clay removal from floodplains in the near future, many lakes will be created which will be exposed to frequent inundations and drawdowns. Although, increased inundation duration will result in decreased species richness and cover of macrophytes, some vegetation types of Charophytes will probably benefit from creation of new lakes in these excavated areas. However, other vegetation types of nymphaeids and helophytes occur only in old lakes. This implies that when cyclic 'rejuvenation' is applied to all lakes with a re-excavation cycle of 25 – 35 years, vegetation types of such more advanced successional phases would disappear from the floodplains.

Waterplanten successie in uiterwaardplassen

Achtergrond van het onderzoek

Naar verwachting zal gedurende de komende decennia de winterafvoer van de Rijn stijgen, waardoor de maximale rivierpeilen toenemen. Om de veiligheid van de rivierdijken te waarborgen, heeft de Nederlandse overheid een analyse uitgevoerd van maatregelen die in de toekomst wateroverlast kunnen voorkomen. Hieruit bleek dat 'oude' oplossingen, zoals dijkverhogingen, ontoereikend zijn om de veiligheid op lange termijn te garanderen. Als alternatief is een pakket van maatregelen opgesteld die de afvoercapaciteit van de rivier tijdens overstromingen vergroot. Voorbeelden van deze maatregelen zijn het verwijderen van obstakels die de waterafvoer belemmeren (zoals steenfabriek-terreinen en veerdammen), de aanleg van nevengeulen die als 'by-pass' voor de rivierafvoer dienen, en grootschalige afgraving van uiterwaarden met 1 à 2 meter. Deze maatregelen leiden tot lagere waterstanden tijdens piekafvoeren van de Rijn, en kunnen gecombineerd worden met reeds bestaande plannen voor natuurontwikkeling langs deze rivier.

Als gevolg van de grootschalige verlaging van het maaiveld zal het aandeel van 'natte natuur' in de uiterwaarden sterk toenemen. De vraag is natuurlijk hoe de plannen voor natuurontwikkeling gecombineerd kunnen worden met maatregelen ter vergroting van de afvoercapaciteit. Aangezien de nieuwe natuur met graafmachines wordt gerealiseerd, kunnen de startcondities bij aanleg bepaald worden. Bepalende voorwaarden voor de ontwikkeling van levensgemeenschappen in uiterwaardplassen zijn ondermeer waterdiepte, plasoppervlak, en tijdsduur van overstroming door de rivier. Voorgaand onderzoek heeft uitgewezen dat een hoge overstromingsduur van de rivier gepaard gaat met een lage soortenrijkdom van waterplanten. Aangezien de overstromingsduur duidelijk toeneemt door maaiveld-verlaging, bestaat de angst dat toekomstige plassen zullen vervallen tot troebele, algen-gedomineerde plassen met een lage soortenrijkdom.

In 1998 startte RIZA samen met Wageningen Universiteit het zogeheten OER-project (Onderzoek Ecologie Rivieruiterwaardplassen). Het OER-project beoogt de factoren te achterhalen die de ontwikkeling van levensgemeenschappen in uiterwaardplassen sturen. In een multidisciplinaire aanpak worden relaties gelegd tussen de samenstelling van levensgemeenschappen en abiotische plas kenmerken (zoals vormgeving, overstromingsduur door de rivier, invloed van grondwater en nutrienten) en biotische interacties (bv. de rol van vis op het phytoplankton). Uiteindelijk heeft het OER-project geleid tot dit proefschrift, dat zich concentreert op waterplanten, en tot het proefschrift

van Frank Roozen, waarin de rol van plankton centraal staat. Aan de hand van de resultaten kan advies gegeven worden over de positie en vormgeving van toekomstige plassen in uiterwaarden langs de Rijn.

Onderzoeksvragen

Dit proefschrift richt zich op twee vragen, namelijk:

- Welke factoren bepalen de bedekking en soortensamenstelling van ondergedoken waterplanten, drijfbladplanten, en helofyten in uiterwaardplassen langs de Rijn?
- Welke richtlijnen kunnen gegeven worden over het ontwerp van toekomstige uiterwaardplassen met hoge natuurwaarden?

Peilfluctuaties in de rivier spelen een belangrijke rol voor de ontwikkeling van waterplanten in uiterwaardplassen. Voorgaand onderzoek heeft uitgewezen dat de aanvoer van nutriënten en slib tijdens rivieroverstromingen een groot effect hebben op de groei van waterplanten. Daarentegen is nog vrij weinig bekend over de invloed van lage rivierpeilen. Om deze reden heb ik onderzocht welke factoren het peilverloop van uiterwaardplassen tijdens lage rivierwaterstanden bepalen (hoofdstuk 2). Via het grondwater kunnen peilfluctuaties van de rivier sterk doorwerken in het peilverloop van uiterwaardplassen. Naarmate een plas op kortere afstand van de rivier ligt, zal het waterpeil in deze plas de fluctuaties van het rivierpeil sterker volgen. Hiernaast bezitten plassen met een zandbodem grotere peilfluctuaties dan plassen met een kleibodem. Bij iedere overstroming sedimenteren kleideeltjes in het sediment van de plas, die gaandeweg tot een kleilaag accumuleren. Deze kleilaag vermindert de doorlaatbaarheid van de bodem, waardoor de peildynamiek afneemt bij een toenemende ouderdom van de plas. De peilfluctuaties hebben grote invloed op de vegetatiesamenstelling van de plassen. Zo blijkt uit hoofdstuk twee dat de soortenrijkdom aan drijfbladplanten en helofyten het hoogst is bij gemiddelde peilfluctuaties, terwijl de soortenrijkdom van ondergedoken waterplanten het hoogst is in plassen met een sterk fluctuerend waterpeil en een (deels) droogvallende bodem.

Aansluitend heb ik onderzocht welke factoren de vegetatiestructuur bepalen in een set van 215 plassen (hoofdstuk 3). De frequentie verdeling van ondergedoken waterplanten was bimodaal, waaruit blijkt dat ondergedoken waterplanten in individuele plassen ofwel een hoge bedekking, ofwel vrijwel afwezig waren. Tegen de verwachting in hadden plassen met een hoge bedekking aan ondergedoken waterplanten eveneens hoge fosfaatgehalten (tot $0.40 \text{ mg total P L}^{-1}$). Bovendien kwamen ondergedoken waterplanten het meest voor in kleine plassen ($< 2\text{-}3 \text{ ha}$), in vergelijking tot grotere plassen met eenzelfde diepteprofiel. Hiernaast nam de kans op ondergedoken waterplanten af bij toenemende waterdiepte, ouderdom en overstromingsduur van de plas. De drijfbladplanten vertoonden een optimum wat betreft waterdiepte, terwijl de bedekking van drijfbladplanten en

helofyten toenam met de leeftijd van de plas. Helofyten vegetaties werden daarentegen minder vaak aangetroffen in de aanwezigheid van vee of bomen op de oever, en in grotere en/of diepere meren. In alle gevallen hing het kritische niveau van de ene factor (bv. plasdiepte) af van de waarde van andere factoren. Zo werden kleinere plassen gemiddeld tot op grotere diepte gedomineerd door ondergedoken waterplanten, en in een vroeger stadium gekoloniseerd door helofyten. Tegen de verwachting in waren verschillen in overstromingsduur door de rivier slechts zwak gerelateerd aan de vegetatiestructuur in de plassen. Mogelijk wordt dit veroorzaakt door de geringe stroomsnelheid van het water tijdens overstromingen, of door het vrijwel achterwege blijven van overstromingen tijdens de zomermaanden van voorafgaande jaren.

In hoofdstuk 4 ga ik nader in op de vraag hoe de vegetatie-ontwikkeling wordt beïnvloed door de afname van de peildynamiek bij toenemende ouderdom van de plassen. De vegetatiesamenstelling in de data-set van 215 plassen was gerelateerd aan de leeftijd van de plas en het percentage drooggevallen oppervlak, het oppervlak en de overstromingsduur van de plas, en de toegang van vee op de oevers. Opmerkelijk genoeg was de vegetatiesamenstelling sterker gerelateerd aan de leeftijd van de plas en het optreden van droogval, dan aan de tijdsduur van rivieroverstromingen. De afname van peilfluctuaties in plassen heeft blijkbaar een grote invloed op de vegetatie-ontwikkeling. Omdat jonge plassen regelmatig droogvallen, groeit in deze plassen een vegetatie die bestaan uit soorten met een levenscyclus waarin tijdelijke droogte wordt getolereerd. Voorbeelden hiervan zijn Veenwortel en kranswier (*Chara* spp.). In oudere plassen neemt de kans op droogvallen duidelijk af, waardoor droogte-gevoelige soorten als Gele Plomp en Witte Waterlelie zich kunnen ontwikkelen.

Langs de Neder-Rijn en Lek is het waterpeil gereguleerd door stuwen. Hierdoor is het waterpeil relatief constant, en komen in de rivier en aangrenzende uiterwaardplassen geen periodes met laagwater en droogval voor. De afwezigheid van peildynamiek heeft een duidelijke invloed op de vegetatiesamenstelling: plassen langs de Neder-Rijn bezaten minder kenmerkende riviersoorten en een lagere soortenrijkdom dan plassen langs de niet-verstuwde Waal en IJssel, terwijl een exoot als Smalle Waterpest daarentegen juist meer voorkwam in plassen langs de Neder-Rijn. Deze resultaten geven aan dat regulering van het rivierpeil tijdens lage rivierafvoer een negatief effect heeft op soortenrijkdom en natuurlijkheid van aangrenzende uiterwaardplassen.

Het waterpeil in de Rijn vertoont van jaar tot jaar aanzienlijke schommelingen. Dit heeft een groot effect op het aantal droogvallende plassen. In sommige jaren droogt er vrijwel geen enkele plas uit, terwijl in andere jaren meer dan de helft van de plassen kan droogvallen. Om een beter inzicht te krijgen in het belang van deze variatie, is de vegetatiesamenstelling van een 70-tal plassen jaarlijks gemonitord in de periode 1999 –

2003 (hoofdstuk 5). Het bedekkingspercentage aan ondergedoken waterplanten fluctueerde sterk van jaar tot jaar, terwijl de bedekking van drijfbladplanten en helofyten veel constanter was. Van 1999 tot 2003 daalde het percentage vegetatierijke plassen van 63% naar 28%. De afname in bedekking van ondergedoken waterplanten was het sterkst in plassen met een grote kans op droogval. Echter, in de periode 1999–2002 zijn deze plassen niet drooggevalen, terwijl dit in 1997 en 1998 wel is gebeurd. Dit wijst erop dat de hoge waterplanten-dominantie in 1999 het gevolg was van droogval in voorgaande jaren. In de daaropvolgende jaren bleef droogval uit, waardoor in veel plassen de ondergedoken waterplanten weer verdwenen. Dit betekent dat bij een regelmatige droogval een groot deel van de plassen zich in een vegetatierijke toestand zal bevinden. In de literatuur wordt vaak aangenomen dat de toename van nutriëntengehaltes verantwoordelijk is voor de afname van ondergedoken waterplanten. Echter, gelijktijdig met de toename van de trofiegraad is in veel plassen ook het waterpeil gestabiliseerd. Deze resultaten tonen aan dat stabilisatie van het waterpeil de gevolgen van eutrofiering kunnen versterken.

In hoofdstuk 6 is een analyse gemaakt van eerder uitgevoerde waterplanten-inventarisaties in uiterwaardplassen over de afgelopen 50 jaar, waardoor een beter beeld werd verkregen van de lange termijn dynamiek van de vegetatiesamenstelling. Hieruit kwam naar voren dat de bedekking van ondergedoken waterplanten verminderde na een zomeroverstroming. Droogval daarentegen resulteerde juist in een verhoogde dominantie van ondergedoken waterplanten, en een afname van drijfbladplanten.

Uit de resultaten van voorgaande hoofdstukken kwam naar voren dat kranswieren (*Chara*) vooral dominant zijn in plassen die regelmatig droogvallen. Om deze reden is gekeken of droogval van sediment de kieming van *Chara* uit zaadbanken kan stimuleren (hoofdstuk 7). Inderdaad resulteerde droogval in een sterke toename van het aantal *Chara*-kiemplanten in het daarop volgende jaar. Dit betekent dat het verloop van het aantal *Chara*-plassen langs de Rijn sterk bepaald wordt door het droogvalregime van de plassen.

Bij toenemende leeftijd van de plassen, verschuift de vegetatiesamenstelling van ondergedoken waterplanten naar drijfbladplanten en helofyten. Dit patroon is in overeenstemming met successiereeksen van waterplanten buiten uiterwaardplassen. Deze successiereeks verloopt in plassen langs de Rijn echter niet volgens een rechte lijn. Regelmatig wordt de vegetatie-ontwikkeling 'teruggezet' door het optreden van extreme waterstanden, resulterend in droogval of zomeroverstromingen (hoofdstuk 6 en 8).

De resultaten in dit proefschrift kunnen van grote betekenis zijn voor het beheer van uiterwaarden langs de Rijn (hoofdstuk 8). Toekomstige plassen in de afgegraven uiterwaarden zullen vaak overstromen en droogvallen. Een verhoogde overstromingsduur van

de rivier gaat vaak gepaard met een lagere soortenrijkdom en bedekking aan waterplanten. Niettemin kunnen bepaalde pioniersoorten zoals kranswier van de aanleg van nieuwe plassen profiteren. Deels betreft dit bedreigde en voor rivieren kenmerkende soorten, zoals Groot Boomglanswier (*Tolypella prolifera*) en Vertakt boomglanswier (*T. intricata*). Daarentegen groeien vegetatietypen van drijfbladplanten en helofyten alleen in oudere uiterwaardplassen. Dit betekent dat vegetatietypen van oudere successiestadia geen kans krijgen zich te ontwikkelen in plassen die gelegen zijn in uiterwaarden waar 'cyclische verjonging' wordt toegepast met een cyclus van 25 – 35 jaar.

Curriculum vitae

Gerben van Geest werd geboren op 23 mei 1969 in 's-Gravenzande. Na het behalen van het HAVO-diploma in 1986 werd de opleiding vervolgd met een botanische opleiding aan het Hoger Laboratorium Onderwijs in Delft (onderdeel van de Polytechnische Faculteit van de Hogeschool Rotterdam en Omstreken). Deze opleiding werd afgesloten met een stage en afstudeervak aan de vakgroep Transportfysiologie van Rijksuniversiteit Utrecht. In 1991 startte hij met de studie Biologie (orientatie Milieu) aan de Wageningen Universiteit, die in 1994 'met lof' werd afrond. Voor deze studie werden twee afstudeervakken uitgevoerd, bij de vakgroep Aquatische Ecologie en Waterkwaliteitsbeheer (AEW) en bij de vakgroep Toxicologie. Van 1995 tot 1997 verrichte hij onderzoek naar de effecten van pesticiden in outdoor mesocosms. Dit onderzoek werd uitgevoerd bij leerstoelgroep AEW (Wageningen Universiteit) in samenwerking met het toenmalige Staring Centrum. In 1997-1998 werkte hij een jaar als aquatisch ecooloog bij adviesbureau Witteveen+Bos in Deventer, alwaar hij diverse opdrachten uitvoerde op het gebied van visstandmonitoring en biomanipulatie. Van 1998 tot eind 2002 werkte hij als assistent in opleiding bij de leerstoelgroep AEW aan de Wageningen Universiteit, waarvan dit proefschrift het resultaat is. Momenteel werkt Gerben als post-doc bij het NIOO-CL in Nieuwersluis, waar hij de effecten van klimaatverandering en ganzen op toendraplassen in Spitsbergen onderzoekt.

List of publications

Journals

- Van Geest, G.J., Coops, H. & Scheffer, M. (submitted) Transient macrophyte dominance in lakes with fluctuating water levels.
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- Van Geest, G.J., Wolters, H., Roozen, F.C.J.M., Coops, H., Roijackers, R.M.M., Buijse, A.D. & Scheffer, M. (in press) Water-level fluctuations affect macrophyte richness in floodplain lakes, *Hydrobiologia*
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