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PRIMARY RESEARCH PAPER

Growth forms and life-history strategies predict the occurrence of aquatic macrophytes in relation to environmental factors in a shallow peat lake complex

Ralph J. M. Temmink · Martijn Dorenbosch · Leon P. M. Lamers · Alfons J. P. Smolders · Winnie Rip · Wouter Lengkeek · Karin Didderen · Gregory S. Fivash · Tjeerd J. Bouma · Tjisse van der Heide

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Abstract Aquatic ecosystems provide vital services, and macrophytes play a critical role in their functioning. Conceptual models indicate that in shallow lakes, plants with different growth strategies are expected to inhabit contrasting habitats. For shallow peat lakes, characterized by incohesive sediments, roles of growth forms, life-history strategies and environmental factors in determining the occurrence of aquatic vegetation remain unknown. In a field survey, we sampled 64 points in a peat lake complex and related macrophyte occurrence to growth forms (floating-leaved rooted and submerged), life-history strategies for overwintering (turions, seeds, rhizomes) and environmental factors (water depth, fetch, and pore-water nutrients). Our survey showed that macrophyte occurrence relates to water depth, wind-fetch, and nutrients, and depends on growth form and life-history strategies. Specifically, rooted floating-leaved macrophytes occur at lower wind-fetch/shallower waters. Submerged macrophytes occur from low to greater wind-fetch/water depth, depending on life-history strategies; macrophytes with rhizomes occur at greater wind-fetch/depth relative to species that overwinter with seeds or turions. We conclude that growth form and life-history strategies for overwintering predict macrophytes occurrence regarding environmental

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R. J. M. Temmink (✉) · L. P. M. Lamers ·
A. J. P. Smolders · W. Lengkeek · T. van der Heide
Aquatic Ecology and Environmental Biology, Institute for Water and Wetland Research, Radboud University,
Heyendaalseweg 135, 6525 AJ Nijmegen, the Netherlands
e-mail: R.temmink@science.ru.nl

R. J. M. Temmink · T. van der Heide
Department Coastal Systems, Royal Netherlands Institute of Sea Research and Utrecht University,
1790 AB Den Burg, the Netherlands

M. Dorenbosch · W. Lengkeek · K. Didderen
Bureau Waardenburg, Varkensmarkt 9,
4101 CK Culemborg, The Netherlands

M. Dorenbosch
RAVON Nijmegen, Toernooiveld 1, 6525 ED Nijmegen,
The Netherlands

L. P. M. Lamers · A. J. P. Smolders
B-WARE Research Centre, Toernooiveld 1,
6525 ED Nijmegen, The Netherlands

W. Rip
Waternet, Amsterdam, Korte Ouderkerkerdijk 7,
1096 AC Amsterdam, The Netherlands

G. S. Fivash · T. J. Bouma
Department of Estuarine and Delta Systems, Royal Netherlands Institute of Sea Research and Utrecht University, 4401 NT Yerseke, The Netherlands

factors in peat lakes. Therefore, we propose an adapted model for macrophyte occurrence for such lakes. Altogether, these results may aid in species-selection to revegetate peat lakes depending on its environment.

Keywords Floating-leaved rooted macrophytes · Submerged macrophytes · Vegetation · Nutrients · Fetch · Water depth

Introduction

Aquatic ecosystems provide a large range of ecological and economic services, including freshwater supply, fisheries, habitats and food for organisms driving biodiversity (Hammer & Bastian, 1989; Jackson et al., 2001; Borst et al., 2018). The occurrence and abundance of aquatic macrophytes, determined by abiotic and biotic drivers, strongly influence these services (Bornette & Puijalon, 2011; Bakker et al., 2013). Abiotic conditions that determine macrophyte occurrence and abundance include water transparency (i.e., light availability), carbon, nitrogen and phosphorus availability in surface water and sediment, water movement and soil phytotoxicity (Søndergaard et al., 2003; Lamers et al., 2013; Verhofstad et al., 2017). Biotic drivers of plant occurrence, abundance and growth include herbivory and bioturbation by water birds, large fish and crayfish (Gulati & van Donk, 2002; Bakker et al., 2013; Bakker et al., 2016).

Aquatic macrophytes occur in a range of freshwater lakes that differ considerably in depth and surface area (Lehner & Döll, 2004; Murphy et al., 2019). In shallow lakes, typically less than 3 m deep, the effect of sediment-water interactions is relatively large (Scheffer, 1997; Bakker et al., 2013). In addition, submerged macrophytes can fill up the entire water column. As a consequence, they increase their competitive advantage over algae by lowering nutrient levels and providing shelter for algae-grazing zooplankton and piscivorous fish feeding on bioturbating and zooplankton- eating fish (Scheffer et al., 2001; Scheffer et al., 2003; Smolders et al., 2006).

Within these shallow lake systems, shallow peat lakes form a specific type. They can be natural or human-made, created by the extraction of peat in combination with erosion of surrounding peatlands (Gulati & van Donk, 2002; Immers et al., 2015). The bottom of these lakes is characterized by very soft, organic sediment that forms a non-cohesive sludge layer (Schutten et al., 2005). Peat lakes therefore have different environmental dynamics compared to for instance sandy-sediment lakes (Bengtsson & Hellström, 1992; Schutten et al., 2005). Because of their soft sediments, peat lakes are much more prone to wind-induced sediment resuspension that negatively affects water clarity (Bengtsson & Hellström, 1992). Furthermore, the non-cohesive structure of the sediment may easily lead to macrophyte uprooting (Schutten et al., 2005). These factors may negatively influence macrophytes occurrence. Bornette & Puijalon (2009) proposed a broadly applicable conceptual model in which they show the expected distribution of five major growth forms along several gradients of several abiotic factors (water transparency, seasonal temperature fluctuations, oxygen availability, substrate grain-size, nutrient level and water movement). For instance, they expected the occurrence of small caulescents (e.g., *Elodea* sp., *Ceratophyllum demersum* L.) at locations with higher water movement, while tall caulescents (e.g., *Potamogeton lucens* L.) and rooted floating-leaved macrophytes (*Nymphaea* sp.) are expected at conditions with lower water movement. They further expected the opposite relationship for nutrient levels for these species. Although they created this model to gain insight into the expected distribution of major macrophyte growth forms in shallow waters, the model was not specifically devised for shallow lakes with thick and non-cohesive sediments, such as peat lakes. Therefore, it remains unknown whether the conceptualized relationships for different macrophyte growth forms holds true for peat lakes.

T. J. Bouma
Delta Academy Applied Research Centre, HZ University of Applied Sciences, Postbus 364, 4380 AJ Vlissingen, The Netherlands

T. J. Bouma · T. van der Heide
Faculty of Geosciences, Department of Physical Geography, Utrecht University, 3508 TC Utrecht, the Netherlands

T. J. Bouma
Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, 9700 CC Groningen, the Netherlands

In shallow peat lakes, we observed large-scale uprooting of aquatic macrophytes after several storms from late summer until winter. This indicates that local survival of aquatic macrophytes can be challenging, probably due to the combination of incohesive sediment and storms (Schutten et al., 2005; Łoboda et al., 2018). Therefore, we hypothesize that the occurrence of macrophytes is not only dependent on growth form and abiotic conditions (Bornette & Puijalon, 2009), but that life-history strategies for overwintering (via seeds, turions or rhizomes) of aquatic macrophytes play an important role in determining their occurrence in peat lakes with unstable sediments. Next to our observation of uprooting, Schutten et al. (2005) showed that peat lakes have a low sediment cohesion relative to lakes with a sand soil. Moreover, they found that plants uproot more easily in sediments with a low sediment cohesion. While some species invest a large part of their energy in subsurface overwintering parts such as rhizomes that also increase anchoring strength, others occur as annuals and produce aboveground reproductive parts such as seeds or turions (Wiegleb et al., 1991; Song et al., 2017). The effectiveness of these life-history strategies depends on environmental conditions, successional stage and hydroperiod. For instance, heavy seeds require firm sediment for germination, because these will sink to depths where they are unable to germinate in non-cohesive sediments (Barrat-Segretain, 1996). Yet, to our knowledge, there are no studies that address the occurrence of aquatic macrophytes in shallow peat lakes and link that to growth form, life-history traits for overwintering and environmental conditions.

In this study, to fill these knowledge gaps for shallow peat lakes, we relate the occurrence of rooted floating-leaved, and submerged vegetation to environmental factors, growth forms and life-history strategies for overwintering. We performed a field survey to relate macrophyte growth form and life-history strategies for overwintering (via seeds, turions or rhizomes) to environmental variables such as fetch, water depth (proxy for light availability) and nutrient availability in a peat lake complex (Stichts Ankeveense Plassen) in the Netherlands. We chose to study these traits, as plants can easily uproot in the incohesive sediments in shallow peat lakes (Schutten et al., 2005) during storms that most frequently occur from late summer to early spring in the Netherlands (The Royal Netherlands Meteorological Institute, KNMI). We hypothesized that submerged and rooted floating-leaved macrophyte occurrence under certain environmental conditions (e.g., water depth and fetch) is driven by their growth forms combined with their life-history strategies for overwintering.

Materials and methods

Study site

Stichts Ankeveense Plassen (SAP) is a complex of connected shallow peat lakes situated in an extensive peat region in the provinces of Holland and Utrecht in the Netherlands (52°16′15.78″N, 5° 4′49.15″E, Fig. 1). The area was exploited for its peat in the 1800s, which created a characteristic landscape of peat ponds (‘petgaten’ in Dutch; pits from which peat was extracted by dredging) and ‘baulks’ (land to dry dredged peat) (Zeeuw, 1978). Over a century, wave-induced erosion and enhanced organic matter degradation due to external eutrophication led to the formation of a complex of connected lakes of $>$ 80 ha with lakebeds of thick layer of organic, non-cohesive sludge (1.26 [1.3] $\pm$ 0.5 m, average [median] $\pm$ SD, lake open water in the survey $\sim$60 ha, Fig. 1b). Over the last 30 years, water quality and related clarity have improved by mitigation measures in a number of lakes in the Netherlands including SAP, and have become sufficient to support the growth of submerged macrophytes (Dorenbosch et al., 2017; Fraters et al., 2017). Specifically, the relatively stable and average light extinction from 2012 to 2016 was 1.9 m (min: 1.3, max: 2.7, n = 58; data from Dorenbosch et al., 2017). Furthermore, the availability of both carbon dioxide (CO_2) (40 μmol L^{-1}) and bicarbonate (HCO_3^-) (1 mmol L^{-1}) in the water layer is relatively low at our study site (Dorenbosch et al., 2017). As there is low recreation pressure in SAP, physical disturbances caused by recreation, mowing of the vegetation and sediment resuspension by boat propellers are negligible, unlike in many other peat lakes.

Survey

To study the occurrence of rooted floating-leaved and submerged vegetation in SAP, we generated 64 random points – sampling stations – inside our study area using QGIS that were sampled in July 2018

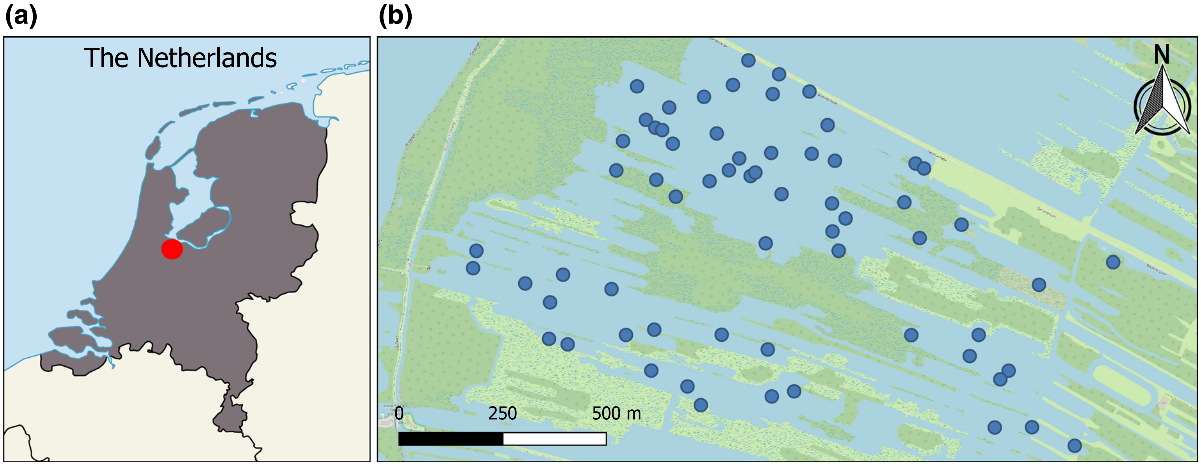


Fig. 1 Study site and experimental setup. (**a**) The Netherlands with the shallow peat lake complex Stichts Ankeveense Plassen (SAP) indicated by the red circle. (**b**) Detail of the study site. Blue circles indicate sampling stations in our field survey. Map data made with Natural Earth (**a**) and OpenStreetMap contributors, CC BY-SA (**b**)

(Fig. 1b). At each sampling station we visually, either by aquascope or eye, determined the total cover of rooted floating-leaved and submerged vegetation (%) and relative abundance per species (%) for a given sampling area of approximately 4 m^2. To account for possible species present underneath the highly dominant vegetation, we additionally used a rake connected to a rope to sample the vegetation (34.5 cm wide rake with 6.5 cm long teeth spaced 2.5 cm apart). We threw the rake four times, once at each corner of the boat, and dragged it one meter across the sediment. If visibility was too low for visual cover estimation, we estimated the cover using the rake (Verhofstad et al., 2017).

Next, we measured water and sludge depth using a stainless steel grid attached to a marked pole (sediment level stave, Eijkelkamp, Giesbeek, the Netherlands). First, the grid rests on the sludge to measure the water level, then the grid is pushed until the hard mineral/peat subsoil, thus measuring the sludge depth. After this, we took a 30 cm deep sediment core of undisturbed and unvegetated sediment using a piston sampler (100 cm long; 4 cm in diameter, Eijkelkamp, Giesbeek, the Netherlands). Sediment concentrations of sulfide were low everywhere, based on the absence of its odor in the sediment (i.e., below 0.3-4 μmol l^{-1}; (National Research Council Committee, 2010). Finally, we stored each sample in an airtight plastic bag, and transported it to the lab, where it was stored at 4 °C overnight.

We grouped all aquatic macrophyte species based on growth form: 1) rooted floating-leaved, and 2) submerged macrophytes (we observed no free-floating and emergent macrophytes in our survey), and life-history strategies related to overwintering 1) turions/winter buds, 2) rhizome or 3) seeds (Table 1). We chose to correlate occurrence to overwintering strategies, because plants are prone to uprooting in unstable sediments during storm events (Schutten et al., 2005), which depends, on among others, on their overwintering root systems. Moreover, plants have different life-history strategies to cope with the cold conditions in winter (daily average temperature in winter 5.2 °C [minimum -8.5 °C] and summer: 18.9 °C 2018 [maximum 37.5 °C]; KNMI weather station de Bilt, the Netherlands). Obviously, many plants produce seeds for reproduction; however, in our study lake in the Netherlands, plants that overwinter follow mainly the depicted classification (Table 1).

Chemical analyses

Sediments were carefully mixed in closed bags, after which porewater was extracted in the dark by inserting a rhizon sampler (Rhizon SMS, Rhizosphere Research Products B.V., Wageningen, the Netherlands) through the plastic, attached to a vacuumed syringe. We focused on the major nutrients for plant growth, namely, nitrogen, phosphorus and potassium. A 10-mL subsample of each sample was conserved by

Table 1 Groups of aquatic macrophyte species, growth form and life-history strategies for each found species including numbers of observations

Submerged			Floating-leaved
Free-floating	Rooted		
Turions/winter buds	Seeds	Rhizome	
Elodea nuttallii (n=1)*	*Najas marina* (n=12)	*Myriophyllum spicatum* (n=1)	*Nymphaea alba* (n=18)
Ceratophyllum demersum (n=9)		*Potamogeton lucens* (n=23)	*Nuphar lutea* (n=8)
		P. crispus L. (n=1)	
		P. perfoliatus L. (n=3)	

*is not free-floating

adding 0.1 mL of nitric acid (HNO_3) (65%) and stored at 4 °C until P-analysis by inductively coupled plasma emission spectrophotometry (ICP-OES iCAP 6000; Thermo Fisher Scientific, Waltham, MA, USA). The rest of each sample was stored in polyethylene bottles at −20 °C prior to further analysis. Ammonium (NH_4^+) was measured colorimetrically with an auto analyzer (Auto Analyzer III, Bran and Luebbe GmbH, Norderstedt, Germany). Potassium (K^+) was determined by flame photometry (FLM3Flame Photometer, Radiometer, Copenhagen, Denmark). Within one day after sampling, pH and alkalinity of the porewater were determined using an Ag/AgCl electrode (Orion Research, Beverly, MA, USA) and a TIM 840 Titration Manager (Radiometer Analytical SAS, Villeurbanne, France). Total inorganic carbon (TIC - HCO_3^- and CO_2) was measured using an infrared carbon analyser (IRGA; ABB Analytical, Frankfurt, Germany), followed by pH-based calculation of CO_2 and HCO_3 – concentrations (van Bergen et al., 2020). Finally, at each sampling station, we determined the fetch as the maximum distance from the sampling station toward the land in north, north-east, east, south-east, south, south-west, west and north-west direction with Google Earth Pro.

Statistical analyses

For the survey data, we used ANOVAs to test for differences between groups and environmental parameters. Macrophytes were categorized in groups based on growth form (rooted floating-leaved and submerged) and life-history trait-categories. This resulted in four groups, namely, (1) rooted floating-leaved (seed/rhizome), (2) submerged & seed, (3) submerged & turion and (4) submerged & rhizome. For, the rooted floating-leaved group, we did not distinguish between seed and rhizome, as the two species that we found are both able to overwinter with seeds and rhizomes. Specifically, we tested whether differences occurred between these groups for water depth (3rd root transformed), southwestern fetch (square root transformed, prevailing wind direction in the Netherlands, Supplementary Fig. S1), porewater P (square root transformed), K and NH_4^+ concentrations (square root transformed). If necessary, variables were transformed to achieve a normal distribution of the residuals. Differences between groups were determined using Tukey post hoc tests. To prevent a large influence of a few individuals, sampling stations with a cover >5% were only used for the analyses. Relationships between environmental parameters were explored using regression analyses between sludge depth and NH_4^+, P, HCO_3^- or alkalinity, and the southwestern fetch and sludge depth. All analyses were performed in R (version 3.6) statistical and programming environment (R Core Team, 2020). All results are shown with average, median and standard deviation (±SD). The significance level was assumed at $p < 0.05$.

Results

In our shallow peat lake complex, thickness of the sludge layer was negatively related to the southwestern fetch ($R^2 = 0.3$, $p < 0.001$), while sediment and porewater nutrient concentrations in turn were positively related to sludge thickness (R^2 = 0.3, 0,3, 0,5 and 0.6 for porewater NH_4^+, P, HCO_3^- and alkalinity, respectively, $p < 0.001$ for all, Fig. 2). The spatial

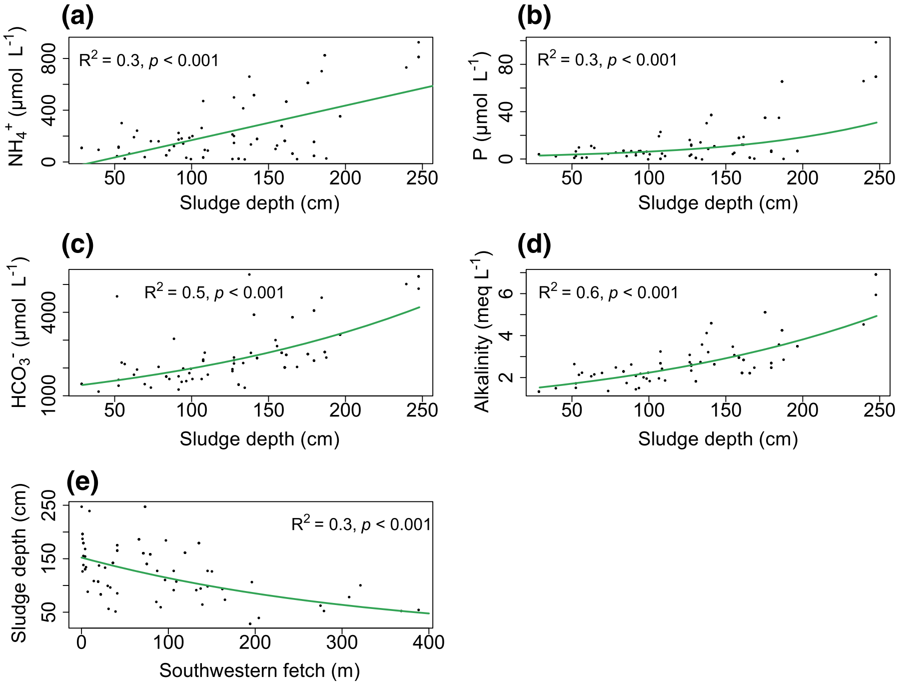


Fig. 2 Abiotic relationships. Relationships between porewater ammonium (μmol L^{-1}, a), phosphorus (μmol L^{-1}, b) bicarbonate (μmol L^{-1}, c) and alkalinity (meq L^{-1}, d) and sludge depth (cm). (**e**) shows the relationship between sludge depth and the southwestern fetch (m). Regression line is depicted in green. Black dots show individual data points

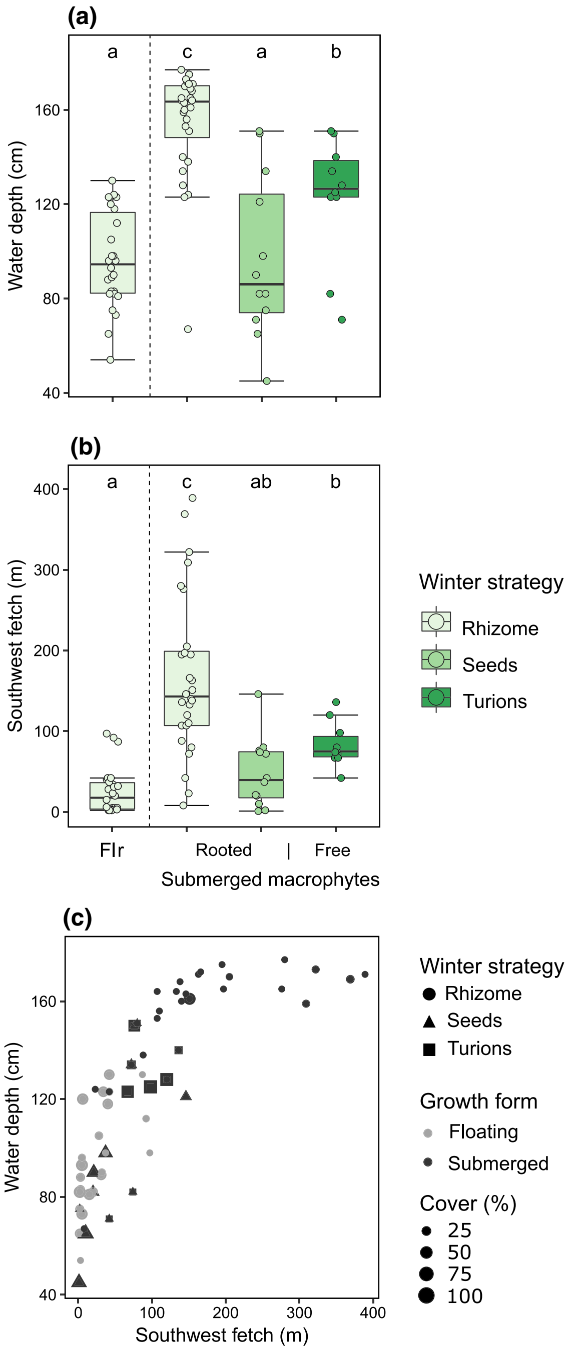
distribution of aquatic macrophytes was found to strongly depend on macrophyte growth form and life-history traits in relation to water depth, fetch and porewater nutrients concentrations (Fig. 3, 4).

In the shallow zone of the lake (40 – 100 cm) with a corresponding low SW fetch (<100 m, Fig. 3), we found the rooted floating-leaved macrophytes *Nuphar lutea* (L.) Sm. and *Nymphaea alba* L. (rhizome/seed) and the submerged macrophyte *Najas marina* L. (seed). At an intermediate depth (100 to 140 cm) with a corresponding SW fetch of 180 m (Fig. 3), we found the rooted floating-leaved macrophytes *N. lutea* and *N. alba*, as well as various species of submerged macrophytes, including *N. marina* (seed), *C. demersum* (free-floating) and *Elodea nuttallii* (Planch.) St. John (turions), *Myriophyllum spicatum* L. (rhizome) and *P. lucens* (rhizome). At the deepest zone of the lake, from 140 to 180 cm depth with a corresponding SW fetch of at maximum 400 m, only submerged macrophytes with rhizomes occurred (*P. lucens,* Fig. 3).

Specifically, we found the rooted floating-leaved vegetation to occur at water depths from 54 to 130 cm (97 [95] ± 21 cm; average [median] ± SD) and submerged vegetation from 45 to 177 cm (average 135 [145] ± 36 cm). Within the submerged vegetation group, macrophytes having rhizomes or turions occurred at depths greater than 120 cm (average 155 [164] ± 24 and 123 [127] ± 27 cm, for macrophytes with rhizomes or turions respectively), while macrophytes that overwinter with seeds showed a great variation in water depth from 45 to 177 cm (average 97 [86] ± 34 cm, $F_{3,72} = 27.26$, $p < 0.001$). The recorded water depth was strongly related to the southwestern (SW) fetch – the predominant wind direction in the Netherlands ($R^2 = 0.7$, $p < 0.001$, Fig. 3c).

Rooted floating-leaved vegetation occurred when SW fetch was less than 100 m (average 26 [18] ± 28 m). In contrast, SW fetch did not affect the occurrence of submerged macrophytes that have rhizomes, as indicated by the large range from 8 to 389 m (average 167 [143] ± 99 m, $F_{3,72} = 28.65$, $p < 0.001$). However, SW fetch strongly affected the occurrence of submerged macrophytes that overwinter via seeds or turions (average 48 [40] ± 43 and 83 [75] ± 28 m for seeds or turions, respectively).

Rooted floating-leaved vegetation occurred at sediment porewater concentrations lower than 12 μmol P L^{-1} (average 4 [3] ± 4 μmol L^{-1}, $F_{3,72} = 25.73$, $p < 0.001$) and 250 μmol L^{-1} for NH_4^+ (average 87 [50] ± 98 μmol L^{-1}, $F_{3,72} = 26.45$, $p < 0.001$) (Fig. 4). Similarly, submerged macrophytes that overwinter



◀**Fig. 3** Environmental conditions related to growth form and winter strategy. Differences between macrophyte characteristics (growth form: Flr [rooted floating-leaved] and submerged [rooted and free-floating; free], and winter strategy: rhizome, seed or turion) and (**a**) water depth (cm), (**b**) southwestern fetch (m), (**c**) the relationship between water depth and south-west fetch. Color: macrophyte form. Symbol: winter strategy. Size of a symbol: vegetation cover (%). Boxplots show the median (middle line), quartiles (boxes), 1.5 times the interquartile range (IQR) (whiskers), and the individual data values (dots). Dots outside the whiskers are extreme values. Different letters indicate significant differences (Tukey post hoc tests, $p < 0.05$). N = 26, 33, 17, and 15 for floating rhizome, submerged rhizome, submerged seed and submerged turions, respectively

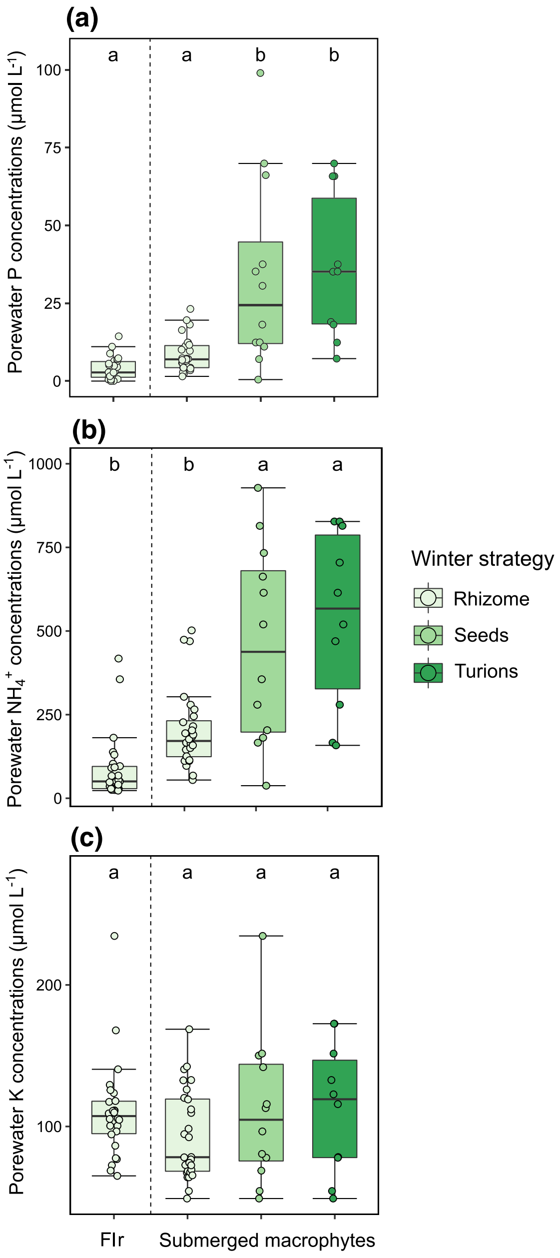
with rhizomes, occurred at low porewater P and NH_4^+ concentrations (average 9 [7] ± 5 µmol P L^{-1}, average 202 [171] ± 115 µmol NH_4^+ L^{-1}). In contrast, submerged macrophytes that overwinter with seeds or turions occurred at higher P (average 33 [24] ± 30 and 37 [35]± 23 µmol P L^{-1}, respectively) and NH_4^+ concentrations (average 458 [438] ± 292 and 538 [567] ± 265 µmol NH_4^+ L^{-1}, respectively). Porewater K concentrations were equal for all groups with average concentrations around 100 µmol K L^{-1} (Fig. 4c, $F_{3,72} = 1.7$, $p = 0.2$).

Discussion

We studied the occurrence of rooted floating-leaved and submerged macrophytes in a shallow peat lake complex characterized by a thick and incohesive sludge substrate. We related their occurrence to growth form and life-history strategies for wintering to gain insight into the functioning of this human-made system. Our survey demonstrates that fetch and water depth differentially affect the occurrence of macrophytes, depending on their growth forms and life-history strategies (Fig. 5). Specifically, tall caulescents (e.g., *P. lucens*) occurred at more exposed locations relative to small caulescents in peat lakes (e.g., *C. demersum*), in contrast to the general model devised by Bornette & Puijalon (2009). Therefore, we propose an adapted predictive model for the occurrence of macrophytes in shallow peat lakes as outlined below. Altogether, these results may aid in species-selection to revegetate shallow peat lakes depending on the environmental context (e.g., exposed versus sheltered; deep versus shallow).

Occurrence of aquatic macrophytes

The occurrence of *N. marina* in the shallowest and lowest-fetch zone of the lake (40-100 cm depth, fetch < 100 m) indicates that light conditions are sufficient to allow submerged macrophyte growth from seeds



◀**Fig. 4** Porewater nutrients related to growth form and life-history strategies. Differences between macrophyte characteristics (growth form: Flr [rooted floating-leaved] and submerged [rooted and free-floating; free], and winter strategy: rhizome, seed or turion) and (**a**) porewater P concentrations (μmol L^{-1}), (**b**) porewater NH$_4^+$ concentrations (μmol L^{-1}), and (**c**) porewater K concentrations (μmol L^{-1}). Boxplots show the median (middle line), quartiles (boxes), 1.5 times the interquartile range (IQR) (whiskers), and the individual data values (dots). Dots outside the whiskers are extreme values. Different letters indicate significant differences (Tukey post hoc tests, $p < 0.05$). N = 26, 33, 17, and 15 for floating rhizome, submerged rhizome, submerged seed and submerged turions, respectively

(Chambers & Kalff, 1987). This is also supported by the 5-year average light extinction (1.9 m) data at this site (Dorenbosch et al., 2017). Interestingly, *N. marina* reached its highest cover at most-sheltered locations where fine particulate matter settles and a thick sludge layer accumulated, but where rooted floating-leaved macrophytes were absent (Supplementary Fig. S2, 3). *N. marina* is known to colonize such areas, because seedling establishment is successful on soft sediments and unsuccessful on firm sediments (Forsberg, 1965; van Vierssen, 1982, Handley & Davy, 2002). However, rooted floating-leaved rooted are not well adapted to very soft sediments, as their heavy seeds can sink to a depth that inhibits germination (Barrat-Segretain, 1996). Furthermore, our data show that rooted floating-leaved macrophytes occur at a water depth up to 120 cm depth and a southwestern fetch of 100 m (Fig. 3a-b, Supplementary Fig. S2), while submerged macrophytes do not occur as frequently in this zone (see e.g., submerged macrophytes with turions/rhizomes in Fig. 3a). As submerged macrophytes occur in the shallowest (seeds) and deeper parts of the lake (seed, turion, rhizomes), but not in the zone dominated by floating-rooted macrophytes, their occurrence may be driven by competition between rooted floating-leaved plants and submerged-growing plants. A possible explanation might be that rooted floating-leaved macrophytes reduce light availability for submerged vegetation. Indeed, *Nuphar* is known to grow dense and strongly block light (Nurminen & Horppila, 2006; Wahl, 2008; Schoelynck et al., 2014), making them superior competitors for light that outcompete submerged-growing plants (Scheffer et al., 2003; Netten et al., 2010; Seto et al., 2013; Strange et al., 2018). Furthermore, perennial aquatic species (e.g., *N. lutea*, *N. alba, Potamogeton* sp.) are known to typically take over communities mainly consisting of seed or vegetatively-dispersed macrophytes during succession (e.g., *C. demersum* or *N. marina*) (Bornette & Puijalon, 2011).

We found that in the deepest zone of the lake with largest fetch, submerged macrophytes with an extensive rhizomal network still occurred (e.g., *P. lucens*), while less strongly rooted or submerged free-floating plants were consistently absent (e.g., *C. demersum,* Fig. 3). The lack of submerged macrophytes other

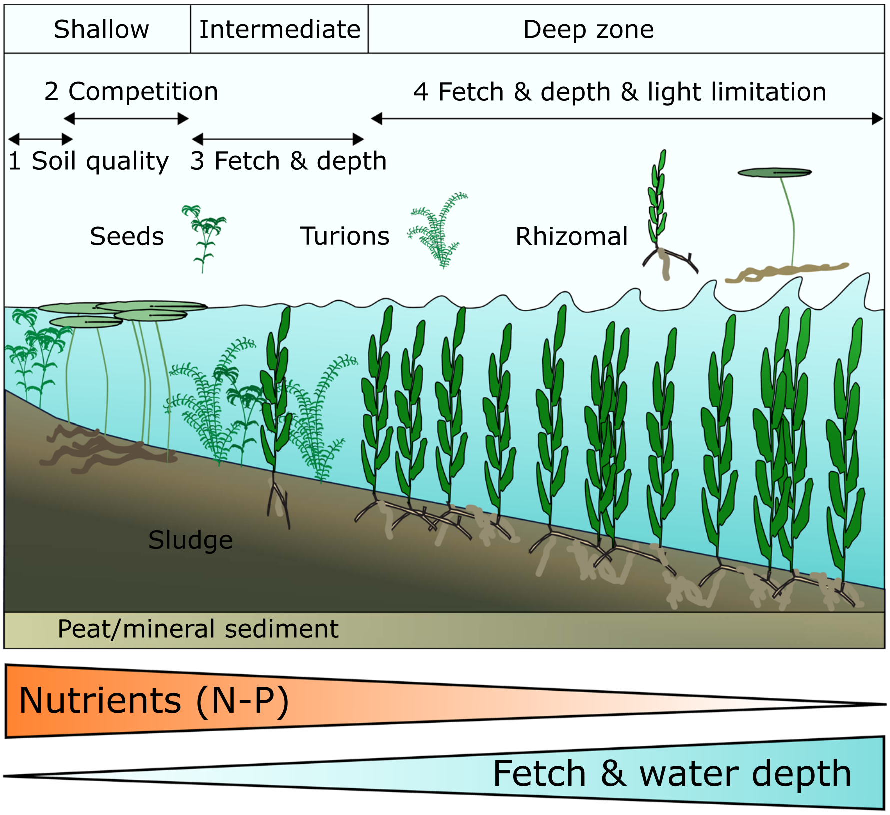


Fig. 5 Graphical summary of the macrophyte zonation in our peat lake-system and its possible driving mechanisms. In the shallow zone, the distribution of floating and submerged vegetation may be driven by (1) sediment cohesion and seed weight, as rooted floating-leaved macrophytes may be unable to germinate in non-cohesive sediment, because their heavy seeds sink into it (Barrat-Segretain 1996), (2) when they are able to germinate, they are very strong competitors, because they shade submerged vegetation, thereby limiting their growth. Rooted floating-leaved vegetation occurrence may be limited when fetch and water depth become too great. In the intermediate zone, when rooted floating-leaved macrophytes vegetation does not occur (3) various submerged macrophyte species occur that differ in life-history strategies for overwintering. At even greater depths and fetch, (4) lower light availability at the sediment level combined with higher changes of uprooting by exposed conditions, most likely inhibits submerged vegetation developing from seeds and turions. Here, only well rooted and tall-growing submerged plants with an extensive rhizomal network are able to cope with lower light levels, most likely because they can utilize energy stored in their rhizomes to invest in the formation of long shoots at the onset of the growing season. Symbols for diagrams courtesy of the Integration and Application Network, IAN Image Library (https://ian.umces.edu/imagelibrary/)

than strongly rooting ones can either be explained by wind-driven waves or lower availability of light. A high fetch, and thus wind-driven waves, may result in macrophyte damage, breakage or uprooting (Schutten et al., 2005). An extensive rhizomal network provides (1) strong anchoring in unstable sediment during storm events, (2) storage of energy in the rhizomes that allows a fast regrowth in spring, and (3) an advantage by forming high stands that reach the water surface, allowing them to cope with poor light conditions (Wiegleb et al., 1991; Schutten et al., 2005; van Zuidam & Peeters, 2012). These observations differ from the expected distribution of major growth forms described by the conceptual model from Bornette & Puijalon (2009). Moreover, as opposed to their model, we found that tall caulescents (e.g., *P. lucens*) occurred at locations with lower porewater nutrient concentrations, while small caulescents (e.g., *C. demersum*) occurred at locations with the highest porewater nutrient concentrations. Also, recent work in China, highlights that *P. lucens* can only cope with hydrodynamic stress when the surface water was not eutrophic, while *C. demersum* and *M. spicatum* were most tolerant species to both eutrophication and hydrodynamic stress (Zhu et al., 2018b). Taken together, we propose an adapted conceptual model for the occurrence of aquatic macrophytes in shallow peat lakes that includes growth form, life-history strategies for overwintering and several abiotic factors (Fig. 5).

Beyond traits for overwintering, *C. demersum* differs with respect to other submerged macrophytes, as it is a free-floating and non-rooted plant and does not directly absorb phosphorus form the sediment, while rooted plants do (Barko & Smart, 1981). This might lead to lower porewater phosphorus concentrations where rooted plants occur (Wigand et al., 1997). These functional differences might be an alternative explanation for the differences in porewater nutrient concentrations between this and other groups of submerged macrophytes. Next to functional differences, aquatic plants can adapt their morphology (e.g., small and streamlined plants) depending on local hydrodynamic stress level and on whether the water is eutrophic or mesotrophic (Zhu et al., 2018a). Future research endeavors related to the occurrence of aquatic macrophytes might more explicitly consider changes in plant morphology.

Implications for shallow lake restoration

In Europe, and in the Netherlands, active revegetation programs and natural revegetation following improved water conditions of unvegetated shallow lakes is important with respect to the European Water Framework Directive (Bouleau & Pont, 2015). This framework sets targets for the ecological quality of water bodies (e.g., composition and abundance of macrophytes). However, restoration is challenging due to various, and often human-induced, bottlenecks including eutrophication, carbon limitation, water clarity and overgrazing (Gulati & van Donk, 2002; Lamers et al., 2002; van de Haterd & ter Heerdt, 2007; Bakker et al., 2013; Phillips et al., 2016). This study provides insight into the occurrence of certain species in a shallow peat lake complex, without light limitation and without recreation and associated disturbances, which could be driven by growth form and life-history traits, water depth and fetch. For restoration measures, this implies that some species can only be expected within a certain fetch and water depth (e.g., *N. lutea* and *N. alba*) or that certain species should be used for restoration measures that can occur at sites with a high fetch and water depth (e.g., *P. lucens*). Beyond our survey, grazing by water birds, crayfish and fish may influence the occurrence of certain species by selective consumption (Bakker et al., 2013; Roessink et al., 2017). To improve the understanding of the functioning of shallow peat lakes, future research might focus on the interaction between grazing and the occurrence of macrophytes that have distinct life-history traits. Altogether, the improved understanding of the biogeochemical and hydromorphological functioning of this peat lake complex may aid in the revegetation and conservation of shallow peat lakes via species-selection depending on the environmental context.

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Availability of data and material All data that support the main findings of this study are available via the Data Archiving and Networked Services (DANS) EASY (https://doi.org/10.17026/dans-xee-h224) (Temmink et al., 2021).

Declarations

Conflict of interest The authors declare that there is no conflict of interest.

Consent for publication All authors agree with the content presented in the manuscript in question.

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