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Primary Research Paper

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 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 hydrologically dynamic lakes will decrease over time. Therefore, we suggest that excavation of new lakes is essential to conserve the successional sequence of floodplain water bodies including conditions of high biodiversity. Shallow, moderately isolated, lakes with occasional bottom exposure 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 (Bornette et al., 1994; Henry et al., 1994; Van den Brink, 1994; Bornette et al., 1998; Van Geest et al., 2003). 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 (Fig. 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).

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 stabilisation 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 vegetation-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.

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 km^2 (Lelek, 1989), of which 25 000 km^2 is situated in the Netherlands. Where the Rhine enters The Netherlands, the discharge varies roughly between 800 and 12 000 m^3 s^{-1}, resulting in a difference between the minimum and maximum water level of up to 8 metres at Lobith (Fig. 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

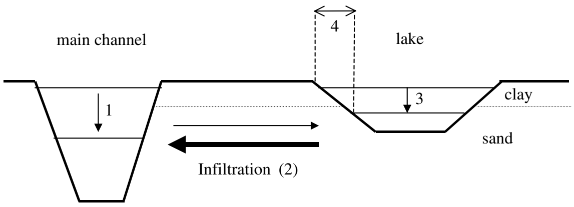

Figure 1. Pathways for groundwater flow between a floodplain lake and the main channel during non-flooded conditions. During low water levels in the river (1), infiltration of lake water to the river (2) will result in a decrease in the lake water-level (3), potentially resulting in sediment exposure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

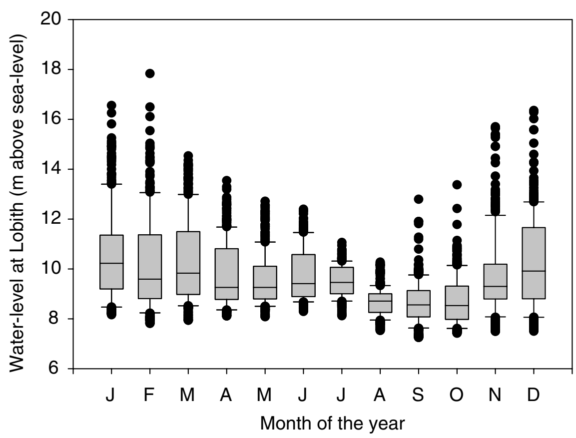

Figure 2. Monthly water-level of the Lower Rhine at Lobith in the period 1990–1999. Each box represents the average, and the 75, 95 percentile values. Dots indicate individual water-level measurements lower or higher than the 5 and 95 percentile value respectively.

splits into three branches: Waal, IJssel, and Neder–Rijn. Due to the construction of major embankments, the active floodplain has been reduced to a narrow belt 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 1960s. All weirs are closed only below the mean river discharge of the Rhine (2200 $m^3 s^{-1}$). 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 (Fig. 3), especially in young lakes.

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

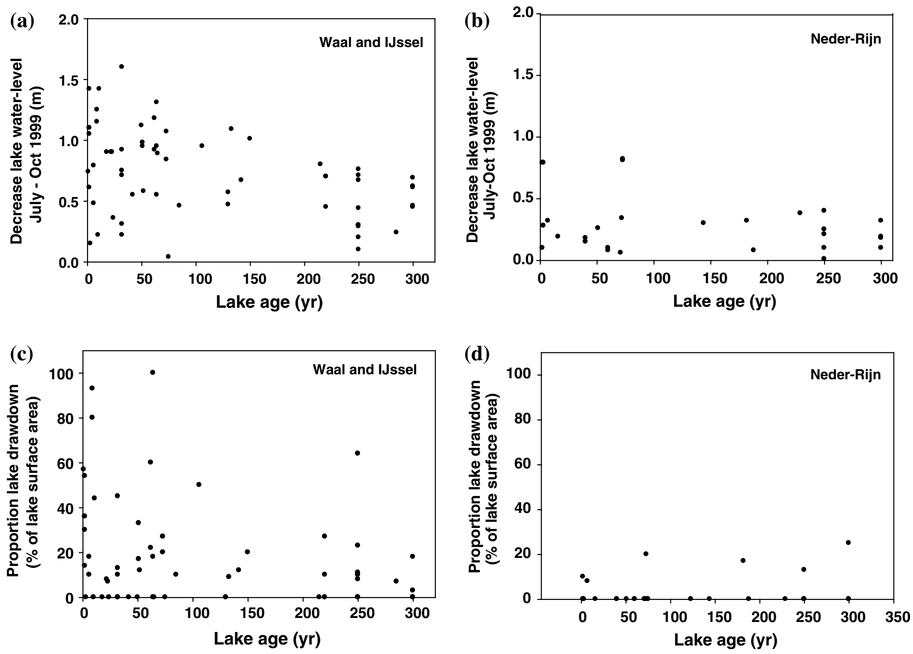

Figure 3. Decrease in lake water-level (3a, b) and drawdown area (3c, d) in relation to lake age along the unimpounded branches Waal and IJssel, and impounded branch Neder–Rijn.

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

	N lakes	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 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 (Fig. 2).

Materials and 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), ± 3–7 years for lakes aged 20–90 y (1980–1910), and ± 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 10 min. 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 $WL_{J–O}$ 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 lineair regression analyses to predict the decrease in water level in the floodplain lakes between July and October 1999

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, 1st–October, 31th 1999
Shortest distance between lake and main channel	m	
Mean lake depth [a]	m	calculated from 5 to 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 the lake sediment

[a] = ln(x)-transformed.

Table 3. Results of forward stepwise regression analysis for decrease in water level in floodplain lakes between July and October 1999

Variable	Unstandardized coefficient ± S.E.	*p*	Standardized coefficient
Water-level river July–Oct 1999	0.319 ± 0.033	< 0.0001	0.697
Distance lake–river	$-3.82.10^{-4}$ ± 0.000	< 0.0001	−0.259
Lake depth[a]	0.157 ± 0.049	< 0.01	0.242
Lake age [a]	$-4.70.10^{-2}$ ± 0.016	< 0.01	−0.189
Lake surface area [a]	$-3.47.10^{-2}$ ± 0.017	< 0.05	−0.144
Constant	0.273 ± 0.090	< 0.01	

(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 which 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.

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–≥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 ($R^2_{adj} = 0.62$, Table 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 ($R^2_{adj} = 0.58$; 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; Fig. 4a,d). 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, Fig. 4b). 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 (Fig. 4c). In addition, lakes

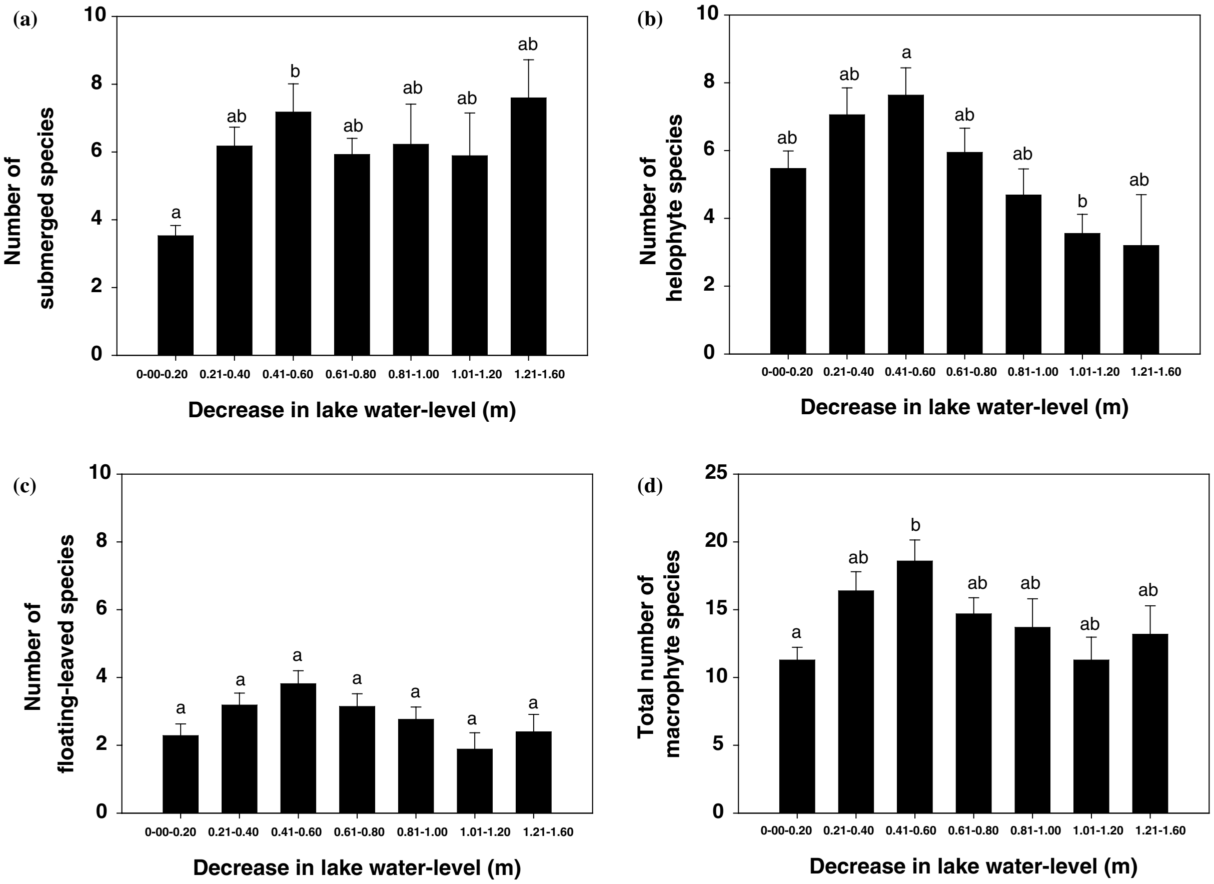

Figure 4. Frequency distribution of species richness of submerged macrophytes, floating-leaved macrophytes, helophytes and total number of macrophytes in lakes ($\pm$ standard error) in relation to decline in lake water-level between July and October 1999. Data for lakes along the impounded Neder–Rijn 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, $p < 0.05$).

with partial drawdown exhibited a significant higher species richness of submerged macrophytes compared to lakes with no drawdown (*t*-test; $p = 0.006$; Fig. 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; Fig. 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 macrophyte dominance, all rehabilitation lakes lost their aquatic vegetation within a few years (Table 4).

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)

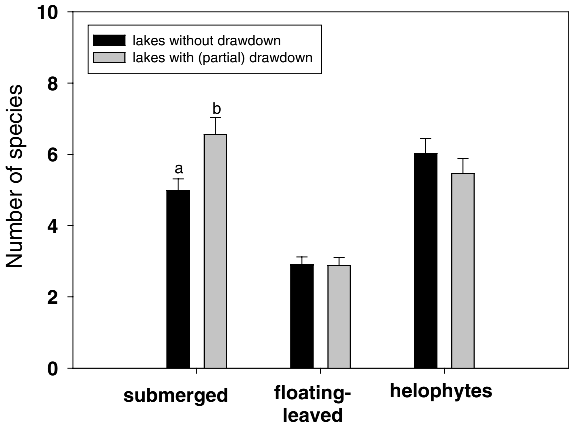

Figure 5. Frequency distribution of species richness of submerged, floating-leaved, and helophyte macrophytes in lakes (± standard error) with and without drawdown (*n* lakes = 48 and 49, respectively). Data for lakes along the impounded Neder–Rijn with an increase in water-level during July–October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

(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 (Keddy & Constabel, 1986; Smits et al., 1989; Coops & Van der Velde, 1995; Bonis & Grillas, 2002). In addition, disturbances caused

Table 4. Vegetation development in rehabilitation lakes in the first years after excavation

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	1992	≥50	3
		1993	≥50	4
		1999	20	4
Koppelerwaard	1996	1999	100	6
		2000	67	4
		2001	< 1	4
		2002	< 1	
		2003	< 1	
Lent	1997	1998	≥50	4
		1999	10	
		2000	< 1	
		2001	< 1	
		2002	< 1	
		2003	30	
Wageningen	1998	1998	≥50	
		1999	60	4
		2000	23	
		2001	7	
		2002	10	
		2003	<1	

Nymphaeids were absent in all years. Data based on own results, Coops et al. (1993), and Lauwaars et al. (1997).

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 (Fig. 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 germinate rapidly 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 reappear, 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 (Van Geest, unpublished data). 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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