

# Mass development of monospecific submerged macrophyte vegetation after the restoration of shallow lakes: Roles of light, sediment nutrient levels, and propagule density



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## ABSTRACT

After restoration, eutrophicated shallow freshwaters may show mass development of only one or two submerged macrophyte species, lowering biodiversity and hampering recreation. It is unclear which environmental factors govern this high percentage of the volume inhabited (PVI<sup>2</sup>) by submerged macrophytes, and whether the development of a more diverse, low canopy vegetation is likely to occur if dominant species decline in abundance.

We hypothesized that (1) adequate light and high sediment nutrient availability leads to massive development of submerged macrophytes, and (2) that macrophyte species richness is low at high PVI, but that this is not caused by a lack of viable propagules of non-dominant species (especially charophytes).

To test these hypotheses, fifteen shallow waters in the Netherlands were studied with respect to submerged vegetation (including propagules), water, and sediment characteristics.

The probability of high submerged macrophyte PVI is highest in shallow waters where light availability in the water layer and phosphorus availability in the sediment are abundant. These conditions typically occur upon restoration of eutrophic waterbodies by reducing water nutrient loading or applying biomanipulation. Other factors, as top-down control, can additionally influence realised PVI. Viable propagules of species other than the dominant ones, including charophytes, were found in most of the sediments, indicating that once the dominant species declines, there is local potential for a diverse submerged vegetation to develop. Results can be used to predict when mass development occurs and to tackle the factors causing mass development.

## 1. Introduction

Shallow waters worldwide suffer from high anthropogenic nutrient input leading to loss of submerged macrophytes by dominance of floating macrophytes, algae or cyanobacteria. Submerged macrophytes are key players in these ecosystems, because they provide a positive feedback for a clear water state and enhance biodiversity (Carpenter and Lodge, 1986). A wide variety of restoration measures have been taken to restore water transparency and submerged macrophyte vegetation in eutrophicated lakes, in particular through the reduction of external nutrient input and the removal of zooplanktivorous and

sediment disturbing fish (i.e. biomanipulation) (Gulati and Van Donk, 2002; Jeppesen et al., 2007). After successful restoration of water transparency, a diverse vegetation of submerged macrophytes can reappear (Bakker et al., 2013; Pot and Ter Heerdt, 2014).

The restoration of clear water in eutrophicated lakes may also lead to massive development of submerged macrophytes, which is often characterised by monospecific stands of eutrophic vascular species with a vertical growth strategy and surface canopy formation, leading to a high percentage of volume inhabited (PVI<sup>3</sup>) in the water column (Hilt et al., 2006; Lamers et al., 2012). These massive stands of tall submerged macrophytes can prevent the development of a more diverse

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<sup>2</sup> PVI: The percent of the water volume inhabited by submerged macrophytes.

<sup>3</sup> PVI: The percent of the water volume inhabited by submerged macrophytes.

vegetation by being superior competitors for light and space over slower growing species, especially isoetid and charophyte species. Additionally, mass development of submerged macrophytes can cause problems for human use of lakes, for example for recreation and navigation (Zehndorf et al., 2015). It is, however, unclear whether these large macrophyte stands are always species poor, or whether other species may still be present below the canopy of the dominant species. It is also unclear whether there is local potential for a more diverse and low-growing vegetation to develop in these ecosystems. In particular the development of charophytes is of interest in this respect, because they maintain low canopies that cause less interference with human use of lakes (e.g. Van Nes et al., 2002a). Charophytes are additionally favoured by water managers because they are promoters of good water quality (Bakker et al., 2010; Blindow et al., 2014), they can maintain large and long-lived propagule banks (Bakker et al., 2013), and they are rapid colonizers of new or restored water bodies (Noordhuis et al., 2002; Pot and Ter Heerdt, 2014). Charophyte species can in principle be a dominant component of a stable clear water state in eutrophic shallow lakes (Van Nes et al., 2002b).

The exact size of the macrophyte stand at which it causes problems depends on the specific ecosystem service provided by the lake (Mitchell, 1996). We will therefore not use a single threshold level to describe problematic stands, but will investigate which factors influence submerged macrophyte PVI in general under field conditions. Both light energy (photosynthetically active radiation, PAR) and nutrient availability highly influence the growth and abundance of autotrophs, including submerged macrophytes (Bornette and Puijalon, 2011). Light availability for the plants can be reduced for example by phytoplankton growth in the water column or by periphyton growth on the macrophytes (Hilt et al., 2006; Bornette and Puijalon, 2011; Phillips et al., 2016). Restoration measures are often aimed at improving light availability (Bakker et al., 2013). An often-overlooked component that may determine whether mass development of macrophytes occurs after water clarity has been restored is sediment nutrient availability (e.g. Bachmann et al., 2002; Eigemann et al., 2016). Rooted submerged macrophytes are able to acquire nutrients from the sediment (Carignan and Kalff, 1980; Halbedel, 2016). Generally, high abundance of macrophytes in the water column, expressed as PVI, may thus occur more frequently at high sediment nutrient conditions (Barko et al., 1991; Carr and Chambers, 1998; Fig. 1). Indeed, laboratory growth experiments have shown that submerged macrophyte species grow faster or taller at increasing sediment nutrient concentrations (e.g. Barko and Smart, 1986; Angelstein et al., 2009; Martin and Coetzee, 2014). However, to our knowledge, field evidence is still largely lacking (Bachmann et al., 2002).

In this study, we hypothesised that: (1) high submerged macrophyte

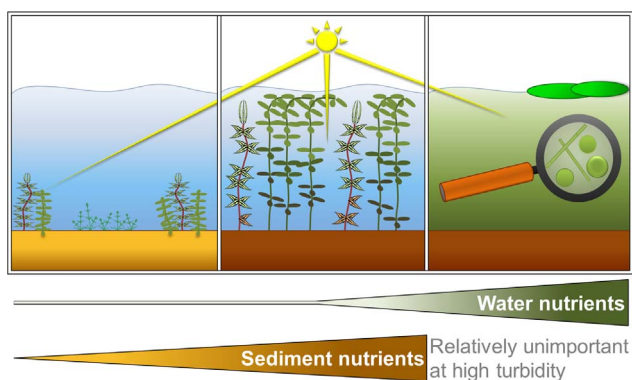


Fig. 1. Theoretical relationship between submerged plant PVI and sediment nutrient levels. At increasing nutrient availability, submerged macrophyte PVI increases, but diversity decreases. At high water turbidity, for example by high water nutrient load, submerged macrophytes are inhibited irrespective of sediment nutrient levels. Figure is adapted from Lamers et al. (2012): Fig. 1.

PVI will occur when sufficient light is available for submerged macrophytes to germinate and grow, and sediment nutrient availability supports high growth rates. (2) Massive stands of submerged macrophytes will consist of a lower number of plant species than stands with lower PVI, but viable propagules of species other than the dominant species will be present in the sediment top layer below massive stands, especially from charophyte species.

To test these hypotheses, we measured vegetation and environmental parameters and sampled the propagule bank in shallow lakes and ponds in the Netherlands, varying in submerged macrophyte abundance, throughout the growing season. We focused on both N and P in the nutrient analyses, because they are both considered to be key nutrients in determining the growth of photoautotrophs in shallow lakes (Moss et al., 2013).

## 2. Methods

### 2.1. Study sites

We selected 15 shallow lakes and ponds throughout the Netherlands that were eutrophicated and have undergone restoration management and/or experienced problems with massive stands of submerged vegetation (see Table 1 & Appendix A Table A1 for restoration methods applied and study site characteristics). Most of the intensive restoration measures have taken place many years ago and will therefore not have influenced the amount of submerged plants present directly, but only indirectly via the abiotic conditions as a result of the management. Most of these abiotic conditions are measured in this study. In several lakes, submerged plants are still harvested locally, but these harvested sites were avoided in our study. The surveyed aquatic ecosystems can be characterized as meso- to eutrophic (based on surface water nutrient concentrations) water with moderate to high surface water alkalinity and pH (lake average alkalinities: 1.4–4.6 meq L<sup>-1</sup> and daytime pH: 8.3–9.6). Total P in the surface water averaged ( $\pm$  SE) 0.13  $\pm$  0.03 mg P L<sup>-1</sup>, whereas total N averaged 0.31  $\pm$  0.03 mg N L<sup>-1</sup> in sites with submerged macrophytes. In sites without submerged macrophytes, total P and N in the surface water averaged 0.09  $\pm$  0.01 and 0.59  $\pm$  0.05 mg L<sup>-1</sup>, respectively.

We selected four sites per ecosystem using the following two criteria: (1) they should be situated in open water, where water depth is between 1 and 1.5 m and (2) their position in the waterbody is most northern (N), eastern (E), southern (S) or western (W), respectively for each site. We avoided areas with apparent direct anthropogenic disturbance including: macrophyte mowing sites, harbours, navigation channels, and areas close to beaches or fishing locations. Sites heavily shaded by large shoreline trees were also avoided.

Because vegetation was expected to vary not only spatially, but also temporally within an ecosystem, sites were visited three times throughout the growing season, using a small flat-bottomed boat. All sites were visited in three rounds: from May 13 until June 26, from July 8 until August 15, and from August 21 to October 4, using a high-sensitivity GPS device to determine each location (eTrex<sup>®</sup> H., Garmin Ltd., Southampton, UK).

### 2.2. Macrophyte survey

At each site we measured water depth and depth of the submerged macrophyte canopy below the water surface (hereafter referred to as ‘canopy depth’), from which submerged macrophyte height was calculated (water depth – canopy depth). We visually estimated total cover (%) and relative abundance per species (%) at four spots around the perimeter of the boat using an aquascope (also known as a bathyscope). This resulted in a survey area of approximately 10–15 m<sup>2</sup> per site. We used submerged macrophyte height and cover, together with water depth, to calculate PVI. To account for possible rare species present underneath the dominant vegetation, we additionally

**Table 1**  
Lake description and recorded management measures.

Waterbody	Coordinates (decimal)	Longest Length (km)	Mean depth (m)	Recorded management measures taken							References management*	
				Reduced external P-loading	Biomanipulation (manipulation fish stock)	Dredging	Sand addition	Introducing macrophytes	Mowing (●) and harvesting	Internal nutrient binding with addition of chemical(s)		Other <sup>#</sup>
Zwemlust	52.194°N : 5.006°E	0.17	1.50									4; 5; 6
Loosdrecht	52.198°N : 5.056°E	4.97	2.20									4; 5; 11
De Waay	51.922°N : 5.995°E	0.48	2.50						●			5; 6; 11
Noorderplassen	52.402°N : 5.226°E	2.69	N/A						●			7
Bleiswijkse Zoom	52.014°N : 4.554°E	1.70	1.10									5; 6
Bergse Achterplas	51.955°N : 4.486°E	0.95	2.00									2
NIOO pond	51.987°N : 5.671°E	0.12	1.00									8
Zevenhuizerplas	51.986°N : 4.574°E	1.98	N/A						●			9
Zuidlaardermeer	53.144°N : 6.698°E	4.04	1.00									6; 11
Nannewijd	52.951°N : 5.864°E	1.72	1.00									3; 6
Sondeler Leien	52.865°N : 5.624°E	1.03	1.00									6
Oldambtmeer	53.198°N : 7.039°E	2.40	1.70									10
Duinigermeer	52.724°N : 6.003°E	0.87	1.00									5; 6
Het Bovenwater	52.496°N : 5.407°E	1.73	1.30									7
Loenderveenseplas Oost	52.219°N : 5.058°E	2.22	2.00									1

\*References: [1] Pot and Ter Heerd (2014); [2] Hoesper et al. (2011); [3] Søndergaard et al. (2007); [4] Dionisio Pires et al. (2004); [5] Gulati and Van Donk (2002); [6] Meijer et al. (1999); [7] Pers. com. Waterboard Zuiderzeeland; [8] Unpubl. data NIOO; [9] Pers. com. Grontmij; [10] Pers. com. Waterboard Hunze en Aa's; [11] Report: Onderzoek meren (Helpdeskwater, NL).

<sup>#</sup>Measures grouped under the 'Other' category were less common and include: herbicide application (Zwemlust in 1968, with no long-term inhibition of plants) and hydraulic isolation of the lake (Loosdrecht Lakes).

used a rake to sample the vegetation (30.4 cm wide rake with: large, 6.6 cm, teeth 2.7 cm apart; and small, 0.6 cm, teeth 0.6 cm apart). The rake was thrown four times, once at each corner of the boat, and was dragged one metre across the sediment. If a species was found using the rake that was not observed by the visual inspection from the boat, the macrophyte was assumed to lie on the bottom (i.e. recorded plant height = 1 cm). All raked macrophytes were collected and abundance per species was estimated as well as total coverage using a conversion table provided by Immers et al. (2015), adapted by our own field observations (see Table A2). If visibility was too low for visual cover estimation, cover was only estimated using the rake (115 cases). In 68% of the 115 cases no submerged macrophytes were found at all. Furthermore, in 96% of the 115 cases with too low visibility the

estimated submerged macrophyte PVI was less than 5%. Therefore possible bias in submerged vegetation measurements due to the different estimation methods is likely very small.

### 2.3. Water and sediment sampling and field measurements

We took four 2 L surface water samples, one from each corner of the plot, and mixed them in a bucket. This mixed sample was used for on the spot turbidity measurements (Turb430IR, WTW GmbH, Weilheim, Germany). Water was filtered using Whatman GF/F glass microfiber filters (GE Healthcare GmbH, Germany) and stored at -20 °C upon arrival at the lab for later inorganic nutrient (N and P) analyses. The filters were dried (60 °C) and stored for suspended solid nutrient

analysis. Light (Photosynthetically Active Radiation: PAR) was measured at regular depth intervals in the ecosystem (LI-250 light meter and underwater quantum sensor, LI-COR inc., Lincoln, NE, USA). The light extinction coefficient of the water was calculated using PAR measurements at 31 and 56 cm depth. The coefficient was not calculated if the aquatic vegetation was too dense, i.e. when vegetation severely shaded the sensor and no open space could be made.

The top 10–15 cm of sediment was collected during the first visit using a core sampler (inner diameter 5 cm). Four cores were taken at each site, one at each corner of the boat, and immediately put into a single airtight bag per site to limit exposure to oxygen. If no sediment sample could be taken during the first round due to equipment failure by hard substrate, the sample was taken during subsequent visits (18/60 cases). On the same day, sediment was homogenized inside the closed bag and porewater was extracted overnight in the dark at 4 °C. To extract porewater, we pierced the bag and inserted a rhizon (Rhizon SMS, RRP B.V., Wageningen, The Netherlands) through the hole. The hole was sealed with tape. Porewater was stored at –20 °C until nutrient analyses. Three subsamples (approx. 45 mL each) of the homogenized sediment were taken from the bag and dried at 60 °C for determination of moisture content and for analyses of total and extractable nutrients.

#### 2.4. Chemical analyses

We measured inorganic nitrogen (NO<sub>2</sub>-N; NO<sub>3</sub>-N; NH<sub>4</sub>-N) and phosphorus (PO<sub>4</sub>-P) concentrations in filtered surface water and sediment porewater colourimetrically with an autoanalyser system (QuAatro SFA, Seal Analytical, Germany). Total carbon and nitrogen of sediment and surface water suspended solids were analysed using a CN analyser (FlashEA 1112 Series, Thermo Scientific, MA, USA). The sediment samples and surface water suspended solids were ashed to determine total P concentration (30 min at 550 °C). We subsequently digested the ashed solids with a 2.5% persulphate solution in an autoclave at 121 °C for 30 min and analysed the solution colourimetrically on the autoanalyser. We calculated total N and P of the surface water by adding the amount of inorganic N or P to the amount of N or P in the suspended solids, respectively.

To estimate the amount of plant available nitrogen in the sediment, a KCl-extraction was performed on the dried sediment as applied by Tang et al. (2017). 12.5 mL 1 M KCl was added to 2.5 g of dried sediment and subsequently shaken for 2.5 h at 250 rpm. Two subsamples (2 mL each) were centrifuged for 10 min at 10,000 rpm and the supernatant was stored at –20 °C for nitrogen analysis on the autoanalyser. We estimated plant available P in the sediment using an adapted P-Olsen protocol, as applied by Tang et al. (2017). 50 mL 0.5 M NaHCO<sub>3</sub> (at pH 8.5) was added to 2.5 g of dried sediment and subsequently shaken for 30 min, after which the solution was immediately filtered (Whatman Grade 42, GE Healthcare Europe GmbH, Eindhoven, the Netherlands). Sulphuric acid (1.04 mL, 2.5 M) was added to 10 mL of the filtrate in an Erlenmeyer flask. The flask was shaken until no more gas development was visible. The filtrate was filtered once more (Whatman Grade 42) and stored at –20 °C until analysis for phosphate on the autoanalyser system. When insufficient sediment material was available for both N and P extractions (n = 13 sites with submerged macrophytes), P-extraction was prioritized and when insufficient sample was present, a corresponding reduction in reagent volume was applied to keep sediment:reagent-ratio equal (n = 2 and 5 sites with submerged macrophytes for N and P, respectively).

We converted sediment nutrient concentration to mmol per litre of sediment ( $\text{mmol L}_{\text{sediment}}^{-1}$ ) by using the sediment moisture content (grams/grams wet weight) and the sediment's specific density (grams wet weight  $\text{L}_{\text{sediment}}^{-1}$ ).

#### 2.5. Germination experiment

To identify viable propagules in the sediment, four samples of the sediment top-layer (approx. 3–5 cm thick) were taken at each field site during the first visit using an Ekman type bottom grab sampler of 15 × 15 cm (1 x w). These four samples were pooled on site and stored in the dark at 4 °C upon arrival at the lab that same day. Samples were kept at 4 °C (cold stratification) for at least 1 week before using them in the germination experiment. We used 1 L of homogenized sediment per site, divided over four containers (1.5 L white PP), each containing 0.25 L of sediment. This created a layer of approximately 1.5 cm, which is thin enough for many submerged species to germinate (Van Zuidam et al., 2014 and literature therein). This sediment was spread on top of a 3 cm thick layer of clean sand (grain size: 0.4–0.8 mm) and the container was filled with 5 cm of tap water. Four aquaria containing only clean sand and tap water were used as negative controls. We gently refilled the water twice a week to compensate for evaporation. Macrophyte germination was followed for at least 2 months in a climate controlled greenhouse between June and August 2013, after which no further germination was observed (air temperature set at 21 °C and 16 °C during the day and night, respectively at natural light). No macrophytes developed in any of the controls.

#### 2.6. Statistical analysis

We performed a logistic regression analysis to test our hypothesis that submerged macrophytes will only be present at a location with adequate light availability ('glm' function in R). For this analysis, we used the average turbidity from all three visits and binary data on whether submerged macrophytes were encountered at any of the sites, during any visit ('1') or not at all ('0'). We used data from the whole ecosystem to test this, as water quality (incl. turbidity) was often highly correlated within an ecosystem. This is likely caused by the relatively small size of the sampled waterbodies (0.1–4.97 km longest length; Table 1).

To test whether the chance of mass development of submerged macrophytes will increase with increasing sediment nutrient availability, we included only waterbodies where more than 1% submerged macrophyte cover was found in at least one of the three visits in the following analyses. We set this limit at 1% because sites with a lower cover often only had loose fragments of submerged plants, making up this 0–1% cover. We therefore believe that this fragment was probably transported into the system via connected ecosystems with more abundant submerged macrophyte vegetation. Another reason for setting the threshold at 1% is that in all of the sites with a year maximum cover of 0–1%, no submerged macrophytes were found at all in at least 1 of the visits. We used the following variables to describe the vegetation: maximum submerged macrophyte cover (%), maximum submerged macrophyte canopy height (%), and maximum PVI (%). The 'maximum' in these parameters refers to the highest value recorded for each individual site over all three visits. Because cover and height were both highly correlated with PVI (Spearman rank correlation:  $\rho = 0.96$  and  $0.70$ , respectively,  $p < 0.001$ ), we only present results on PVI.

To test whether the maximum PVI of submerged macrophytes related positively with the sediment nutrient parameters, we used mixed models with a sediment nutrient parameter as fixed factor and 'Waterbody ID' as random factor. The 'Waterbody ID' factor is a character variable stating the name of the waterbody. For several sediment parameters, 1–3 waterbodies had to be excluded from this analysis due to missing data. We used the 'lme'-function in R for the analyses ('nlme' package version 3.1–118) and p-values were conservatively adjusted to correct for multiple tests by Bonferroni's method.

The restoration potential with regard to local development of diverse submerged vegetation with charophytes was assessed by comparing species richness found in the field with species richness of the plants germinated in the greenhouse from gathered sediment from

the waterbodies, using paired-sample *t*-tests ('t.test' function). There is local potential for creating a more species diverse vegetation with charophytes if the amount of species found in the field is lower than the amount of species germinating from viable propagules in the sediment collected from the same site.

To explore possible correlations between variables, Spearman rank correlations between all measured environmental parameters and maximum PVI can be found in Table A3. We used the 'rcorr' and 'corrplot' R functions from 'Hmisc' version 3.17-0 and 'corrplot' version 0.73 packages, respectively. For these correlations, the critical *p*-value ( $\alpha$ ) was adjusted for multiple comparison with the number of other parameters tested against PVI ( $\alpha = 0.05/29$ ).

All statistical analyses were performed using the R programme (version 3.1.2).

### 3. Results

#### 3.1. Submerged macrophyte PVI and light

The probability that submerged macrophytes were present at a location was inversely related to waterbody turbidity, with almost no submerged macrophyte presence above a turbidity of 14 NTU (Fig. 2). This corresponds to 1–4% light reaching the bottom, calculated from linear regression between the measured light extinction coefficient (LEC) and turbidity (Trb) values ( $LEC = 0.59 \cdot Trb + 0.598$ ;  $R^2 = 0.76$ ;  $p < 0.001$ ,  $n = 132$ ). Below this critical turbidity level the PVI varied extensively, with no significant correlation between turbidity and submerged macrophyte PVI ( $R^2 = 0.06$ ,  $p = 0.11$ ).

#### 3.2. Submerged macrophyte PVI and sediment nutrients

When the light availability did not prevent submerged plants from growing, no significant relation between sediment nutrient concentrations and submerged macrophyte PVI was found using the mixed model analyses (Table 2). However, non-parametric correlation analyses between PVI and environmental variables of sites where submerged macrophytes were found did show a significant positive correlation between plant-available P in the sediment and yearly maximum PVI ( $\rho = 0.53$ ;  $p_{adj.} = 0.045$ ; Fig. 3A), but not for any of the other sediment nutrient parameters (Fig. 3B–F; Table A3). A high submerged macrophyte PVI was possible over a wide range of sediment nutrient levels

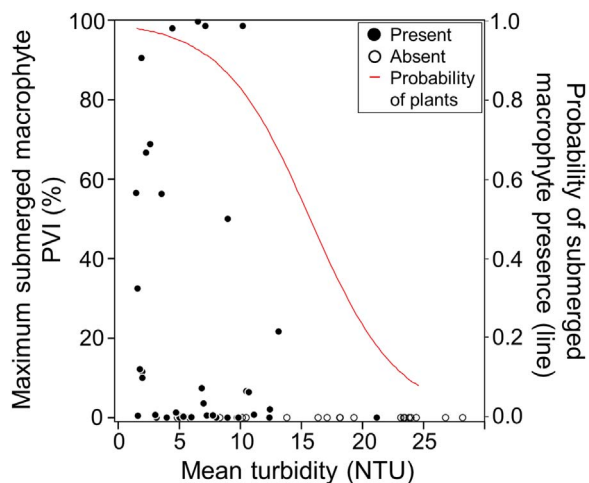


Fig. 2. Maximum PVI of submerged macrophytes per site ( $n = 60$ ) in relation to the average turbidity of the surface water of the entire lake (left y-axis). The maximum of the 3 PVI's measured in one site during 3 visits is taken as 'Maximum PVI'. Site with and without submerged vegetation are represented by closed and open circles represent, respectively. Line: Logistic regression on average turbidity per waterbody in relation to the presence or absence of submerged macrophytes at any of the 4 sampled sites in the waterbody ( $p = 0.04$ ; right y-axis).

(Fig. 3).

#### 3.3. Local restoration potential: species richness and viable propagules

Submerged macrophyte species were found in 11 of the visited ecosystems and species richness in the field was positively correlated with submerged macrophyte PVI ( $R_{adj.}^2 = 0.32$ ,  $p < 0.001$  on log transformed data, Fig. A1). However, this positive correlation is driven by a sharp increase in species richness when PVI increases from  $< 1\%$  to  $5\%$ , whereas at  $> 5\%$  PVI species richness appears unrelated to macrophyte PVI (Fig. A1).

In the 11 ecosystems where submerged macrophytes were encountered in the field, submerged macrophytes also emerged from the incubated sediment (Table 3). Charophyte species emerged from the sediments from 8 of these waterbodies. Significantly more charophyte species emerged from the sediment compared to the number of charophyte species found in the corresponding field site, on average 1.0 and 0.5 species from the sediment and the field, respectively (paired-sample *t*-test on sites with submerged macrophytes:  $t = 2.55$ ;  $df = 39$ ;  $p = 0.015$ ). No submerged macrophytes emerged from the sediments from the 4 waterbodies where no submerged macrophytes were found at any of the four sampled sites in the field (Table 3).

### 4. Discussion

We found that submerged macrophytes almost exclusively occurred (i.e. cover  $> 1\%$ ) at turbidity levels below 14 NTU, confirming the first part of our hypothesis. When turbidity was below 14 NTU, a weak correlation between PVI and plant-available P in the sediment was found (also see Sterner et al., 1997), with high PVI mainly occurring at Olsen P levels above  $0.35 \text{ mmol L}_{\text{sediment}}^{-1}$ . Interestingly, a high PVI was observed over a wide range of sediment nutrient levels. The local propagule bank in sites with submerged vegetation contained additional species to the ones present in the vegetation itself, often including charophyte species. This confirms our hypothesis that most sites had the potential to develop submerged vegetation of higher macrophyte diversity.

#### 4.1. Submerged vegetation, light and nutrients

In our study, submerged macrophytes were almost exclusively present at sites where light (PAR) at the bottom was higher than 1–4% of the irradiance at the water surface. This threshold is also applicable for many other submerged macrophyte species than the ones found in our study (Bornette and Puijalon, 2011). Mixed model analyses of our field data did not support the hypothesis that this variation was primarily caused by sediment nutrient availability. Using Spearman rank correlation, we did demonstrate that the chance of mass development of submerged macrophytes increased with increasing sediment P availability for plants (Fig. 3; Table A3). These conflicting statistical results are partly caused by the limited number of sites sampled within one waterbody on which the mixed model regression is based ( $n = 4$ ). The significant Spearman rank correlation can thus be the result of the higher number of data points available for this test. Whereas controlled experiments do show positive effects of sediment nutrients on submerged plant growth (e.g. Barko and Smart, 1986; Angelstein et al., 2009; Martin and Coetzee, 2014), the relationship between nutrient availability and submerged plant PVI under field conditions is weak (this study; Backmann et al., 2002; Demars and Edwards, 2007), pointing at either nutrients being non-limiting for PVI in our sites or at additional controlling factors.

#### 4.2. Other factors impacting PVI

Here we will discuss these possible reasons for the lack of a strong relationship between PVI and sediment nutrient availability under field

**Table 2**

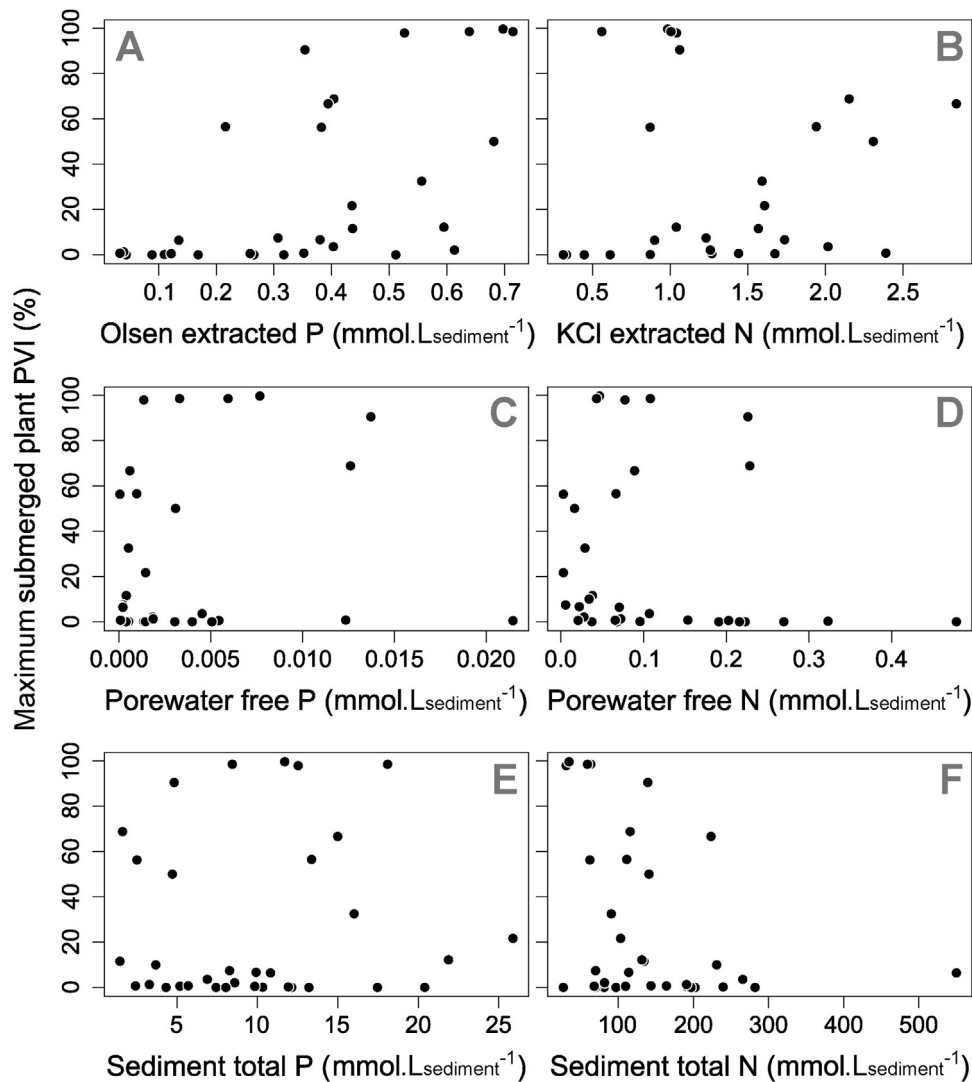
Correlation between environmental nutrient parameters (predictor variables) and maximum submerged plant PVI (dependent variable) with Waterbody ID (i.e. ecosystem name) as random factor. The maximum of the 3 PVI's measured in one site during 3 visits is taken as 'Max submerged plant PVI'. Predictor variables were expressed in mmol L<sup>-1</sup>. P-values were adjusted for multiple tests using the Bonferroni method for multiple comparisons. Unadjusted P-values are also provided.

Dependent variable	Predictor variable	df (num,den)	F	P	P <sub>adjusted</sub>
Max. submerged plant PVI	Olsen Extracted P	1,17	0.43	0.52	1
	KCl Extracted N	1,17	2.16	0.16	1
	Porewater free P	1,23	0.16	0.69	1
	Porewater free N	1,23	5.14	0.03	0.26
	Sediment total P	1,23	1.78	0.20	1
	Sediment total N	1,23	8.34	0.008	0.07
	Mean surface water total P	1,26	0.52	0.48	1
	Mean surface water total N	1,26	1.25	0.27	1

conditions. First, shallow freshwater ecosystems are particularly vulnerable for submerged macrophyte reaching high PVI. Light availability will generally be higher in shallower water due to the limited depth of the water column. This enables submerged macrophytes to germinate and meet their light requirements for growth in shallow waters, even when the actual light attenuation in the water is high (i.e. high turbidity; Søndergaard et al., 2013). Additionally, several fast-growing

species may still grow 1–2 m tall, and thus reach the water surface, even if environmental conditions limit their growth rates (e.g. Rattray et al., 1991). Our data substantiated this, as macrophyte stands with a high PVI occurred over a wide range of sediment nutrient levels.

Second, whereas the probability of the occurrence of high submerged macrophyte PVI may increase with sediment nutrient level, the realised PVI may not reach its full potential due to inhibition by other



**Fig. 3.** The relationship between sediment nutrient parameters and submerged plant volume (PVI) in sites with submerged macrophytes (i.e. > 1% cover). The maximum of the 3 PVI's measured in one site during 3 visits is taken as 'Maximum submerged plant PVI'. For all PVI values, see Table A4.



factors. Abiotic factors, such as carbon limitation (e.g. low CO<sub>2</sub> levels due to higher pH) and high sediment organic matter content, can reduce macrophyte abundance (e.g. Barko and Smart, 1986; Raun et al., 2010). Strong effects of carbon limitation on PVI do not seem likely in our ecosystems, as surface water pH did not significantly correlate with submerged macrophyte PVI during the first two sampling dates (Table A3). During the last sampling date, surface water pH correlated positively with maximum PVI, indicating that the high pH (and potentially low CO<sub>2</sub>) was more likely a consequence of high plant growth than a factor that severely limited macrophyte growth. In addition, most of the dominant species in our ecosystems, for example *E. nuttallii* and *M. spicatum*, are also able to take up and use HCO<sub>3</sub><sup>-</sup> for growth when CO<sub>2</sub> concentrations are low (Eighmy et al., 1991; Hussner and Jahns, 2015). Strong growth limitation by high sediment organic matter content is also not probable in our sites with submerged plants, as organic matter content did not significantly correlate to PVI during our visits and only few sites (8) had more than 20% sediment organic matter (data not shown; Barko and Smart, 1986). However, even when sediment and water properties are optimal for macrophyte growth, the realised macrophyte abundance can still be regulated top-down. Herbivory by invertebrates, fish, or waterfowl can strongly regulate submerged vegetation composition and abundance (Van Donk and Otte, 1996; Gross et al., 2002; Bakker et al., 2016). This has also been observed in one of our sampled ecosystems, Lake Zwemlust, where coots (*Fulica atra*) and rudd (*Scardinius erythrophthalmus*) substantially decreased macrophyte abundance (Van Donk and Otte, 1996). Additionally, periphyton can also regulate submerged macrophyte growth by reducing light availability to the plants (Phillips et al., 2016), which may severely limit plant standing crop, even more so in combination with grazing (Hidding et al., 2016). We therefore propose that these additional top-down factors severely limit submerged macrophyte PVI under field conditions, which can thus obscure bottom-up mechanisms underlying the mass development of submerged macrophytes.

#### 4.3. Development of macrophytes during eutrophication and after restoration of clear water

Here we will discuss when massive stands of submerged macrophytes are likely to develop and we outline these concepts in Fig. 4. The chance of high macrophyte PVI will increase with eutrophication of oligo- to mesotrophic waterbodies (Fig. 4: panel 1–2). Indeed, it has been observed that macrophyte abundance can be enhanced during eutrophication when water is still clear, leading to mass development (e.g. Hasler, 1947), before the system is dominated by floating macrophytes or algae after continued eutrophication (Sand-Jensen and Borum, 1991; Sayer et al., 2010; Fig. 4: panel 2–4).

When lakes are restored by gradually reducing the nutritional status of the water, the potential for high submerged macrophytes PVI will most likely increase when water transparency improves, while the sediment is still high in historically loaded nutrients (Fig. 4: panel 4–2), as high water nutrient levels lead to sediment storage (Tang et al., 2017). One condition first needs to be met, however: viable propagules need to be present for the vegetation to develop at all (this study; Hilt et al., 2006). When propagules are present, the reduction in nutrient loading and the improvement of water transparency in temperate lakes has enabled macrophytes to return (Jeppesen et al., 2005), and has facilitated mass development of macrophytes (Hilt et al., 2006; Zehnsdorf et al., 2015; Fig. 4: panel 4–2a).

A similar effect can be expected after the removal of sediment disturbing or zooplanktivorous fish (i.e. biomanipulation). Below a certain threshold of nutrient concentrations, biomanipulation can instantly improve water transparency (e.g. Meijer et al., 1999; Bernes et al., 2015), while the concentration of nutrients in the ecosystem remains similar (Fig. 4: panel 4–2a). Indeed, many lakes initially show a rapid increase in water transparency after biomanipulation (Bernes et al., 2015), which may well result in mass development of submerged

macrophytes (Strand and Weisner, 2001; Van De Bund and Van Donk, 2002; Pot and Ter Heerdt, 2014).

#### 4.4. Restoring target vegetation

When submerged macrophytes finally reappear after successful restoration of eutrophicated ecosystems, species with a vertical growth strategy (for example several *Potamogeton*, *Myriophyllum*, or *Elodea* spp.) are most likely able to benefit from this ‘new’ situation with clear water and high sediment nutrient availability (Meijer et al., 1991; Hilt et al., 2013). In our study, *E. nuttallii* was often dominant and showed the highest PVI, but seven other species also became dominant in macrophyte stands, including several *Potamogeton* species. All these dominant species are known to possess a vertical growth strategy and can form canopies at the water surface.

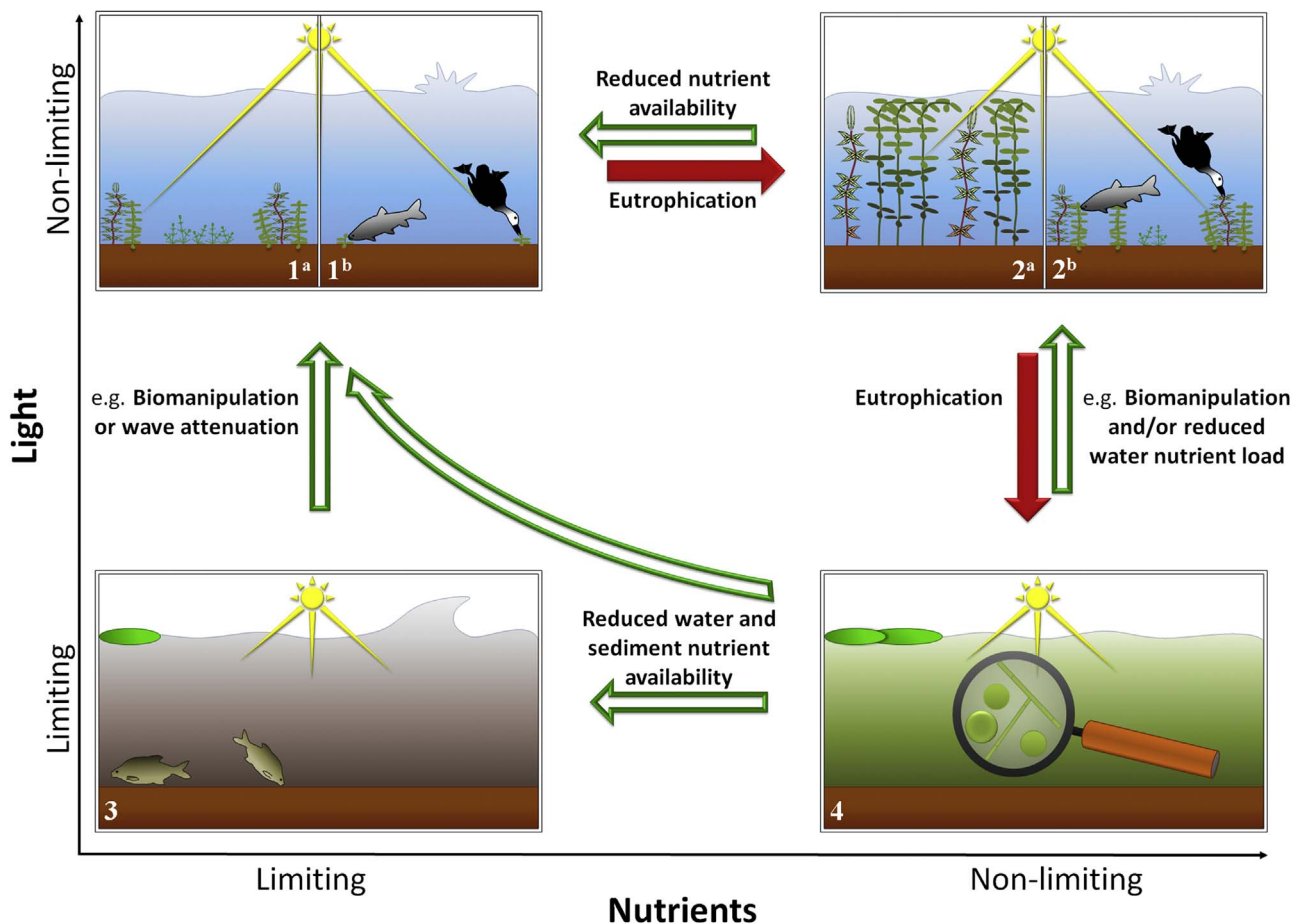
When management efforts further decrease nutrient availability by either physically removing (e.g. dredging) or chemically binding them, other species, in particular charophytes, can potentially outcompete these dominant vascular plants (Hidding et al., 2010; Richter and Gross, 2013), provided that viable propagules are present. In our study, there was a local species pool (including charophytes) from which other species could take over once the dominant species declines in abundance. The period of mass development of tall growing species may thus be a transient phase that can give way to the development of a less dense diverse submerged vegetation including charophytes, as recently observed in one of the water bodies studied here: Loenderveense Plas Oost (Pot and Ter Heerdt, 2014). Such a shift from vegetation dominated by species with a vertical growth strategy to vegetation with shorter species has also been observed in several other lakes during oligotrophication. In Lake Krankesjön in Sweden for example, submerged vegetation redeveloped after a period of high turbidity (Hargeby et al., 1994). *Potamogeton pectinatus* first expanded in Krankesjön, but was largely replaced by *Chara tomentosa* within 6 years, which coincided with a decrease in total P levels in the lake (Hargeby et al., 1994). Similarly, in Lake Veluwemeer in the Netherlands, the P load of the surface water was reduced leading to recovery of submerged macrophytes. In this lake *Potamogeton perfoliatus* expanded first, while a subsequent transition towards charophytes took place (Noordhuis et al., 2002).

Reducing external nutrient input alone, however, does not guarantee a rapid transition towards a diverse vegetation that will not cause nuisance to people, as macrophyte recovery may potentially take decades (Eigemann et al., 2016). Additional reduction of the availability of nutrients stored in the sediment by, for example dredging or chemical P-binding, is likely required and has promoted the development of a more desired vegetation in several ecosystems (Immers et al., 2015; Spears et al., 2016). However, the extent of nutrient reduction required may not be achievable for all ecosystems (Zehnsdorf et al., 2015), as mass development can already occur under low nutrient concentrations and even charophytes can occasionally grow to problematic proportions (personal observation on *Nitellopsis obtusa* in lake Duinigermeer; Sidorkewicz et al., 1998; Schneider et al., 2013). When substantial nutrient reduction is not feasible, or when macrophyte species remain to cause nuisance after nutrient reduction, other management techniques can be applied to reduce nuisance locally. For example, mowing and removing macrophyte biomass (i.e. mimicking high grazing pressure) could directly reduce localized nuisance problems and simultaneously remove nutrients from the system, which can then be reused as fertilizer for example (e.g. Quilliam et al., 2015; Kuiper et al., 2017).

#### 4.5. Conclusions

Light availability and propagule presence determine if submerged macrophytes are encountered or not. Under adequate light levels, sediment nutrient availability was not the major driver in determining





**Fig. 4.** Graphical representation of factors impacting macrophyte PVI. Main abiotic factors are different nutrient levels (x-axis) and light availability (y-axis), which can be limiting or non-limiting for submerged macrophyte growth. Standing submerged macrophyte PVI is further impacted by top-down pressures, e.g. herbivores (represented as fish or waterfowl), but also shading by periphyton. Red (filled) arrows indicate eutrophication first leading to increased submerged macrophytes production, but eventually leading to disappearance of submerged macrophytes. Green (open) arrows indicate restoration measures to regain submerged macrophytes either through reducing nutrient availability or additional measures such as biomanipulation. Panel 1: Low growing diverse vegetation (1<sup>a</sup>) or almost no submerged vegetation due to high top-down pressures (1<sup>b</sup>). Panel 2: Massive development of tall growing submerged macrophytes (2<sup>a</sup>) or less vegetation and no mass development due to high top-down pressures (2<sup>b</sup>). Panel 3: No submerged plants due to low light, mainly caused by suspended particles other than algae (e.g. suspended sediment). Panel 4: No submerged plants due to low light, mainly caused by algae, cyanobacteria and possibly also by floating plants. Part of the information presented in this figure is based on literature instead of our own data, including the effects of herbivory, wave-action and extreme nutrient limitation. See discussion for more details. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rooted submerged macrophytes PVI. We found that high submerged macrophyte PVI was possible over a large range of sediment nutrient levels. The presence of viable propagules, including charophytes, in most of our ecosystem's sediments indicates that once the dominant species diminish, either as a result of oligotrophication over time or after active management, there is local potential for a more diverse submerged vegetation to develop. We propose that the enhanced risk of mass development of submerged macrophytes may be a typical phase when restoring eutrophic shallow ecosystems to a more oligotrophic state. During this transition, water becomes clear, but the sediment still holds ample nutrients. This increases the risk of mass development of submerged macrophytes, but whether mass development is realised depends on other limiting factors, in particular top-down control by herbivores, which can be mimicked by active mowing and removal of aquatic macrophytes.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.aquabot.2017.04.004>.

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