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Plant-mediated equilibrium between phosphorus immobilization and mobilization: a mini-review

Abstract

Aquatic (submerged) macrophytes stands represent an important phosphorus (P) retention structure, crucial in stabilizing the clear water state of shallow waters even at an increasing P loading. Particularly reviewed are processes often regarded only in a biased presentation since mainly studied exclusively during the plant's growing season: 1) Beside the P uptake by plants during their growth, they can considerably translocate P to other biota by mobilizing mineral P forms, and by accumulating organic matter stimulating redox processes being related to an iron-bound P release. 2) Definite stands preferentially accumulate matter during growing season, which is usually fine grained and rich in organic matter and P, representing a high resuspension potential. Macrophyte senescence regularly leads to temporary and higher resuspension rates (P entrainment) compared to non-vegetated areas. 3) In-lake P precipitation translocates P towards the sediment surface limiting pelagic P availability, but providing an important P resource for the recovering eutraphent macrophyte species. The key role of submerged macrophytes in shallow waters is more directly related to modifying the dynamic equilibria between the seasonally different vegetation particle trapping and resuspension, i.e. between retention and mobilization of P in the plant's life cycle. This makes obvious, that studies quantifying and balancing the transient matter retention and the net effect of macrophytes should include at least a complete annual life cycle of the dominating species.

Keywords: Sediment, sedimentation, resuspension, entrainment, river, shallow lake, phosphorus release, iron

1 Introduction

Aquatic macrophytes are a substantial part of aquatic ecosystems. They are important habitats for a variety of fish and macrozoobenthos species, and crucial in stabilizing the clear water state of shallow waters even at an increasing nutrient loading (e.g. SCHEFFER et al. 2001). Because of their low mean water depth, usually <5 m (JEPPESEN et al. 1990), and thereby light transmission up to the bottom, shallow lakes are often colonized by submerged macrophytes. However, if a certain waters-specific threshold of burden of nutrients such as the key nutrient phosphorus (P) is exceeded the lake can abruptly switch toward a turbid, plankton-dominated macrophyte-free state (SCHEFFER et al. 1993). This turbid state is self-stabilizing since the low light availability restricts the macrophytic growth. The feedback between water turbidity and macrophyte occurrence causes a hysteresis. As a consequence, a strong reduction in nutrient loading below the previous threshold becomes necessary to reach a re-colonization by macrophytes and thus the clear water state (SCHEFFER et al. 1993). Within a certain span of P loading alternative stable states are a characteristic feature of shallow lakes, i.e. at the same P loading they can be clear or turbid.

The weathering of P-containing minerals in the catchment area is usually a slow process (SHARPLEY et al. 1999). Thus, usually only a small quantity of P is mobilized and accumulated in different type of waters (KLEEBERG et al. 2010a). However, processes occurring at the sediment water interface may considerably enhance P mobilization, as often mediated by macrophytes. Colonisation, growth and decomposition of macrophytes can considerably influence P cycling, and thus the energy flow in aquatic ecosystems (BARKO & JAMES 1998; DINKA et al. 2004). During the growing season, macrophytes accumulate P from both sediments and water (e.g. PELTON et al. 1998). When the macrophytes die, the resulting decomposition processes can, in turn, substantially regulate the recycling of P in fresh water ecosystems over an extended period of time (PIECZYŃSKA 1993; SHILLA et al. 2006).

Living macrophytes alter sediment biogeochemistry, resulting in varying pore water P, solid-phase P, and metal levels (WIGAND et al. 1997). Decomposing macrophytes supply organic matter (OM) (BÄRLOCHER & GRACA 2005) which can stimulate microbial and redox processes (LONGHI et al. 2008) within a lake. Furthermore, it has been hypothesized that elevated nutrient concentrations may be an important factor in controlling decomposition rates (XIE et al. 2004; SHILLA et al. 2006), as nitrogen and P demands associated with decomposition often exceed the P supply from the material being decomposed.

Resuspension, the hydrodynamically induced entrainment of already deposited particulate matter and dissolved sediment constituents due to impact of wind and waves (e.g. SHINOHARA & ISOBE 2010; KLEEBERG et al. 2013a) as well as due to the locomotive activity by benthivorous fish can considerably contribute to an increase in turbidity particularly in shallow lakess (VAN DONK & VAN DE BUND 2002) and rivers (KLEEBERG et al. 2010b). This applies also to the entrainment of sedimentary particulate and dissolved P forms (e.g. SCHEFFER 1998; KLEEBERG et al. 2013a). Thus, resuspension is an important mechanism in shallow aquatic systems, where the translocation and transport of sediment-associated P often constitutes a high percentage of the total annual P flux. However, stands of submerged macrophytes can significantly contribute to stabilize the sediment against waves and benthivorous fish and thus lowering the concentration of suspended particulate matter (SPM) (e.g. JAMES et al. 2004; MADSEN et al. 2001).

The aim of the present mini-review is to provide arguments that macrophytes mediate important long-term matter accumulation which is a seasonal equilibrium process particularly in respect to P mobilization. Compiled are preferentially processes often regarded only in a biased presentation; that is why the mini-review does not complain to be complete. Particularly, the following three issues are being addressed: 1) the role of macrophytes in the benthic pelagic P cycle (P mobilization, release), 2) their effects on P transport (sedimentation, resuspension), and 3) plant recovery following restoration measures (P supply).

2 Role of macrophytes in the benthic pelagic phosphorus cycle

Macrophyte stands represent an important P retention structure within a lake where P is accumulated in the lake sediment. Internal biochemical processes, however, can considerably enhance P mobilization (e.g. RODEN & EDMONDS 1997), and macrophytes can also enhance benthic P mobility.

Coupled mechanisms of carbon (C) turnover and P mobilization can lead to positive feedback effects. Figure 1 illustrates the main processes of the benthic-pelagic P cycle in a shallow macrophyte-dominated system. An increasing allochthonous C input (process #1) and the biomass produced by pelagic and benthic production lead to deposition and accumulation of OM. Event-related changes of sedimentation (#2) and resuspension (#3) lead to the formation of transport- and accumulation-zones at the bottom (e.g. KLEEBERG et al. 2013a). Due to the selective transport of particles, sediment is spatially sorted according to sediment properties. Hence, the basic morphology, wind exposure, location, runoff and particulate matter load of tributaries determine whether and to what extent which materials are translocated and thus which C and P compounds temporarily accumulate in the sediment or are entrained into the pelagial. Moreover, resuspension is often related to milieu changes, which in turn influence the redox-controlled P binding onto iron (GERHARDT et al. 2005) or lead to sorption/desorption of P (KROGERUS & EKHOLM 2003).

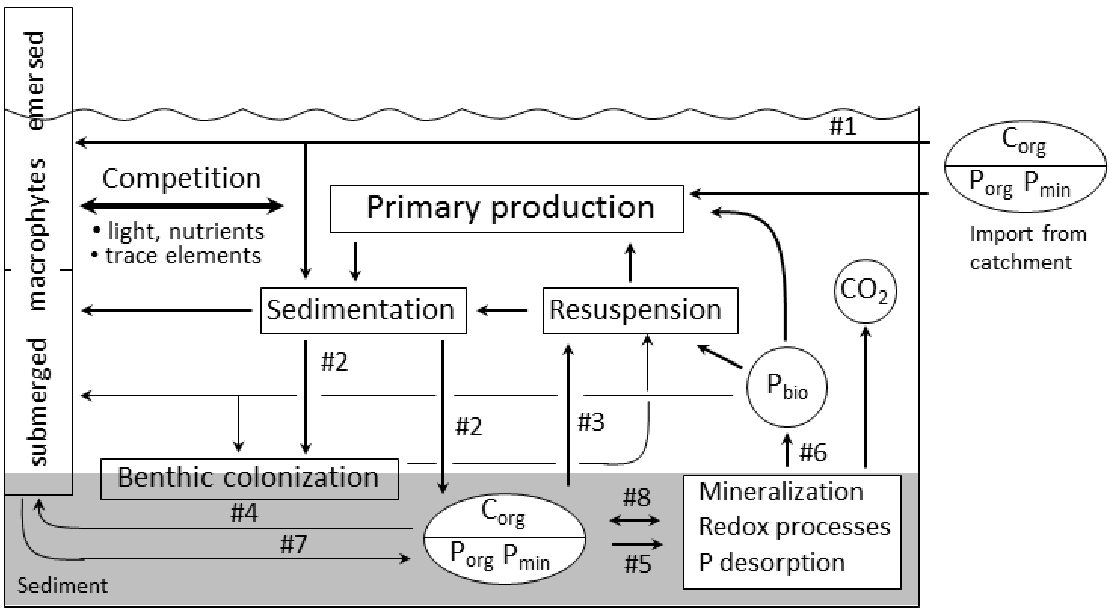

Fig. 1: Conceptual model illustrating the main processes of the pelagic benthic P cycle in a shallow macrophyte-dominated aquatic system. C_{org} – organic carbon, P_{org} – organic bound phosphorus, P_{min} – phosphorus bound in minerals.

One well described positive feedback involves acceleration of P cycling by submersed macrophytes (reviewed by BARKO et al. 1991; BARKO & JAMES 1998). Accordingly, sediment P, even if rather tightly (metal) bound, is taken up by roots (#4). Macrophytes can mobilize particulate bound P since they influence the biogeochemical conditions in the rhizosphere on a small scale. Due to the release of acids and exudates, the root surface forms a reactive surface for different chemical and microbial processes (SORRELL et al. 2002), which can influence the stability of mineral phases (#5). Short-chain organic acids mobilize P sorbed to iron hydroxides (e.g. THOMSEN et al. 2005). Macrophytes thus act as a 'P pump', transporting P towards the water body (SMITH & ADAMS 1986; #6). In this manner, P is mobilized and translocated to shoots (#4) and subsequently released rapidly upon seasonal senescence (#7). This P recycling increases P availability in the open water where P can be used by phytoplankton leading to a further C fixation, which in turn accelerates OM production and accumulation at the surface sediment which in turn can induce redox processes at the sediment water interface (#8). As in terrestrial systems, the quality of the OM and the availability of electron acceptors determine the decomposition rate (GRIMM et al. 2003).

The decomposition of OM, especially via iron and sulfate reduction, is crucial for the mobilization of inorganic P, bound by sorption to iron hydroxide surfaces (RODEN & EDMONDS 1997; #5). Briefly, the formation and precipitation of insoluble complexes of sulfide with ferrous iron can disrupt the iron-phosphate cycle which results in a lack of iron for P binding, and an excess of mobile P species (e.g. KLEEBERG et al. 2012) and their release (#6).

Due to aerobic and anaerobic redox processes, not only organic C compounds, but also organic P compounds are turned over (TURNER et al. 2005; #8). A further succession of vegetation in the lake will generate biologically available P forms (e.g. BARKO & SMART 1980; #6) which are favourable for the intensification of the lake internal P cycle.

In conclusion, usually an increasing import of OM both from terrestrial and aquatic vegetation increasingly contributes to accumulation of OM stimulating microbial and redox processes. In this manner, primarily aquatic macrophytes can accelerate the shift from a 'pure' geochemical to a biogeochemical sediment diagenesis and essentially drive the evolution of a sedimentary P cycle by mobilizing and translocating P to other biota. Still a key unresolved issue is whether the biota at a given site determine their own future by modifying their environment, or the development of an ecosystem is simply determined by the external environment (MITCH & GOSSELINK 2000).

3 Effects of macrophytes on sedimentation and resuspension

Aquatic macrophytes play a key role in structure and functioning of aquatic ecosystems, which applies to fluvial systems (e.g. SAND-JENSEN et al. 1989) in a very similar manner to shallow, wind- and wave-exposed standing waters (e.g. SCHEFFER 1998). The seasonally different extent of increasing or decreasing the accumulation and mobilization of matter and P by macrophytes is illustrated in their annual life cycle (Fig. 2).

3.1 Macrophyte effects during growing season

During growth, despite the very low concentrations of soluble reactive P (SRP) in the pore water, rooted macrophytes are known to be fully capable of deriving their P nutrition exclusively from the sediment (Fig. 2). As reported by BARKO & SMART (1980), P absorption and translocation into shoots (i.e., mobilization) was substantial, and in some cases suggested a more than 1000-fold turnover of pore water SRP over a 3-month period. For example BARKO & SMART (1980) reported macrophyte-mediated P release rates, for *Egeria* spec. 1.64-2.88 mg m^{-2} d^{-1}, *Hydrilla* spec. 0.27-1.37 mg m^{-2} d^{-1}, and *Myriophyllum* spec. 0.41-4.38 mg m^{-2} d^{-1}.

In definitive stands, macrophytes locally reduce flow velocities by mechanical obstruction of water flow (BUTCHER 1933), and improve water quality, trap extensive SPM, and accumulate and stabilize fine-grained cohesive sediments (SCOFFIN 1970; MADSEN & WARNCKE 1983; SAND-JENSEN et al. 1989; MARSHALL & WESTLAKE 1990; MADSEN et al. 2001). Furthermore, the retention and release processes strongly regulate the fluxes of P (HAGGARD et al. 2004; KLEEBERG et al. 2007). The reduction of flow velocities, increases both sedimentation and P retention, and decreases the potential for resuspension at high biomass levels (Fig. 2) (FONSECA & CAHALAN 1992; JAMES & BARKO 1994; MADSEN et al. 2001; JAMES et al. 2004).

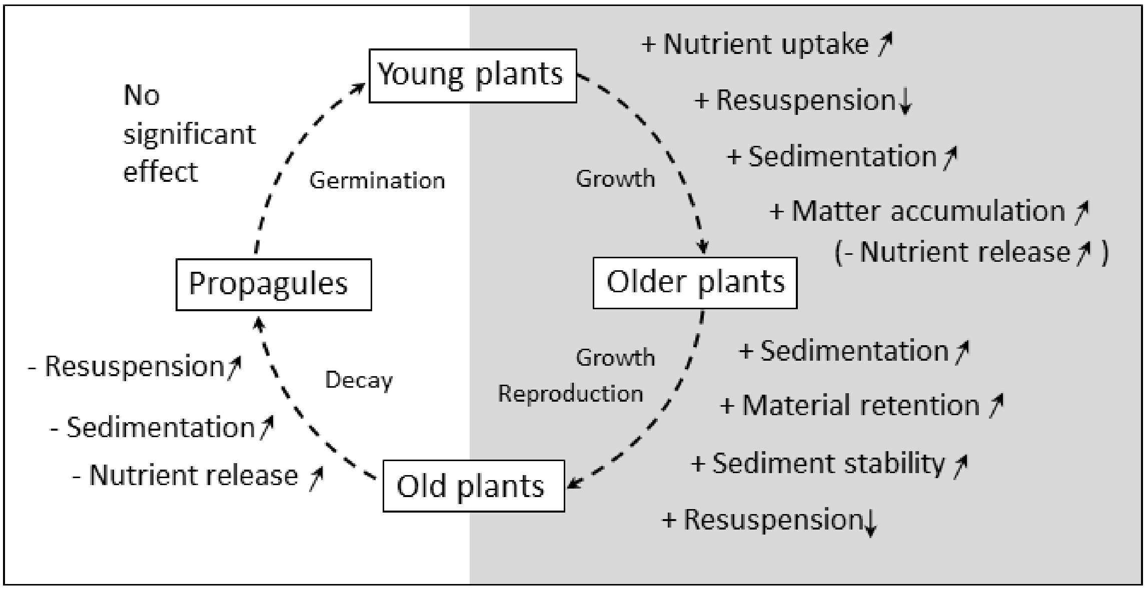

Fig. 2: Schematic presentation of the possible effects of macrophytes on sediment water interactions in a shallow, wind-exposed lake with macrophytes. An upturned arrow indicates the increase in the intensity of a process; a downward arrow indicates the opposite. The respective process can either have a positive (‘+‘) or a negative effect (‘-‘) on the water quality.

For example, these effects were studied during the growing season (May-August) in three different zones of a stand of the emergent *Typha angustifolia* L. in shallow Kirkkojärvi basin of Lake Hiidenvesi, SW Finland (HORPPILA & NURMINEN 2001). The authors reported that within the stand (5 m from the edge), both the concentration of SPM and the entrainment rate were significantly lower than at the edge and outside the stand (5 m from the edge). The differences between the zones increased towards the end of summer together with the growing stem density. During the 82 d study, on dry weight basis, 2210 g m^{-2} of sediment was resuspended in the outer zone. At the edge and in the inner zone, the corresponding numbers were 1414 and 858 g m^{-2}, respectively. The P entrainment rate was 39.4 mg m^{-2} d^{-1} outside the stand, 22.4 mg m^{-2} d^{-1} at the edge, and 13.4 mg m^{-2} d^{-1} within the stand. The authors admit that in early summer, the concentration of SPM had a highly significant positive effect on SRP concentration in the water, whereas, in late summer (*Typha* senescence) no effect was found. During the study period, P retention by emergent macrophyte stands corresponded to only 3-5% of the present annual external P loading of the Kirkkojärvi basin (HORPPILA & NURMINEN 2001).

In a similar study, i.e. at the same site and time HORPPILA & NURMINEN (2003) studied sedimentation and resuspension in a submerged plant community. During the 83 d study period, 793 g m^{-2} of sediment was resuspended within a stand formed by *Ranunculus circinatus* SIBTH., *Ceratophyllum demersum* L., and *Potamogeton obtusifolius* WERT. et W.D.J. KOCH. Outside the stand, 1701 g m^{-2} sediment resuspension was determined. Water turbidity and SPM concentration were significantly lower within the plant bed compared with the surrounding water area. With the resuspended sediment, the P entrainment rate was 11.8 mg m^{-2} d^{-1} within the stand and 24.5 mg m^{-2} d^{-1} outside the stand. Within the macrophyte stand, resuspended particles absorbed P from the water (indicated by the inverse relationship between SPM and SRP), which was probably connected to the lowered P concentration of surface sediment due to uptake by macrophytes (HORPPILA & NURMINEN 2003). The latter is astonishing. Usually, seasonal changes in sedimentary TP are not to detect since first, the variability particularly in plants stands is too high to find any significant uniformity, and second, the dissolved P pool of sediment usually represents not more than 1-2% of TP (BOSTRÖM et al. 1988).

In essence, in definitive stands during growing season, macrophyte-mediated effects improving the water quality are dominating, i.e. mainly due to the P uptake from the sediment into biomass, and by accumulating matter within their stands.

3.2 Macrophyte effects during plant senescence

It is obvious that the matter accumulated during growing season is preferentially fine grained and rich in OM and P representing a respective resuspension potential (KLEEBERG et al. 2010b). Thus, the senescence of macrophytes, a sudden increase in discharge of a running water or an inflowing tributary, wind and waves, or a possible plant cutting, all lead to resuspension and entrainment of organic material (SAND-JENSEN et al. 1989; SCHULZ et al. 2003; JAMES et al. 2004), and release of nutrients into the water column (WAINRIGHT 1990; KLEEBERG et al. 2010b).

The extent of resuspension depends on both (i) the vertical distribution of sediment properties in the bed, such as dry weight representing time after deposition, OM, and P concentration of pore water (WITT & WESTRICH 2003; TENGBERG et al. 2004; KLEEBERG et al. 2007), and (ii) the hydrodynamics such as flow velocity and bottom shear stress, which also influence floc formation and aggregation at the sediment-water interface (DROPPO et al. 1998). Although the impact of all these parameters is qualitatively known, it is not possible to predict the resuspension behaviour of the sediment (such as critical erosion thresholds and entrainment rates) from one or more easily measurable sediment parameters (e.g. El Ganaoui et al. 2004). Hence, each sediment and plant type must be investigated independently.

The importance of the hydrodynamically induced transport processes relative to the total flux of nutrients through the system is often not known. In particular, the P fluxes due to resuspension associated with macrophyte stands under changing wave and flow conditions are poorly understood (Reddy et al. 1999; Steinman et al. 2008). Consequently, often the impact of 'in-stream' or 'in-lake' hydrologic conditions on the extent of benthic P entrainment is poorly documented, both for the magnitude and source strength from sediment and pore water. Moreover, accurate determination of critical shear stress for resuspension is only attained through direct, in situ measurements (Paterson & Black 1999).

Moreover, macrophytes and their interactions with sediment and overlying water may be considered from small scale (individual plant) to large scale (vegetation mosaic); intermediate scales are vegetation patches, which are assemblages of certain dominating species growing in relatively uniform physical conditions with defined spatial boundaries (Pringle et al. 1988). Assembling of individual plants into patches means establishing certain interactions between plants, and assumes an increased level of interaction with the flow such as vegetation resistance, frictional energy loss and volume displacement (e.g. Green 2005). Because of this complexity (see Sand-Jensen & Pedersen 1999), most of the basic interactions have been conceptualized only at the individual plant and patch scale. At all scales there are only limited studies providing quantitative data of the definitive relationships (see review by Madsen et al. 2001).

A more recent paper by Kleeberg et al. (2010) quantified resuspension, in particular the P entrainment, under well-defined hydrodynamic conditions in a stand of the arrowhead *Sagittaria sagittifolia* L. in shallow lowland River Spree, Brandenburg, Germany. *In situ* resuspension experiments with a hydrodynamically calibrated erosion chamber were conducted. Concurrent measurements of the prevailing flow characteristics and bed load were used to quantify the seasonal dynamics of matter deposition and mobilization (Fig. 2) inside and outside (free path) of a representative patch of *S. sagittifolia*. Increasing entrainment rates (E) of particles (E_{SPM}) and TP (E_{TP}), with increments of shear velocity (u*) from 0.53 to 2.42 cm s^{-1}, were significantly higher inside the plant patch than outside. Indeed, E_{SPM} and E_{TP} at the lowest u* were 8- and 12-fold higher inside than outside the patch, reflecting the resuspension potential of the upper nutrient-enriched layer and the extent of pulsed P inputs even at small increases in u*. Vertical distribution of velocity (u) revealed a flow pattern of a mixing layer inside the *S. sagittifolia* patch, and that of a boundary layer in the free path. The highest gradient of u in the mixing layer was located in the water column at about 0.5 m depth, whereas the highest gradient of u for the boundary layer was found near the riverbed. The maximum of u* (1.65 cm s^{-1}) was only 4 mm above the sediment. Thus, a plant mosaic provides a low-energetic environment promoting extensive particle trapping and the accumulation of a fine-grained, P-enriched sediment, and forming a large resuspension potential. Consequently, during plant decay and the concomitant increase of u* this material is preferentially entrained (Fig. 2) at higher rates. Hence, the key role of submerged macrophytes in lowland rivers, as in shallow lakes, is more directly related to modifying the dynamic equilibria between vegetation trapping and resuspension, i.e. the retention and mobilization of P.

3.3 Macrophyte effects during decomposition

During decay, the majority of plant constituents, e.g. nutrients, is rapidly leached and released back to the sediment pore water or overlying water (Fig. 2). For example, BELOVA (1993) studied the decomposition of several lake macrophytes in the littoral of two lakes with different levels of macrophyte development. Weight loss during 40-60 days of decomposition for fast-decomposing plants was 60-95% and after 365-day of incubation *Potamogeton perfoliatus* L. lost nearly 100% of its initial weight. Slow-decomposing plants lost 20-50% of their initial weight after 40-60 days of incubation, and *Phragmites australis* (CAV.) TRIN. ex STEUD. lost 84% of its initial weight after 365 days. TP in plants did not decrease at the first stages of decomposition. The proportion of macrophyte OM entering the biological cycle in two lakes amounted 3.5% and 26% of phytoplankton primary production (BELOVA 1993).

An additional view, it can be assumed that metals concurrently released during plant decomposition could contribute to P binding (KLEEBERG 2013), thus decreasing the direct P availability to decomposers and the release to the water column and other biota (Fig. 1). This applies particularly to Fe, which is known to be an efficient P binding partner. Phosphorus is co-precipitated with oxidized Fe- and Mn-species, and adsorbed to their amorphous oxyhydroxides (CHRISTENSEN et al. 1997). Briefly, inorganic Fe exists in the reduced ferrous (Fe^{2+}) or the oxidized ferric (Fe^{3+}) form, depending upon pH and oxidation-reduction potential. Thus, Fe^{3+} compounds such as $Fe(OH)_3$ strongly sorb P and form an oxidized ‘microzone’ at the sediment surface. Minerals such as $FePO_4$ are also formed, but the primary P retention in sediments is by solid $FeOOH{\sim}PO_4$ complexes whose effect is greatest across a pH range of 5 to 7 (MARTYNOVA 2010). In the reduced state, Fe^{2+} becomes soluble and associated P is released. This change occurs rapidly, so that even brief periods of oxygen consumption lead to P release. Both the mineralization of organic P compounds and the dilution of solid Fe minerals could contribute to a transition from less mobile to more mobile (i.e., redox-sensitive) Fe-bound P (Fig. 1). However, in studies on aquatic macrophyte decomposition, P binding partners are usually not yet been examined (KLEEBERG 2013). Furthermore, the availability of elements such as Fe can influence macrophyte species composition (LAMERS et al. 2002).

In essence, both sedimentation of OM and the uptake of P, and the resuspension of different sediment constituents and P and its binding partners within the plant’s life cycle, all with different intensity, emphasize the importance of submerged macrophytes in mediating the water quality. However, the plant-dependant properties of the sediment known to influence sediment consolidation and the respective hydrodynamic thresholds for resuspension are often not known. Thus, it becomes obvious, that studies quantifying and balancing the equilibrium processes and the net effect of macrophytes on retaining OM and P, respectively, should include at least a complete annual life cycle of the dominating species.

4 Effects after macrophyte recovery following restoration measures

The pristine state of lakes is often poor in P, clear and rich in aquatic macrophytes. The lakes with low P concentrations have mostly growth-restricted plants. With increasing load of OM and P and its availability the aquatic plant biomass increases (see Fig. 1); dense stands might occur which thrive within the whole water column up to the water surface (SCHEFFER 1998). However, if a certain threshold of P concentration is exceeded the lake can switch toward a turbid, plankton-dominated macrophyte-free state (SCHEFFER et al. 1993).

The case study of dimictic Lake Groß-Glienicke, Berlin/Potsdam, Germany, illustrates that a single in-lake Fe application can be a suitable lake restoration tool to initiate the re-colonialization of a certain community of submerged macrophytes which in turn is contributing to a stabilization of a new, long-lasting equilibrium.

Following the reduction of the external P loading, the previously highly eutrophic Lake Groß-Glienicke has been treated once, between December 1992 and February 1993, with solid ferric hydroxide ($Fe(OH)_3$) and dissolved ferric chloride ($FeCl_3$), each at 250 g Fe m^{-2} (KLEEBERG et al. 2012). Due to reduced external P loading and the in-lake P precipitation, the concentrations of total P (TP) and chlorophyll a (Chl a) decreased on average (1989-1992 to 1993-1996) from 485 to 55 μg l^{-1}, and from 41 to 13 μg l^{-1}, respectively; decreases have continued down to today's mesotrophic level (TP 20 μg l^{-1}, Chl a 7 μg l^{-1}). The secchi depth visibility increased to maximum 6 m (KLEEBERG et al. 2013b) providing a better light availaibility.

With the recolonialization of submerged macrophytes and their massive dispersion since about the year 2000 mesotrophic conditions at a TP concentration around 22 μg L^{-1} have been reached. The maximum macrophytic colonization depth of about 3 m in 2000 increased on average to 6.3 m in 2008, and the numbers of species within the same period of time from 7 to 14 species. The macrophyte evaluation using the reference index according to SCHAUMBURG et al. (2006) resulted in the ecological status class 3.0 ('moderate') for the lake. The evaluation according to the macrophyte index Brandenburg (PÄZOLT 2007) resulted in an ecological status class 1 ('excellent'). Surveying and mapping in 2010, in the same manner as before, resulted in 13 species of aquatic macrophytes. The colonization of the submerged macrophytes with water depth increased to 7.2 m. Nevertheless, the evaluation of the macrophytes indicated only an 'unsatisfactory' ecological status of the lake; because the species which represent a 'good ecological quality' such as *Chara* spp. are missing or completely under-represented. Guidelines that critically assess the potential development of submerged vegetation, considering into account the complex factors and interrelations that determine their occurrence, abundance and diversity exist (e.g. HILT et al. 2006). Nevertheless, it remains difficult to predict when and which submerged macrophyte species will probably re-colonize a lake after a certain restoration measure.

The in-lake measure, more than 20 yrs ago, is sustainable (KLEEBERG et al. 2013b). Due to the iron addition the pelagic P was almost completely precipitated and translocated towards the sediment surface. This is the main reason why particularly eutraphent species of submerged macrophytes recolonized the bottom of the litoral zone. The highly competitive plant species benefit from the high iron-bound P supply at the sediment surface, translocating via their roots the P in the same manner as described above (Fig. 2). However, decisive is that the P, taken up from the P-rich surface layer of sediment, is seasonally stored in the biomass, thus being not available for phytoplankton growth. Hence, the rooting macrophytes contribute to a stabilization of the mesotrophic, i.e. low level P conditions in the water column.After senescence of biomass, the P leaked can be retained by oxidized iron compounds.

Zusammenfassung

Bestände aquatischer (submerser) Makrophyten repräsentieren eine bedeutende Retentionsstruktur für Phosphor (P), die entscheidend den Klarwasserstatus eines Flachgewässers, selbst bei zunehmender P-Last, stabilisieren. Insbesondere betrachtet werden Prozesse die oft einseitig interpretiert wurden, da sie hauptsächlich nur zur Wachstumssaison der Pflanzen untersucht wurden: 1) Neben der P-Aufnahme der Pflanzen während ihres Wachstums, können sie in erheblichem Maße P zu anderen Organismen verlagern in dem sie mineralisch P-Formen mobilisieren und durch die Akkumulation organischen Materials Redoxprozesse stimulieren, die wiederum die eisengebundene P-Freisetzung begünstigen. 2) Ausgeprägte Bestände akkumulieren präferentiell während der Wachstumssaison Material welches feinkörnig und reich an organischem Material und P ist, das zugleich ein hohes Resuspensionpotential repräsentiert. Der Makrophytenzerfall führt folglich regelmäßig und kurzzeitig zu höheren Resuspensionraten (P-Eintrag) im Vergleich zu vegetationsfreien Flächen. 3) Eine seeinterne P-Fällung verlagert den P zur Sedimentoberfläche und begrenzt so die pelagische P-Verfügbarkeit, stellt jedoch eine wichtige P-Ressource für die sich wiederansiedelnden eutraphenten Makrophytenarten dar. Die Schlüsselrolle der submersen Makrophyten in Flachgewässern ist insgesamt eher auf die Modifizierung eines dynamischen Gleichgewichts zwischen dem saisonal unterschiedlichen Partikelfang in der Vegetation und der Resuspension gerichtet, d. h. zwischen der Retention und Mobilisierung von P im Lebenszyklus der Pflanzen. So wird deutlich, dass Untersuchungen, die die vorübergehende Materialretention und den Netto-Effekt der Makrophyten quantifizieren und bilanzieren sollen, mindestens einen jährlichen und somit vollständigen Lebenszyklus der dominanten Art(en) berücksichtigen sollten.

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