

MINIREVIEW

THE ROLE OF PERIPHYTON IN PHOSPHORUS RETENTION IN SHALLOW FRESHWATER AQUATIC SYSTEMS¹

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Eutrophication caused by phosphorus (P) leads to water quality problems in aquatic systems, particularly freshwaters, worldwide. Processing of nutrients in shallow habitats removes P from water naturally and periphyton influences P removal from the water column in flowing waters and wetlands. Periphyton plays several roles in removing P from the water column, including P uptake and deposition, filtering particulate P from the water, and attenuating flow, which decreases advective transport of particulate and dissolved P from sediments. Furthermore, periphyton photosynthesis locally increases pH by up to 1 unit, which can lead to increased precipitation of calcium phosphate, concurrent deposition of carbonate-phosphate complexes, and long-term burial of P. Actively photosynthesizing periphyton can cause super-saturated O₂ concentrations near the sediment surface encouraging deposition of metal phosphates. However, anoxia associated with periphyton respiration at night may offset this effect. Linking the small-scale functional role of periphyton to ecosystem-level P retention will require more detailed studies in a variety of ecosystems or large mesocosms. A case study from the Everglades illustrates the importance of considering the role of periphyton in P removal from wetlands. In general, periphyton tends to increase P retention and deposition. In pilot-scale constructed periphyton-dominated wetlands in South Florida, about half of the inflowing total P was removed.

Key index words: eutrophication; microalgae; microphytobenthos; periphyton; phosphate; phosphorus; tertiary treatment; water quality

Periphyton can be involved in P cycling both as epibenthic and as epiphytic organisms (Fig. 1). In both cases, the periphyton can assimilate P, alter hydrodynamics, and modify the local chemical environment in ways that ultimately influence P retention by an aquatic system. While it is evident that periphytic organisms are not the only ones involved in P retention, the fact that major P fluxes can be altered by algal biofilms suggests that careful examination of their

potential role will be beneficial to both managers interested in P control and scientists interested in basic ecosystem function.

Periphyton can play an active role in P interception in many ecosystems. Periphyton led to a net increase in short-term nutrient flux from the water column into the sediments in small artificial systems (142%, Confer 1972), lake mesocosms (~130%, Hansson 1990), a shallow lake (Havens et al. 2001), and generally in shallow waters such as wetlands and estuaries (Sand-Jensen and Borum 1991, Vaithyanathan and Richardson 1998). Epibenthic periphyton in lentic habitats obtain nutrients from the water column as well as intercepting nutrients that diffuse upward from the sediments (Hansson 1989). Thus, periphyton-dominated wetlands show promise for removal of unwanted P from surface waters (Wu and Mitsch 1998), and other shallow freshwater systems may as well. For example, about 90% of P-loading from some mountainous agricultural areas in China appeared to be retained by a centuries-old practice of maintaining periphyton-dominated artificial ponds downstream of cropland (Yin et al. 1993).

Given the ability of periphyton to alter P fluxes, the goal of this mini review is to assess key aspects of periphyton that should be considered relative to their ability to function as agents of P removal. I will first describe how periphyton assemblages influence rates of P retention through uptake and hydrological influence. Next, the effects of periphyton on biochemical process rates will be explored. Finally, a case study that illustrates the potential role of periphyton in P retention in a wetland is considered.

Periphyton assemblages can play several roles that lead to increased retention of nutrients. First, they can remove nutrients from the water column and cause a net flux of nutrients toward the sediments. Second, they can slow water exchange across the sediment/water column boundary thus decreasing advective transport of P away from sediments. Third, they can intercept nutrients diffusing from the benthic sediments or senescent macrophytes. Fourth, they can cause biochemical conditions that favor P deposition. Finally, they can trap particulate material from the water column (Adey et al. 1993). Advective and molecular diffusion of solutes toward and away from the sediments and macrophytes are related to these processes and will be considered first.

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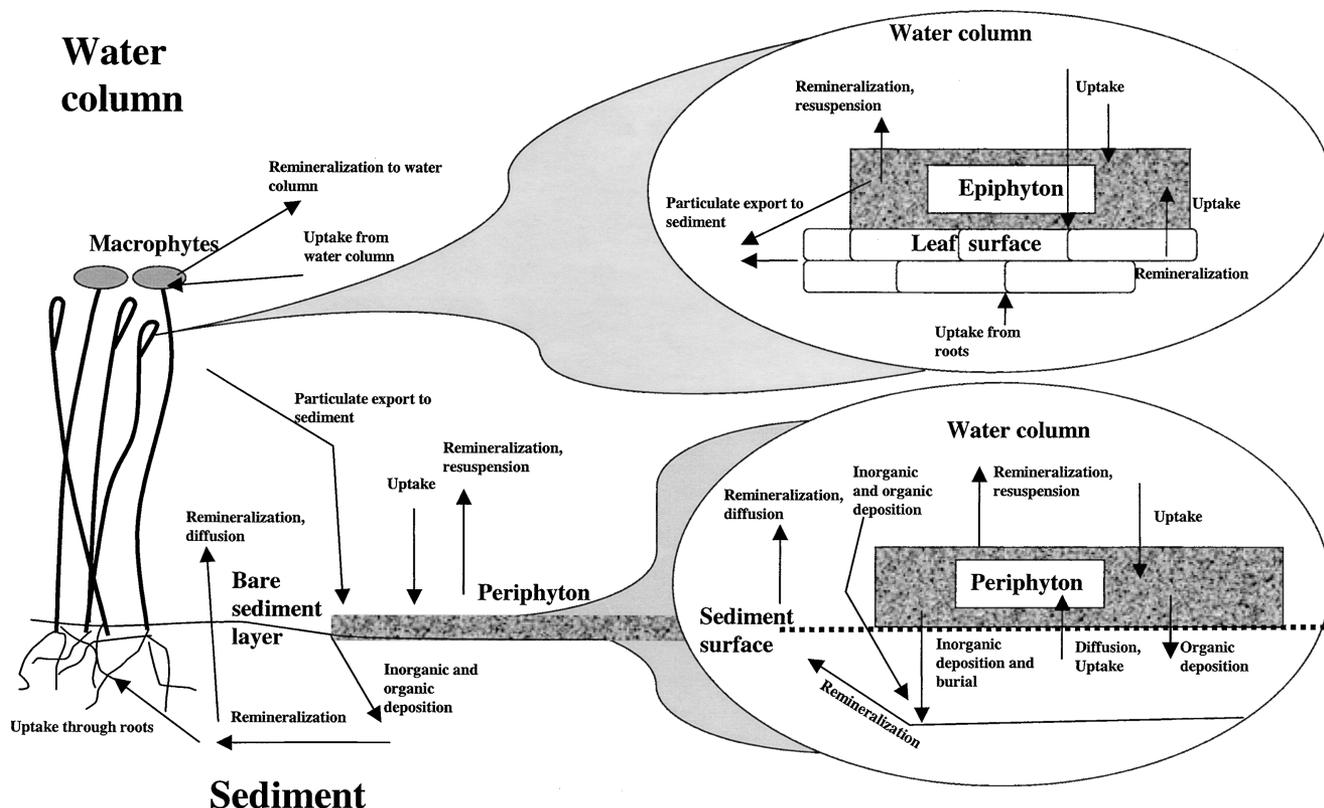


FIG. 1. Conceptual diagram of nutrient flux to and from sediments as modified by periphyton. The inset on the top-right details processes occurring at the surface of macrophytes, the inset at the lower right details processes at the sediment-periphyton interface.

PHOSPHORUS FLUX: HYDRODYNAMICS

Advective transport is a key factor in how periphyton assemblages acquire nutrients from the water column and block transport of nutrients from the sediments. Rates of advective nutrient transport exceed rates of molecular diffusion by several orders of magnitude (Vogel 1994). Growth form dictates flow attenuation and is directly related to nutrient uptake capacity (Steinman et al. 1992). Algal species with a high surface area to volume ratio such as filamentous algae have up to two-times greater nutrient uptake rates than prostrate gelatinous forms because advective transport can move nutrients into looser assemblages much more quickly. Thus, attenuation is crucial in determining how P moves into and through periphyton masses.

The attenuation of flow by algal masses is exponential (Fig. 2) and is generally determined by biomass density. Attenuation coefficients (η) range from 0.29 – 0.96 mm^{-1} according to the relationship $U_z = U_{z-d} e^{-\eta z}$ where U_z is water velocity at depth z , and U_{z-d} is water velocity at a known depth above point depth z , but still within the mass (Dodds and Biggs 2002). Dense assemblages can reduce water velocity to approximately zero within several millimeters of the surface of the mat. Even filamentous algal assemblages can attenuate water velocity by 90% within 10 mm

into the assemblage (Fig. 2). This translates into a 90% reduction in advective transport with a 1 cm thick periphyton layer. These data were collected from streams, where water velocity is considerably higher than in wetlands. Assuming that water velocity extinction coefficients are roughly similar in algal masses in wetlands, little or no flow-mediated transport should occur through dense periphyton mats in wetlands. Thus, in areas of wetlands with dense benthic periphyton growths, molecular diffusion or very low rates of advective transport should dominate movement of materials across the sediment/ water column interface. For example, in a slowly flowing ditch with extensive filamentous algal cover, the central open water channel had water velocity of $50 \text{ cm}\cdot\text{s}^{-1}$, but most of the channel had water velocities $<1 \text{ cm}\cdot\text{s}^{-1}$ (Dodds 1991a), leading to an expected 50-fold decrease in rates of advective transport.

The ability of periphyton to retard flow may increase short-term nutrient retention simply by increasing water retention time. Mulholland et al. (1994) documented that high periphyton masses increased water retention by increasing the relative area of dead zones in stream channels by 6 times as compared to low periphyton treatments. The high periphyton biomass treatments had turnover rates of P about 2 times longer than the low biomass treatments, indicating enhanced

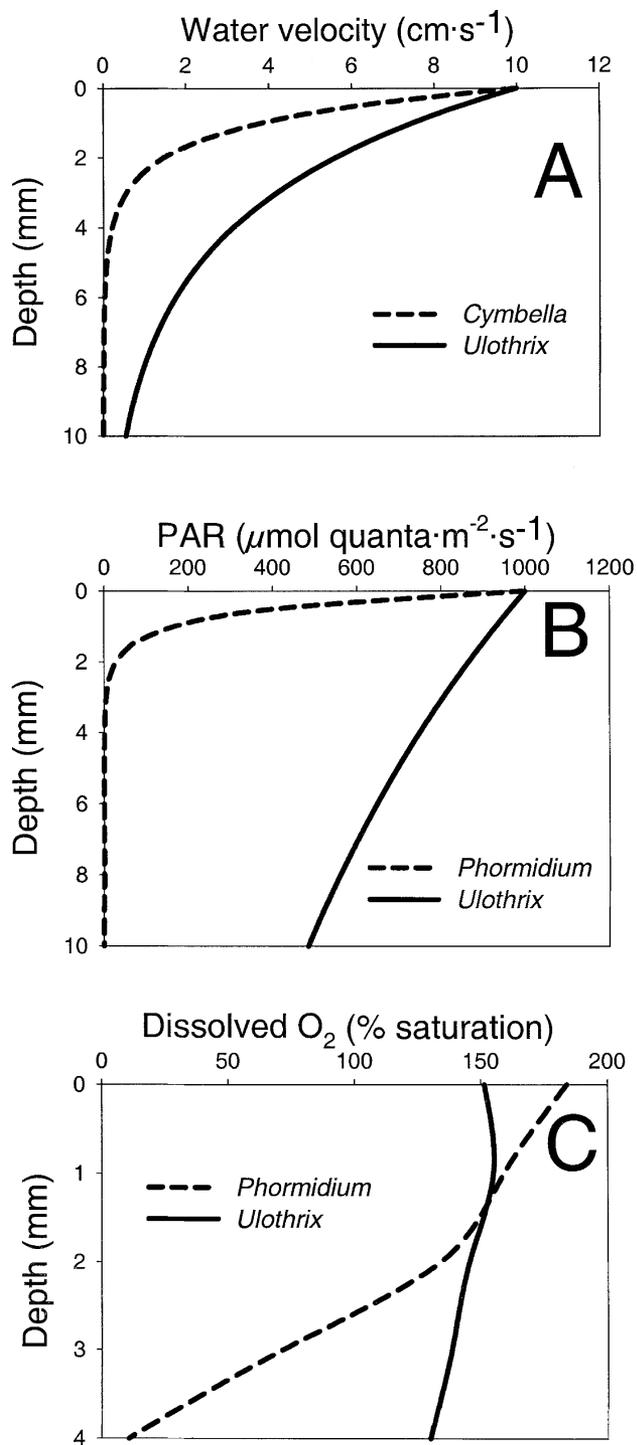


FIG. 2. Variations in water velocity (A), PAR (B) and Dissolved O₂ (C) with depth for dense algal assemblages (*Cymbella* or *Phormidium* dominated) or a loose filamentous assemblage (*Ulothrix*). Data in (A) calculated from flow extinction coefficients in Dodds and Biggs (2002), data in (B) from extinction coefficients in Dodds et al. (1999), and data in (C) unpublished data from assemblages described in Dodds et al. (1999).

internal nutrient cycling and retention. This effect occurred in experimental stream channels at a water velocity of 7 cm · s⁻¹. Since advective transport appar-

ently played a role in these experiments, lower water velocity habitats such as wetlands should demonstrate these effects to even a greater degree because exchange with the dead zones decreases proportionally with decreases in water velocity.

In addition to retarding advective transport of dissolved materials, filamentous algal assemblages can serve as filters or create areas of reduced flow, which has the net effect of removing suspended particulate materials from the water column (Stevenson 1996). For example, in still water mesocosms, phytoplankton cells in filamentous algae were concentrated 100 times over water-column cell counts. This effect accounted for rapid loss of P from the water column (Confer 1972). Filtering particulates may be important in lotic waters where turbulence tends to keep particulate materials containing bio-available P suspended, and in shallow lakes, where wind-induced resuspension is a common occurrence. Experiments with *Cladophora* demonstrated a greater than 10 fold concentration of particulate material relative to the water column (Dodds 1991b). Logically, the trapped particulate material is more likely to be deposited into the sediments once it is retained in the algal mass because the water velocity is lower and the fall rates of the particulates will be greater. The enhancement of sedimentation rates will be system-specific.

PHOSPHORUS FLUX: UPTAKE

Periphyton mediated P uptake rates vary over five orders of magnitude in natural systems (Table 1). A number of investigators have attempted to optimize systems for P removal from sewage effluent, and have achieved P uptake rates comparable to the maximum rates seen in natural lakes and wetlands (Table 1). Phosphorus uptake rates are influenced by periphyton biomass, periphyton metabolic activity, and advective transport of P to periphyton assemblages. Biomass, activity, and advective transport all vary and this may explain why natural systems often take up P at less than maximum rates.

A number of factors may influence accumulation of periphyton biomass. Grazing and sloughing losses for stream periphyton are reviewed by Biggs (1996); it is not known how well the sloughing rates apply to wetlands, where there is less turbulent sheer stress. A maximum limit of biomass of periphyton can accrue because self-shading (Fig. 2) leads to reduced growth of the lowermost layers. Such shading is also common with epiphytes, where a relatively thick (20 mg dry mass · cm⁻² leaf area) layer of epiphyte can remove 90% of incoming irradiance (Brush and Nixon 2002). Grazing of periphyton can lead to half the area-specific P uptake compared to ungrazed controls (Table 1), and periphyton growth must offset these losses if an active assemblage is to be maintained.

An upper limit on metabolic activity, and thus growth, is set by temperature. DeNicola (1996) and Hashimoto and Furukawa (1989) quantified maximum production as a function of temperature for a

TABLE 1. Range of phosphorus uptake rates for periphyton from natural and constructed systems.

System	Source water P (mg P · L ⁻¹)	Range of uptake rates (mg P · m ⁻² · d ⁻¹)	References
Recirculating laboratory streams—no grazing	0.005–0.007	7.2–15.6	Steinman et al. 1991
Recirculating laboratory streams—snail grazing	0.005–0.007	4.32–6.72	Steinman et al. 1991
Recirculating chamber—dairy manure nutrients	7–14	80–116	Wilkie and Mulbry 2002
Algal turf scrubber—sewage effluent	3.1	250–1820	Craggs et al. 1996
Algae in secondary clarifier—sewage effluent	0.1–10.4	24–1903	Davis et al. 1990
Assemblages on screens harvested weekly	0.012–0.148	100–130	Adey et al. 1993
Lake assemblages ^a		0.14–43,100	
Wetland assemblages ^b		0.4–2,200	

P, phosphorus. Source P concentrations were only available for constructed systems, soluble reactive P values only available for Steinman et al. 1991, total P was reported for the rest.

^aCalculated assuming 1.1–12,300 mg dry mass · m⁻² · d⁻¹ (Wetzel 2001) at 0.04–0.96% P (Vymazal 1995).

^bCalculated assuming fixation of 0.5–119 gC · m⁻² · d⁻¹ (Vymazal 1995, Goldsborough and Robinson 1996), dry mass of 50% C and 0.04–0.96% P content (Vymazal 1995).

variety of periphyton assemblages. These values of net photosynthetic rates were converted to P uptake rates (Fig. 3), and illustrate the tremendous range of rates that is possible under a maximum limit of growth rate as determined by temperature. Simple relationships between temperature and P uptake may not occur in part because of community-specific properties; some P accumulating microorganisms in a wastewater treatment biofilm were not tolerant of high temperatures so high temperatures lowered P uptake (Panswad et al. 2003).

Uptake of P is a biotic process, and depends in part upon the affinity of organisms for P. This affinity is generally described with a Michaelis-Menten relationship. Nutrient uptake parameters for several periphyton species and associated growth parameters were summarized by Borchardt (1996) who considered 7 separate studies. In general these studies demonstrated that half saturation constants for uptake ranged from 0.62–1271 µg P · L⁻¹, with most values falling below 60 µg P · L⁻¹. Pure cultures of organisms generally have half saturation constants for uptake far below 60 µg P · L⁻¹, so environmental factors must influence uptake rates.

Variable rates of advective transport of P to and into periphyton assemblages may explain the wide range of observed uptake kinetic parameters. Research from streams (Dodds et al. 2002), and marine mesocosms (Sanford and Crawford 2000) indicated that both the degree of advective transport and biotic affinity for P influence nutrient uptake by organisms associated with benthic habitats. These studies demonstrated that relatively low rates of advective transport lead to high half-saturation constants of the Michaelis-Menten relationship for uptake versus concentration, particularly for dense periphyton assemblages where water velocity is very low and molecular diffusion dominates. Thus, the amount of advective transport may limit uptake to some degree, even in streams where water velocity and turbulence are high, and advective transport is maximized. Wetlands have low water velocity, low turbulence, and relatively low

advective transport. Thus, high half saturation constants for P uptake by periphyton assemblages in wetlands are expected.

The discussion thus far has avoided the issue of the spatial distribution of periphyton cover. Areas with open sediments may contribute substantially more P to the water column. For example, sediments with periphyton activity had about three-fourths the rates of P flux from the sediments compared to those without periphyton activity (Carlton and Wetzel 1988). In a lake study, sediments without periphyton activity (incubated in the dark), had P release rates of about 1 mg P · m⁻² · d⁻¹, whereas those that were lighted had release rates that were <0.1 mg P · m⁻² · d⁻¹ (Van Luijn et al. 1995).

Furthermore, periphyton growth occurring on macrophytes may influence P uptake. Over 60% of the P uptake from the water column associated with macrophytes has been attributed to epiphytic algal

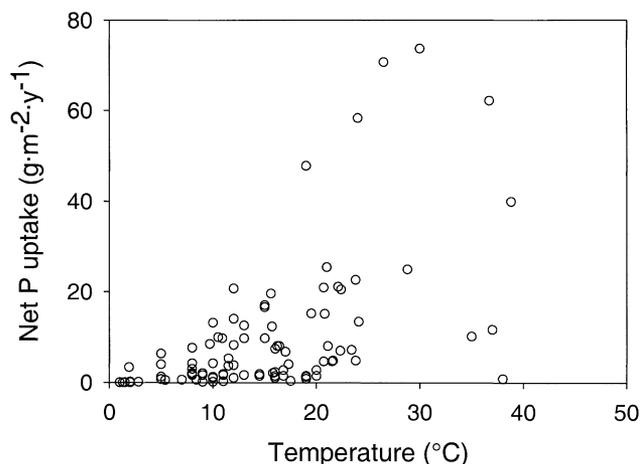


FIG. 3. Relationship between temperature and calculated net P uptake using published data on net photosynthesis from DeNicola (1996) and converting to P assimilation rates, assuming new cells use phosphate according to the Redfield ratio.

and microbial communities (Richardson and Marshall 1986). The pattern of epiphytes dominating P uptake from the water column has been documented in other studies (Wetzel 2001). This uptake by periphyton may ultimately lead to deposition of P onto sediments when the epiphytes slough off of the macrophytes, or when the macrophytes die and drop into the sediments.

At the ecosystem level, P deposition values are potentially influenced by the degree and distribution of periphyton cover on sediments and macrophytes as well as P concentration, grazing, sloughing, temperature, and advective transport. Detailed whole-system or large-scale mesocosm experiments are necessary to dissect the influence of these factors on P retention in ecosystems.

PHOSPHORUS BIOGEOCHEMISTRY AND RELATIONSHIPS TO PERIPHYTON

The role of periphyton in mediating P movement across the sediment/water interface is not limited only by hydrological influences and the capacity to assimilate P. Periphyton is also intimately involved in the biogeochemical cycling that allows for long-term sediment storage. Flux of P from sediments is a complex function of chemical, hydrodynamic, and biological properties, which is probably why specific rates are not reported for most sediment types under a wide variety of potential environmental conditions. Some important factors altering P flux include movement of organic P from sediments (Hannapel et al. 1964a, b, Wetzel 1999), adsorption and release from organic components (Stewart and Wetzel 1981, Stewart and Tiessen 1987), interference of organic compounds with adsorption to sediments (Kastelan-Macan and Petrovic 1996), sediment porosity (Cabrera et al. 1981), microbial mobilization of P (Hannapel et al. 1964a), hydrology (Kadlec 1999), and bioturbation increasing material flux rates from and into sediments (Fisher et al. 1980). In acidic sediments, absorption of P to Fe^{3+} and Al (Richardson 1985, Vymazal et al. 1998) can be important. Mineral deposition is dominated by Ca and Mg phosphates (Boström et al. 1988) if pH is above 6.5 (Wetzel 2001), or 7 (Vymazal et al. 1998). Periphyton can directly or indirectly influence all of these properties, but the strongest effects are on metal-phosphate deposition and co-precipitation with Ca and Mg phosphates, so these processes will be examined most closely.

Metal complexation with phosphate dominates at lower pH when the water column is oxic. In this case, the availability of metals that bind phosphate (Fox and Kamprath 1971, Danen-Louwerse et al. 1993) can be crucial to how much P is deposited. The availability of metals to react with phosphate can ultimately be driven by sulfate loading. Sulfate is reduced to sulfide by microbial action, and sulfide binds metals so they will not bind with phosphate at the oxic/anoxic interface (Caraco et al. 1990, Cooke et al. 1992, Smolders and Roelofs 1993, Golterman 1995). Sulfate reduc-

tion by microorganisms begins as redox falls below about 100 mV (Wetzel 2001), thus simple measurements of sediment anoxia are not sufficient to determine how sulfate reduction may be related to P deposition. Deposition and subsequent decomposition of organic carbon produced by periphyton photosynthesis may be sufficient to drive the redox low enough to cause the sediment to become a net producer of sulfide. Experiments are necessary to delineate the exact amount of carbon deposition caused by periphyton that ultimately leads sediment to become a net producer of sulfide.

Super-saturation of O_2 resulting from periphyton photosynthesis (see e.g. Fig. 2C) keeps the surface of sediments oxidized under lighted conditions. If the water column above the sediments becomes anoxic, then metal-phosphate complexes dissociate and phosphate enters the water column. Organic P compounds are also more likely to enter the water column under anoxic conditions (Golterman 1995). If a large periphyton mass dies or experiences low light, respiration may cause anoxia, leading to greater rates of P diffusion from the sediment into the water column above. For example, diurnal changes in light led to low rates of P release under periphyton-dominated sediments in the day, and accelerated release by several fold during the night when respiration decreased O_2 to 50% of saturation at the sediment surface (Carlton and Wetzel 1988).

High pH (above ~ 7) encourages the precipitation of Ca-phosphate compounds. This precipitation occurs concurrently with carbonate deposition (Otsuki and Wetzel 1972). There are a large number of apatite compounds that may form, including Ca-phosphate compounds (Nriagu 1984), and they undergo complex weathering reactions (Altschuler 1973, Flicoteaux and Lucas 1984). In general, these phosphate compounds are soluble at lower pH (Brown 1973). Interestingly, iron and aluminum can influence rates of P deposition even in calcareous systems where pH is high (Golterman and De Groot 1994, Olila and Reddy 1997).

Actively photosynthetic periphyton increase pH values at the surface of sediments. For example, Carlton and Wetzel (1988) documented a pH value of 9.0 in actively photosynthesizing periphyton, with pH values of 8 in the water column above and 7 in the sediments below. Greater pH increases rates of formation of Ca-phosphate compounds (Boström et al. 1988, House 1990) and formation of phosphate complexes with carbonate and calcium (Graetz and Nair 1999, Dittrich et al. 2000). The relationship between photosynthesis and P release from sediments, as related to pH shifts caused by photosynthesis, has been established for periphyton (Carlton and Wetzel 1988), and is partially related to increased iron precipitation of phosphate under oxic conditions and partially to increased pH favoring phosphate/ carbonate deposition (Cabrera et al. 1981). The increase in pH associated with photosynthesis by algal biofilms in a waste

water treatment system encouraged P precipitation and led to increased efficiency; during lighted periods, total P concentrations in sewage effluent dropped from 6 to 3 mg P · L⁻¹ as pH was raised from 8 to 9 by photosynthetic processes (Schumacher and Sekoulov 2002).

Experiments may be necessary to assess the ability of sediments to sequester P in any particular habitat. These experiments need to consider the role of periphyton, given that algal assemblages can alter numerous biogeochemical factors that influence rates of P deposition including pH, dissolved oxygen (Patrick and Khalid 1974), and redox. Results from sterile sediments were not necessarily comparable to those obtained with an active microbial community (de Montigny and Prairie 1993, Eckert et al. 1997). Phosphorus adsorption/desorption isotherms depend upon sediment type, calcium concentrations, and pH levels (Kadlec and Knight 1996, Rhue and Harris 1999). A diurnal lighting scheme with PAR levels representative of those found in the outdoor system could recreate diurnal fluctuations in pH, O₂, and redox caused by periphyton.

Periphyton substantially alter biogeochemical conditions at the surface of sediments. These influences will vary depending on the chemistry of the system of interest, with pH being of prime importance. Periphyton are probably most important in influencing P deposition by facilitating conditions conducive to carbonate deposition (i.e. high pH, high alkalinity habitats). The degree of periphyton cover, the activity of the mat, and conditions that influence photosynthetic rates of periphyton will all impact rates of long-term P deposition.

PHOSPHORUS DEPOSITION RATES FOR NATURAL AND CONSTRUCTED SYSTEMS

The best estimate for long-term performance for P removal of wetlands comes from P accretion rates in sediments measured over historical times in P-enriched areas. Several estimates are available; 1-3 mg P · m⁻² · d⁻¹ appears to be a rough estimate of the upper limit of long-term accretion rates (Craft and Richardson 1993, Richardson and Craft 1993, Kadlec 1994a, Moustafa et al. 1999, Richardson 1999), and this is consistent with P deposition rates of Lake Okeechobee sediments (Brezonik and Engstrom 1998), and other macrophyte-based wetlands (Mitsch et al. 1995). Thus, the maximum rates of deposition correspond roughly with the minimum rates reported for short term P uptake by periphyton (Table 1).

The process of deposition may be sensitive to temporal and spatial scale. For example, when artificial wetlands are established, initially there can be a large amount of P retention due to uptake associated with rapidly growing plants and algae (Richardson and Schweigler 1986). Alternatively, if wetlands are established on P-rich soils, they may release P. In one experiment, P flux from hydrated soils formerly used for dairy operations had initial equilibrium water column

concentrations of about 40 times that required for successful P removal, and after 3 to 4 hydration cycles still released substantial amounts of P (Pant and Reddy 2003). Thus, not all wetlands retain P as they age. Johnston (1991) reviewed 24 studies of wetlands and found that 9 served as nutrient sources. Kadlec (1994b) reviewed 19 studies of wetlands and found one that was a net source of P. Clearly, P retention is variable across wetlands; understanding why will be crucial to mitigating excessive P loading. Perhaps periphyton plays a key role in these differences among wetlands.

Since wetland geomorphology is generally driven more by depositional processes than rivers and streams, it is assumed that wetlands can accumulate P at substantially greater rates. However, P deposition rates in both habitats are variable. If periphyton growth is seasonal, retention over weeks or months may occur, but over the course of a year, sloughing may release all the retained P. In lotic systems particularly, deposition may occur for years, but a single very large flood may transport all the retained materials. Wetlands are generally less prone to such flushing with the exception of riparian wetlands.

CASE STUDY: THE EVERGLADES

Nutrient contamination from agricultural runoff could threaten this very large naturally oligotrophic native wetland (Lodge 1994). Nutrient addition encourages invasion by cattail (*Typha domingensis*) to the exclusion of the dominant native sawgrass, *Cladium jamaicense* (Davis 1994), and gradual loss of natural periphyton assemblages, altering basic nutrient cycling pathways and rates (McCormick et al. 2001). Periphyton in the Everglades takes up P from the water column, triples dissolved O₂ concentrations at the surface of the mat and pushes pH a full unit greater than values observed in the water column (Vaithyanathan and Richardson 1998). Periphyton dynamics appear to be intimately linked to P dynamics of the Everglades.

Efforts are underway to identify methods of treating agricultural runoff, and one method includes construction of periphyton-dominated wetlands to retain nutrients. Construction of these nutrient-removal systems requires knowledge of the natural processes that lead to P retention in the Everglades.

As discussed above, pH is a key factor in determining deposition rates related to the influences of periphyton. The pH of peat sediments and soils in the Everglades area is near 7 (Snyder 1994), so it is unclear if metal or calcium related precipitation dominates. Redox is low in the sediments (Qualls et al. 2001), so phosphate dissociation from metal phosphates will occur. Data suggest that in the peat soils in the Everglades, Fe/Al-bound and Ca-bound P are equally important (Scinto 1997), but Ca precipitation can dominate in some areas (Richardson and Vaithyanathan 1995). However, many areas of sediments are calcareous and calcareous deposits are associated

with formation of calcium/carbonate/phosphate complexes. The high pH caused by periphyton photosynthetic activity encourages carbonate deposition and associated Ca-bound P. These relationships between periphyton and calcareous deposition indicate the key role periphyton have in maintaining the naturally low levels of P found in the Everglades.

Initial research on adsorption/desorption has been conducted on low-nutrient peat sediments from the Everglades (Scinto 1997). Because a variety of soil types are present in South Florida (Harris and Hurt 1999), the type of sediments could vary between and within existing natural and treatment wetlands. Some data are available on adsorption/desorption processes from nearby Lake Okeechobee sediments (Pollman 1983, Olila et al. 1995, Olila and Reddy 1997, Brezonik and Pollman 1999). In general, muddy sediments from Lake Okeechobee had soluble P release rates 2-3 times greater than sandy sediments, and anoxic release rates were more than 5 times greater than sediments under an oxic water column (Moore et al. 1998).

The concentration of P in the water column of wetland areas upstream of the Everglades and P content of the periphyton were correlated, suggesting that periphyton is able to take dissolved P from the water column and incorporate it into biomass (Grimshaw et al. 1993). When areas within the Everglades with moderate density of macrophytes and substantial periphyton cover were contrasted with dense stands of cattails, there was about 10 times more total P in the water column in the areas with low amounts of periphyton. These types of observations, in part, led to the idea that areas with substantial periphyton growth could be set aside to remove P from the water. Pilot experiments have been implemented to assess the possibility of using periphyton-based storm water treatment areas (very large nutrient filtering wetlands) to lower nutrient loading to the Everglades.

Experimental cells were constructed to assess the effects of substrate, vegetation removal, and hydrology on the ability of periphyton-dominated wetlands to remove P (CH2M Hill 2000, 2001a, b, c). Some results from these treatment cells included: 1) sediments released P early in the process of wetland establishment on soils where agriculture previously occurred, 2) periphyton removed a substantial amount of P over a year-long cycle (long term average input was $25 \mu\text{g P} \cdot \text{L}^{-1}$ and output was $11 \mu\text{g P} \cdot \text{L}^{-1}$), 3) considerable effort (e.g. herbicide application or periodic drying) was necessary if macrophytes were removed and periphyton encouraged, and, 4) hydrology had strong effects on P removal (deposition rates of P in treatments with water levels that were varied were roughly half of those in treatments with static water depth).

It is estimated that construction and operation of periphyton-dominated wetlands to remove P would cost \$300-400 million U.S. to lower total P to $20 \mu\text{g} \cdot \text{L}^{-1}$ (CH2M Hill 2003). It is not certain if chemical treatment, periphyton-based wetlands, macrophyte-based

wetlands, or some combination of the above will be attempted. There is certainly a need for more long-term data on the ability of periphyton-based wetlands to remove P, and the role of periphyton in P removal in macrophyte-dominated wetlands.

SUMMARY

Those interested in P dynamics in shallow aquatic ecosystems, including P management, should consider the role of periphyton. While benthic algal assemblages can remove P from the water column and retain it in biomass, rates of P uptake are likely to exceed long-term retention (i.e. over months-years) unless the biomass is removed regularly. For this reason, maximal nutrient uptake rates of periphyton often exceed the long-term average rates of deposition in wetlands and streams. In systems where periphyton biomass is not removed, the deposition and burial of algal biomass may be responsible for some retention, but it appears that the role of periphyton in altering biogeochemical conditions at the sediment/water interface is at least as important.

When actively photosynthesizing, periphyton can influence water at the sediment/water column interface, causing super-saturation of dissolved oxygen and increasing the pH up to one unit compared to the water column above. High pH can increase the rates of calcium phosphate precipitation and co-precipitation with carbonates. Oxic conditions discourage dissolution of metal-phosphate complexes but anoxia induced by respiration in the dark may counteract this high dissolved oxygen effect. Furthermore, periphyton layers can attenuate flow and trap suspended particulate material, and thus decrease advective transport of P from the sediment surface.

A case study in a wetland illustrates the potential role of periphyton in P retention. In the Everglades, the system may be protected from some P pollution because of the natural ability of periphyton to encourage P deposition. This natural ability could be taken advantage of by constructing periphyton-dominated wetlands to help protect the native ecosystem from P-rich agricultural runoff. Pilot experiments demonstrated about half of the total P was removed from water flowing through experimental periphyton-dominated wetlands. Further research is necessary to test the degree of protection afforded by periphyton-dominated wetlands, and to conduct cost-benefit analyses of such treatment plans.

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