Freshwater Biology (2003) **48**, 1993–2008

Phosphorus cycling and partitioning in an oligotrophic Everglades wetland ecosystem: a radioisotope tracing study

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SUMMARY

1. Our goal was to quantify short-term phosphorus (P) partitioning and identify the ecosystem components important to P cycling in wetland ecosystems. To do this, we added P radiotracer to oligotrophic, P-limited Everglades marshes. $^{32}PO_4$ was added to the water column in six 1-m^2 enclosed mesocosms located in long-hydroperiod marshes of Shark River Slough, Everglades National Park. Ecosystem components were then repeatedly sampled over 18 days.

2. Water column particulates (>0.45 μm) incorporated radiotracer within the first minute after dosing and stored 95–99% of total water column ^{32}P activity throughout the study. Soluble (<0.45 μm) ^{32}P in the water column, in contrast, was always <5% of the ^{32}P in surface water. Periphyton, both floating and attached to emergent macrophytes, had the highest specific activity of ^{32}P (Bq g^{-1} ^{31}P) among the different ecosystem components. Fish and aquatic macroinvertebrates also had high affinity for P, whereas emergent macrophytes, soil and flocculent detrital organic matter (floc) had the lowest specific activities of radiotracer.

3. Within the calcareous, floating periphyton mats, 81% of the initial ^{32}P uptake was associated with Ca, but most of this ^{32}P entered and remained within the organic pool (Ca-associated = 14% of total) after 1 day. In the floc layer, ^{32}P rapidly entered the microbial pool and the labile fraction was negligible for most of the study.

4. Budgeting of the radiotracer indicated that ^{32}P moved from particulates in the water column to periphyton and floc and then to the floc and soil over the course of the 18 days incubations. Floc (35% of total) and soil (27%) dominated ^{32}P storage after 18 days, with floating periphyton (12%) and surface water (10%) holding smaller proportions of total ecosystem ^{32}P.

5. To summarise, oligotrophic Everglades marshes exhibited rapid uptake and retention of labile ^{32}P. Components dominated by microbes appear to control short-term P cycling in this oligotrophic ecosystem.

Keywords: Everglades, nutrient cycling, oligotrophic, phosphorus, wetland

Introduction

Nutrient enrichment strongly affects aquatic ecosystems (Schindler, 1974; Carpenter *et al.*, 1998; Downing *et al.*, 1999; Howarth *et al.*, 2000), including wetlands

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(Mitsch & Gosselink, 1993; Verhoeven, Koerselman & Meuleman, 1996). Anthropogenic additions of nitrogen and phosphorus (P) alter many aspects of the structure and function of these ecosystems, such that they are frequently identified as targets of restoration (National Research Council, 1992). Oligotrophic ecosystems, in particular, are more sensitive to nutrient enrichment than those that are more productive (Morris, 1991; Smith, 1998). Therefore, understanding nutrient cycling in oligotrophic ecosystems enables prediction, detection and amelioration of changes because of nutrient enrichment.

In the oligotrophic Florida Everglades, numerous studies have identified alterations in surface water, periphyton, soils, macrophytes and consumers following modest P enrichment (reviewed by Davis, 1994; Noe, Childers & Jones, 2001; McCormick *et al.*, 2002). Many of these focused studies have documented changes in total phosphorus (TP) concentration, biomass and species composition in particular biotic components (e.g. Koch & Reddy, 1992; McCormick & O'Dell, 1996; Miao & Sklar, 1998; Turner *et al.*, 1999; Childers *et al.*, 2003). Others have also shown alterations to biogeochemical processes in soil and detritus (e.g. Amador & Jones, 1993; Drake *et al.*, 1996; Miao & DeBusk, 1999; Reddy *et al.*, 1999; Qualls & Richardson, 2000). However, knowledge of whole-ecosystem cycling of P in the oligotrophic Everglades is limited. A holistic understanding of the system is critical for predicting the effects of future changes (increases or decreases) in P loading on the most pristine areas of the Everglades. This information would also benefit models of the impacts of nutrient enrichment on other oligotrophic wetland or shallow aquatic ecosystems. In addition, almost all Everglades studies have relied on gradients or experimental P additions (^{31}P) to document P cycling under natural, oligotrophic conditions. Yet water column concentrations of soluble reactive P are typically near the limit of colorimetric detection in the oligotrophic Everglades (*ca.* 0.01 μM; McCormick & Scinto, 1999).

Our goal in this study was to document the cycling rate of P without altering its ambient concentration. Unlike ^{31}P dosing experiments, carrier-free ^{32}P radiotracer additions provide a sensitive marker of activity while adding insubstantial amounts of P. For these reasons, we used ^{32}P to track the cycling and partitioning of P in oligotrophic Everglades wetlands. We dosed ^{32}P into field mesocosms and repeatedly quantified the ^{32}P activity and standing stock in most ecosystem components through time. These components included water, periphyton, flocculent detrital organic matter (floc), soil, macrophytes and aquatic consumers; we were unable to include organisms higher in the food web, such as large fish, alligators or wading birds. We hypothesised that ecosystem components with the highest turnover rates and greatest biotic activity would dominate P cycling in this short time scale (≤18 day). The periphyton and floc, sites of intense microbial activity (both autotrophic and heterotrophic), should accumulate P more rapidly than other system components. In addition, ^{32}P incorporated into detritus should be found in microbially bound forms. Finally, because oligotrophy is associated with efficient P uptake and retention mechanisms (Odum, 1985), we also hypothesised that labile ^{32}P would occur at very low concentrations throughout the study. In this paper, we test these hypotheses and report patterns of P cycling and partitioning in the different ecosystem components. We will provide more detailed, quantitative information on P fluxes in another paper.

Methods

Site description

We installed six 1-m^2 mesocosms in wet prairie marshes in central Shark River Slough (SRS), Everglades National Park (Latitude 25°38′, Longitude −80°44′), in close proximity to an experimental flume-based P dosing study (Childers *et al.*, 2002), site SRS-2 of the Florida Coastal Everglades Long-Term Ecological Research project and the 16 km site of the SRS transect from Childers *et al.* (2003). These sites were oligotrophic with a mean water column TP concentration of 6 μg L^{-1} and 40 cm-deep peat soils containing 215 μg P g^{-1} (0–10 cm; unpublished data). The hydrology of wet prairies in this subtropical climate is characterised by deeper, faster flowing water in the wet season (up to *ca.* 2.5 cm sec^{-1}) compared with shallower, non-flowing water in the dry season. These wet prairies are rarely completely dry, although water supply to Shark River Slough is substantially controlled by management of water control structures at the Tamiami Canal (Sklar *et al.*, 2002). Vegetation was dominated by the emergent macrophyte *Eleocharis cellulosa* Torr. and other

commonly present species included *Eleocharis elongata* Chapm., *Panicum hemitomon* Schult., *Paspalidium geminatum* (Forssk.) Stapf and *Sagittaria lancifolia* L. The submerged aquatic macrophytes *Utricularia purpurea* Walter and to a lesser extent *Utricularia foliosa* L., were also abundant. A floating, calcareous periphyton mat (metaphyton) associated with *U. purpurea* was the dominant form of periphyton, while smaller amounts of periphyton were also attached to macrophyte stems (epiphyton).

Experimental design

Watertight mesocosm chambers were built by forming an open-ended cylinder from 3.2-mm thick, clear Lexan plastic sheeting with bolted and silicone-sealed seams. The mesocosms were inserted approximately 20 cm into the soil by cutting the peat with a knife. Each of the six mesocosms was located in separate sloughs. Each mesocosm enclosed 1 m^2 of marsh surface, including surface soil, floc, surface water, emergent and submerged macrophytes, periphyton and aquatic micro- and mesoconsumers (consumers). Mesocosms were allowed to equilibrate for about 72 h prior to radiotracer addition.

Known activities of ^{32}P (as $H_3^{32}PO_4$ in 0.02 M HCl) were added to each mesocosm [mean = 18.4 MBq in 2 L of distilled, deionised H_2O ($DDIH_2O$)]. With the mean surface water volume of 582 L and mean total P concentration of 6.1 μg L^{-1} in the mesocosms (unpublished data), the expected initial activity of ^{32}P in the surface water of the mesocosms was 5744 Bq μg^{-1} ^{31}P, assuming complete mixing. The $^{32}PO_4$ solution was added evenly throughout the water column over a 2 min period via a perforated Tygon tube connected to a 2 L bottle. Radiotracer was added between 9 : 00 and 11 : 00 am at each site. Because of logistical constraints, dosing was initiated in two mesocosms per week. ^{32}P dosing began on 6 October and ended on 27 October 2000, towards the end of the wet season.

All ^{32}P activities were measured on a liquid scintillation counter (Beckman 3801) using Cherenkov counting (L'Annunziata, 1998) and were corrected for radioactive decay, component-specific quenching rates, Cherenkov counting efficiency and background radiation over the duration of the study. Negative counts after corrections were considered zero. We found the Cherenkov counting efficiency to be independent of sample volume. Finally, we also measured the ^{31}P content of each sample in order to calculate the specific activities of ^{32}P (Bq μg^{-1} ^{31}P) in ecosystem components. The concentration of ^{31}P was quantified after drying the sample (with the exception of water samples) and storing for 6 months to eliminate radioactivity. Total ^{31}P was measured in all samples using the ashing/acid hydrolysis method of Solorzano & Sharp (1980). The resulting soluble reactive phosphorus (SRP) was measured colorimetrically using an RFA-500 rapid flow analyser (ALPKEM Corporation, Wilsonville, OR, U.S.A.; EPA (365.1), 1983).

Sample collection and processing

Subsamples of each of the wetland ecosystem components were collected repeatedly over the 18 days following radiotracer addition. Live and dead macrophytes, periphyton and consumers were also removed at the end of the 18 day incubations to determine the mass of each component in each mesocosm. In addition, volumetric samples of soil, floc and water were collected at day 18. Soil cores were also collected in order to estimate root biomass.

Surface water was sampled immediately before and after dosing (*ca.* 1 min) and nominally at 5 min, 15 min, 30 min, 1 h, 1 day, 4 days, 10 days and 18 days after dosing. Water was collected from the middle of the water column in a 500 mL Nalgene bottle covered with an 88-μm Nitex screen. A subsample was transferred to a 120 mL bottle and returned to the laboratory, where 5 mL was transferred to a glass scintillation vial (vial) and analysed for ^{32}P. A 25 mL aliquot of the original sample was syringe filtered (0.45 μm membrane filter, Fisher Scientific, Pittsburgh, PA, U.S.A.) in the field to separate soluble and particulate fractions. Five millilitre of filtrate was collected in a vial and analysed for soluble ^{32}P. The filter was placed face upward into a vial, 2 mL $DDI\text{-}H_2O$ was added to cover the filter and the filters were then analysed for particulate ^{32}P. Surface water depth was also measured at three locations in each mesocosm on each sampling day.

Metaphyton (a matrix of algae, heterotrophs, detritus, $CaCO_3$, associated *U. purpurea* and microconsumers) was sampled at 1 h, 1 day, 4 days, 10 days and 18 days. We collected metaphyton by placing a small cutting board under the floating mat and removing cores with a 20.5 mm inner diameter (ID) corer. Five

cores were collected at each sampling and combined into one sample, stored on ice and transported in the dark to the laboratory. The sample was then weighed, homogenised and subdivided for analyses. A known mass (*ca.* 0.5 g) was homogenised in 10 mL DDI-H_2O in a vial and analysed for ^{32}P. At the end of the 18 day incubation, all the remaining metaphyton was collected and weighed.

Phosphorus uptake and availability can be associated with $CaCO_3$; this may be particularly important in calcareous periphyton. We quantified the amount of metaphyton ^{32}P that was associated with Ca by extraction with HCl. A subsample (*ca.* 1 g) of each metaphyton sample was placed in 10 mL of 0.1 M HCl and occasionally stirred for 2 h; the pH of the extractant was 2.0–3.0. The metaphyton/HCl solution was then vacuum filtered (Whatman glass-fibre filter (GF/F) followed by 0.45 μm membrane filter; Whatman International, Maidstone, U.K.) and 5 mL of the filtrate was analysed for acid-extractable P (Ca-associated ^{32}P) in a vial. ^{32}P associated with the biotic fraction of metaphyton was calculated as the difference between total and Ca-associated activity.

One live and one dead stem of the dominant macrophyte at each site were cut at the soil surface and collected with their associated epiphyton, when present. Samples were collected at 1 h, 1 day, 4 days, 10 days and 18 days, placed into separate sample bags and returned to the laboratory on ice. Stems and leaves were then gently scraped with a scalpel to remove epiphyton and weighed. Each macrophyte sample was wiped clean, subsampled, weighed, homogenised with 10 mL DDI-H_2O in a vial and analysed for ^{32}P. Epiphyton from both live and dead stems was each weighed, added to a vial with 5 mL of DDI-H_2O, homogenised and analysed for ^{32}P. The epiphyton did not appear to be calcareous, so we did not perform HCl extractions.

All aboveground macrophyte biomass was harvested from each mesocosm at the end of the incubation. Live stems of *E. cellulosa* and other species were cleaned of epiphyton and weighed. All dead stems of *E. cellulosa* and their associated epiphyton were also collected and weighed together. The total mass of epiphyton on live stems in each mesocosm was estimated as the product of the mass of the live stems of *E. cellulosa* at 18 day and the average mass of epiphyton per mass of live stem during the incubations. The final mass of epiphyton on dead stems of *E. cellulosa* was calculated from the total mass of dead macrophytes and associated epiphyton and corrected for the average amount of epiphyton mass per mass of dead stem during the incubations. Additionally, all *U. purpurea* and *U. foliosa* plants were removed at the end of incubation, separated by species, weighed and analysed for ^{32}P. *Utricularia purpurea* often serves as the substratum for the formation of metaphyton. We operationally defined *U. purpurea* as sections of plant that were not encrusted with calcified periphyton. This restricted our sampling to plants that were in the middle of the water column but that probably still harboured a microbial community.

Floc was collected at 1 h, 1 day, 4 days, 10 days and 18 days. We sampled floc by inserting a 23.6-mm ID corer through the water column and floc layer into the soil surface and then removing the intact core and recovering the floc (see Noe *et al.*, 2002, for details). This procedure was repeated for two additional cores and all three floc samples were combined into one composite sample per mesocosm. Samples were placed on ice in the dark and returned to the laboratory. The floc sample was then weighed, hand homogenised and subdivided for analysis. A 5 mL subsample was weighed, added to a vial and analysed for ^{32}P. An additional subsample was vacuum filtered (0.45 μm) and 5 mL of the filtrate was added to a vial and analysed for floc interstitial water ^{32}P.

All floc samples that had sufficiently large ^{32}P activities (>5.0 Bq) were extracted and analysed for microbial and labile ^{32}P by slight modification of the methods of Hedley & Stewart (1982). A floc subsample of known mass (*ca.* 2 g) was transferred to a vial and 0.5 mL of chloroform was added to lyse microbial cells. This vial was vortexed for 30 s and left to incubate overnight at room temperature. The vial cap was then removed and the $CHCl_3$ was allowed to evaporate in a hood for 8 h. A similar sample did not have $CHCl_3$ added (non-fumigated samples). Both sets of vials received 10 mL of 0.5 M $NaHCO_3$ to extract inorganic phosphorus, were laid horizontally on a slow speed shaker for 16 h and then were vacuum filtered (GF/F followed by 0.45 μm membrane filter). A 5 mL portion of the filtrate was added to a vial and analysed for either labile ^{32}P (non-fumigated sample) or labile and microbial ^{32}P (fumigated sample). This extraction technique recovers only approximately 40% of total microbial biomass P (Hedley & Stewart, 1982;

Walbridge, 1991). Given this uncertainty, we report raw (uncorrected) concentrations from the extractions and do not report microbial partitioning as a percentage of total activity.

Vertical profiles of total, labile and microbial-based ^{32}P activity in the floc were characterised at the end of the incubations (day 18). Three intact cores of floc were collected from each mesocosm, returned to the laboratory, sectioned into depth increments of 0–1, 1–2, 2–5, 5–10 and 10+ cm by pipetting from the surface downward and combined into one sample per depth increment. These samples of the floc depth profile were treated identically to the other floc samples.

Soil was collected at 1 day, 10 days and 18 days. In order to minimise soil disturbance during the study, small diameter cores (23.6 mm ID) were taken at 1, 10 and 18 days for soil analysis in a manner similar to the floc coring method. Cores were carefully inserted into the soil to a depth of 20 cm, but compaction was typically *ca.* 50%. The intact soil cores (two per mesocosm per sampling) were collected, sectioned in the field into 0–1, 1–2, 2–5, 5–10 and 10+ cm depth increments (when present), and composited by depth increment for each mesocosm. We then returned samples to the laboratory on ice, hand homogenised each sample, removed roots and snail shells, and weighed and subdivided each sample for analysis. A 0.5–1.0 g sample was mixed with 10 mL DDI-H_2O in a vial, homogenised and then analysed for ^{32}P. Three large diameter cores (57 mm ID) were collected at 18 day, combined into one sample per mesocosm, and roots were removed in the laboratory by visual inspection, hand collection and wet sieving through a U.S.A. Standard Testing Sieve No. 10 (2 mm). Roots were weighed, added to 10 mL DDI-H_20 in a vial, homogenised and analysed for ^{32}P.

Soil interstitial water was collected at 1 h, 1 day, 4 days, 10 days and 18 days via porewater samplers. The filter (nominal porosity = 60 μm; Porex 6810, Porex Corporation, Fairburn, GA, U.S.A.) attached to each sampler was inserted 10 cm deep into the soil. Five samplers were installed 72 h prior to dosing in each mesocosm. A composite water sample was made from three samples taken from three arbitrarily chosen samplers at each sampling. A large syringe (140 mL) was connected to the sampler, suction was applied, the first few mL were purged, and then approximately 15 mL of soil solution was withdrawn. Each sample was then filtered through a syringe filter (Whatman GF/F) into a 30 mL polyethylene sample bottle (rinsed three times). Samples were stored in ice until returned to the laboratory, and then a 5 mL aliquot was transferred to a vial and analysed for ^{32}P.

Gambusia holbrooki Girard (eastern mosquitofish) is a dominant aquatic consumer in the Everglades (Turner *et al.*, 1999). One *G. holbrooki* individual was collected from each mesocosm (mean density = 5.8 individuals m^{-2}) at 1, 10 and 18 days. Exceptions included one mesocosm where *G. holbrooki* were not observed at 1 and 10 d. After vegetation was removed at the end of the incubations, the mesocosms were allowed to settle for approximately 1 h. Three people then simultaneously collected aquatic consumers with dip nets (each with 130 cm^2 openings) for a total of 15 min (very few consumers were being collected at that time). All vertebrates were sacrificed with tricane methlysulphionate (MS-222). The invertebrates were stored on ice in the field and later frozen in the laboratory. All consumer groups were identified, sorted, blotted dry, weighed, added to 10 mL DDI-H_2O in a vial, homogenised and analysed for ^{32}P.

Early in the study it became apparent that the consumers were accumulating high activities of ^{32}P. We conducted a study of P uptake mechanisms to test if fish were obtaining ^{32}P through consumption or simply by being in a dosed mesocosm (e.g. gill uptake). *Gambusia holbrooki* were collected near the mesocosms and returned to the laboratory. Nine fish were placed in separate beakers each with 100 mL DDI-H_2O. Six of these beakers were each spiked with 3.14 kBq$^{32}PO_4$, and three beakers served as controls. Fish were then sacrificed using MS-222 after 24 h, removed from the beakers, blotted dry, homogenised and analysed for ^{32}P.

Integration

The concentration (specific activity; Bq μg^{-1} ^{31}P), content (Bq m^{-2}) and partitioning (percentage of total recovered Bq m^{-2}) of ^{32}P in each ecosystem component at each time interval was quantified. The ^{32}P content of solid samples was calculated from estimates of mass (g m^{-2}) and measured activity, whereas volume was used to determine content in the water column. Estimates of the total amount of ^{32}P recovered in each mesocosm were made by summing the ^{32}P content of all sampled ecosystem components.

Results

Immediately after the study began, the South Florida Water Management District stopped the flow of water into SRS by closing water control gates on the Tamiami Canal. From the day of dosing until day 18, mean water level decreased from 58 to 51 cm as a result of this action. However, water depth was consistent among replicate mesocosms.

^{32}P cycling

The specific activity (Bq μg^{-1} ^{31}P) of ^{32}P in surface water decreased through time, with large reductions occurring between 60 min to 10 days after dosing (Fig. 1). In the first hour after dosing and in the final 8 day of the incubations, however, ^{32}P activity in the water changed little. Immediately after dosing (*ca.* 1 min), the particulate fraction (>0.45 μm) comprised 95% of total water column ^{32}P activity (Fig. 1). This particulate fraction in the water column increased to more than 99% of total at 1 day after dosing, but then decreased again to 95% at day 18. The soluble fraction (<0.45 μm) of total ^{32}P activity exhibited the inverse trend, by definition, decreasing from 5 to <1% of total activity at 1 day and then increasing to 5% of total water-column activity at 18 day.

The calcareous metaphyton quickly incorporated ^{32}P, showing activity when first sampled at 60 min (Fig. 2). Mean ^{32}P activity then increased roughly 50% from 60 min to 10 day and decreased slightly by the end of the incubations at day 18. However, variation in metaphyton ^{32}P activity among mesocosms was high and the decrease in mean activity at day 18 was within the range of this variation. The proportion of ^{32}P in metaphyton that was associated with Ca quickly decreased through time. This inorganic fraction, extracted with HCl, was 80.8% of total activity at 60 min and then decreased to a stable, low proportion of total activity (mean ± 1 SE: 13.7 ± 1.4%) from day 1 through day 18.

Periphyton growing on emergent macrophyte stems (epiphyton) had similar ^{32}P activity as metaphyton at 60 min and 1 day after dosing (Fig. 2). Epiphyton ^{32}P activity then increased greatly from 4 to 10 days and decreased at 18 days. Of the two types

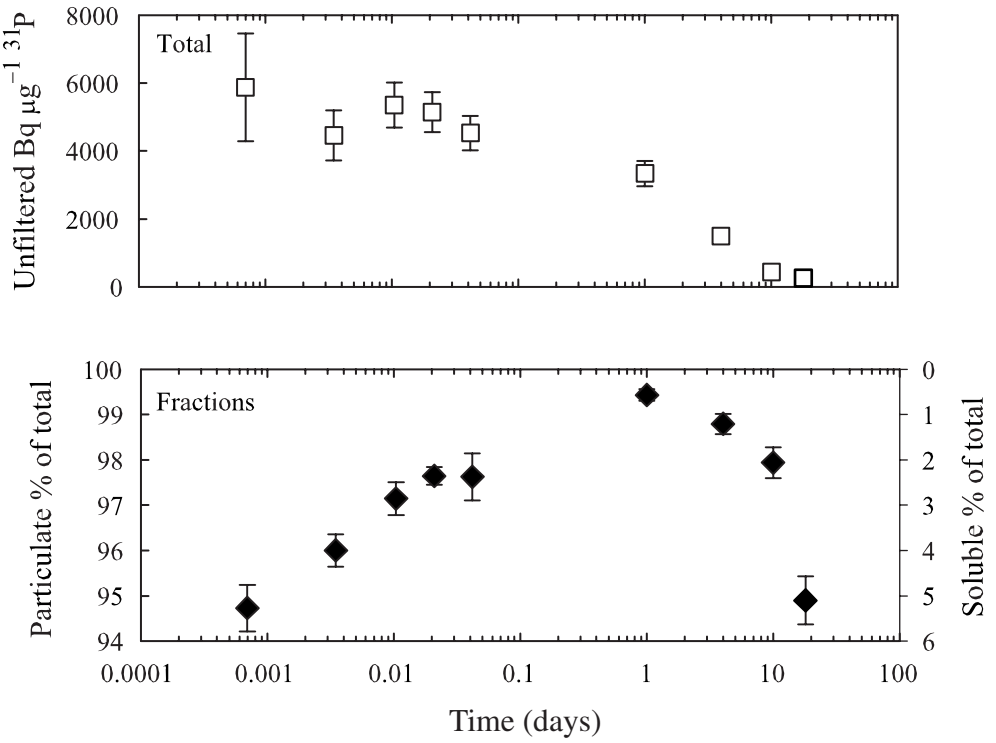

Fig. 1 Specific activity of ^{32}P in unfiltered surface water (total) and partitioning of total surface water activity into the particulate and soluble fractions (fractions) (mean ± 1 SE) through time.

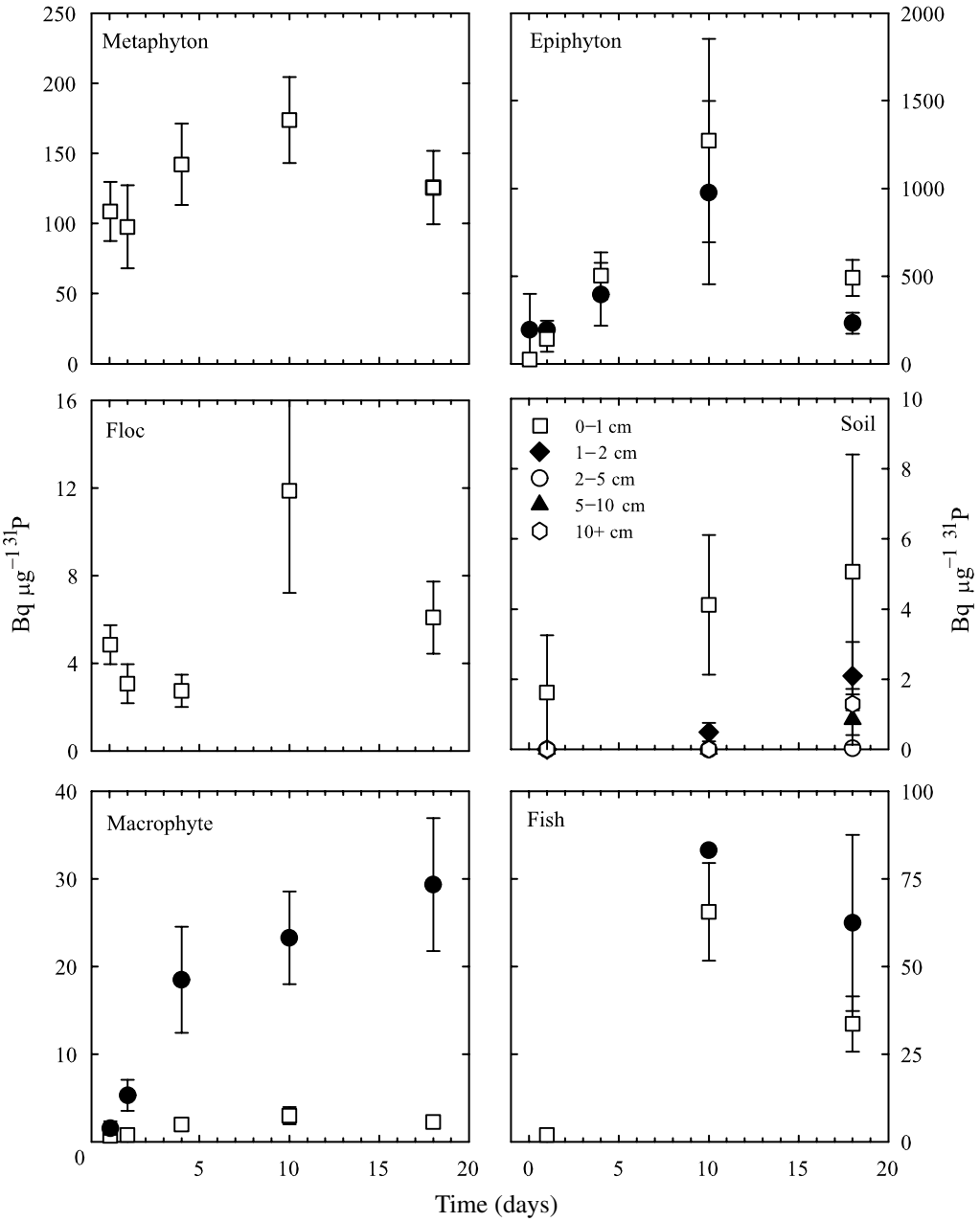

Fig. 2 Specific activity of ^{32}P (mean ± 1 SE) through time in wetland ecosystem components: metaphyton, epiphyton (on live stems = open squares, on dead stems = closed circles), floc, soil, macrophytes (live stems = open squares, dead stems = closed circles) and fish (*Gambusia holbrooki* = open squares, *Heterandria formosa* = closed circles).

of epiphyton, that growing on live stems had greater ^{32}P activity towards the end of the study than epiphyton on dead stems. However, epiphyton on live stems weighed less than that on standing dead stems (mean ± SE: live stem = 7.0 ± 4.3 g stem^{-1}, dead stem = 26.8 ± 7.2 g stem^{-1}). While epiphyton growing on live stems had less mass, it had twice the ^{31}P content as epiphyton on dead stems (mean ± SE: live stem = 346.1 ± 65.7 µg g^{-1}, dead stem = 187.1 ± 33.6 µg g^{-1}).

Patterns of ^{32}P cycling in floc were erratic and variable through time (Fig. 2). The ^{32}P activity in floc decreased slightly from 60 min to 1 day, did not change up to 4 days, increased greatly and peaked at

Table 1 Total, labile and microbial ^{32}P specific activity (Bq μg^{-1} ^{31}P; mean ± 1 SE) in different floc depth increments at the end of the incubations, 18 days. Low total ^{32}P activity in the lower depth increments precluded measurement of labile and microbial ^{32}P

Floc depth increment (cm)	Total		Labile		Microbial	
	Mean	SE	Mean	SE	Mean	SE
0–1	35.4	9.1	5.8	1.5	7.1	9.8
1–2	13.8	3.0	4.3	1.1	8.7	2.5
2–5	5.0	0.8	3.5	1.7	7.0	2.8
5–10	1.7	0.3				
10+	0.6	0.1				

10 days and finally decreased somewhat at the end of the incubations. The floc layer showed vertically stratified ^{32}P activity at day 18 (Table 1). The 0–1 cm depth increment (exposed to water column) had much higher ^{32}P activity than the 1–2 cm increment; both surficial increments had greater activity than lower depths or the whole-profile samples collected at that time. However, the bottom of the floc layer had acquired ^{32}P by the end of the incubations. Finally, floc interstitial water had low and relatively constant ^{32}P concentrations (1.21–2.06 Bq μg^{-1} ^{31}P).

The microbes in the floc quickly acquired and retained ^{32}P. Floc microbial ^{32}P activity was often much greater than floc labile ^{32}P activity, beginning at the first sampling at 60 min (Fig. 3). However, by day 18 the P in the labile fraction became increasingly labeled with ^{32}P. The temporal pattern of both microbial and labile fractions was similar to the temporal pattern of floc total ^{32}P activity, indicating little net cycling among fractions. In addition,

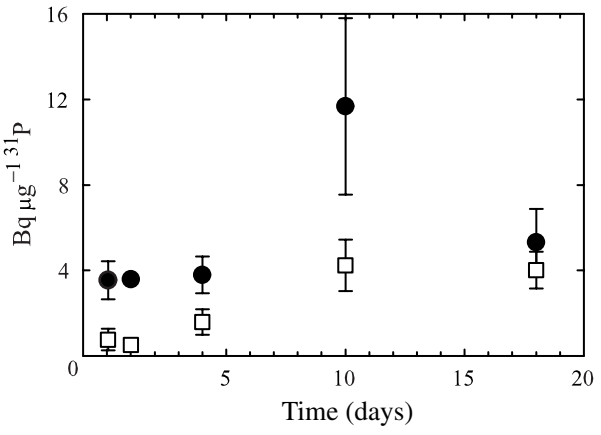

Fig. 3 Activity of labile ^{32}P (open squares) and microbial ^{32}P (closed circles) in the floc layer (mean ± 1 SE) through time.

microbial ^{32}P activity slightly exceeded labile activity throughout the vertical profile of the floc layer at day 18 (Table 1). Finally, labile and microbial activity was a much smaller proportion of total ^{32}P in the surface centimetre of floc than other depth increments at 18 day, suggesting greater importance of refractory ^{32}P. One possible mechanism for this pattern is the sedimentation of refractory ^{32}P from periphyton in the water column onto the surface of the floc layer.

Low but measurable ^{32}P activity was found in surficial soils (0–1 cm) when they were first sampled at day 1 and activity increased gradually through time (Fig. 2). Radiotracer moved downward in the soil profile by day 18. In general, variability in soil ^{32}P activity between mesocosms was high. The ^{32}P activity in soil interstitial water was also low and increased through time (0.01–0.30 Bq μg^{-1} ^{31}P).

The ^{32}P activity in the live aboveground stems of the dominant emergent macrophyte, *E. cellulosa*, increased slowly through time (Fig. 2). The activity of ^{32}P in standing dead shoots of *E. cellulosa* also increased, but greatly exceeded the activity of live shoots. At the end of the incubations, the aquatic macrophytes *U. purpurea* and *U. foliosa* (both with associated microbes) had greater ^{32}P activity than the live stems of the emergent macrophytes *E. cellulosa*, *E. elongata*, *P. hemitomon*, *P. geminatum* and *S. lancifolia* (all without associated epiphytic microbes; Table 2). Aboveground shoots of the emergent macrophyte species had similar ^{32}P activity, but the rhizomes of *E. elongata* had higher activity.

Adventitious roots of *P. hemitomon*, growing into the water column, were collected from stems harvested at the end of the incubation. These adventitious roots had ^{32}P activity of 23.9 kBq g^{-1} (sample mass was insufficient for ^{31}P analysis), which was one to two orders of magnitude higher than in the live stems and leaves of the same *P. hemitomon* culm (when expressed on a mass basis). Belowground roots also had lower ^{32}P activity per unit mass than adventitious roots, but had specific activities similar to the surrounding soil (Fig. 2; Table 2).

In the laboratory experiment, none of the *G. holbrooki* placed in $^{32}PO_4$-dosed water incorporated ^{32}P after 24 h. In the field, *G. holbrooki* showed ^{32}P activity after the first sampling (day 1; Fig. 2). The ^{32}P activity in *G. holbrooki* increased dramatically by day 10 and then decreased nearly 50% at the end of the incubations. *Heterandria formosa* Agassiz (least

Table 2 ^{32}P specific activity (Bq μg^{-1} ^{31}P; mean ± 1 SE) in different ecosystem components at the end of the incubations, 18 days. The number of sites (*n*) where each component was found is listed

	Mean	SE	*n*
Consumers			
Fish			
Fundulus chrysotus Gunther	116.5	59.0	5
Gambusia holbrooki	33.6	7.9	6
Heterandria formosa	62.5	25.1	6
Lucania goodei Jordan	69.7	17.7	6
Poecilia latipinna Lesueur	50.4	19.2	2
Invertebrates			
Anisoptera	37.6	1.9	4
Belostoma sp. (Heteroptera)	85.5	28.8	2
Hyalella azteca Saussure (Amphipoda)	54.0	3.4	4
Palaemonetes paludosus Gibbs (Decapoda)	85.4	27.5	6
Pelocoris femoratus Palisot-Beauvois (Heteroptera)	42.7	25.2	3
Pomacea paludosa Say (Gastropoda)	366.6	—	1
Procambarus sp. (Decapoda)	242.6	194.2	2
Zygoptera	123.8	108.2	2
Macrophytes			
Emergent			
Eleocharis cellulosa	2.3	0.5	6
Eleocharis elongata	3.5	1.6	4
Eleocharis elongata rhizome	23.0	13.4	2
Panicum hemitomon	4.0	0.3	3
Paspalidium geminatum	8.0	1.6	3
Sagittaria lancifolia	4.9	2.1	2
Sagittaria lancifolia rhizome	0.8	—	1
Roots (belowground)	3.0	0.9	6
Aquatic			
Utricularia foliosa	86.7	7.7	3
Utricularia purpurea	103.9	22.0	6

killifish) ^{32}P activity also declined from day 10 to 18. The activity of ^{32}P ranged widely among the fish and macroinvertebrate taxa collected at the end of the incubations (Table 2).

Partitioning

Partitioning (the proportion of the total amount of recovered ^{32}P in the mesocosms that was stored in each of the routinely sampled ecosystem components) changed through time. Nearly all of the ^{32}P remained in the surface water 60 min after dosing (Fig. 4). The percentage of ^{32}P in the water column decreased throughout the study with greatest reductions between 1 and 4 days. Metaphyton accumulation of ^{32}P increased from 1 to 4 days and then stabilised until the end of the study. Storage of ^{32}P in floc generally increased steadily through time. The ^{32}P content in soils also gradually increased throughout the incubations, but more slowly than in the floc. With the exception of a large peak of ^{32}P storage in the epiphyton on dead macrophyte stems at day 10 (which was because of an extremely high measurement in one mesocosm), all of the other components changed only slightly during the incubations. To summarise, the location of large ^{32}P pools moved from the water column, to periphyton and floc, and then finally to floc and soils.

We recovered 64% of the added radiotracer at the end of the incubations. The fate of the unaccounted radiotracer is unknown, although it is possible that a biofilm on the inner walls of the plastic mesocosms could have sequestered radiotracer or that ^{32}P could have leaked from the seams in the mesocosms. When the mesocosms were harvested at day 18, the relative rank of ^{32}P storage by the different components differed from the relative rank of ^{32}P specific activities because of differences in component biomass or volume and ^{31}P content. At the end of the incubations: (i) floc stored the most ^{32}P, followed by (ii) soil, (iii) metaphyton, (iv) water and (v) *U. purpurea* (Table 3). Other ecosystem components each held <5% of the

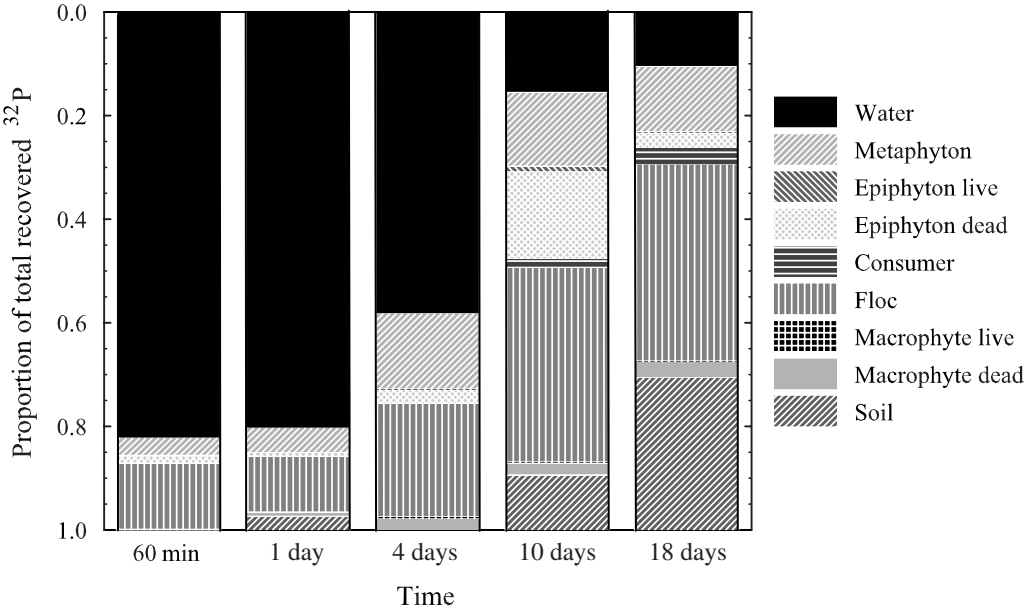

Fig. 4 Mean proportion of total recovered ^{32}P per mesocosm found in different ecosystem components over time.

Table 3 Percentage of total recovered ^{32}P present in each ecosystem component (mean ± 1 SE) at the end of the 18-days incubation

Component	Mean	SE
Floc	34.7	5.7
Soil	26.7	8.5
Metaphyton	11.6	2.7
Water	9.7	1.7
Utricularia purpurea	5.2	0.8
Consumer	3.1	1.2
Emergent macrophyte (dead)	2.7	0.5
Epiphyton (on dead stems)	2.6	0.5
Utricularia foliosa	1.4	1.0
Roots	1.3	0.6
Emergent macrophyte (live)	0.8	0.2
Epiphyton (on live stems)	0.3	0.1

radiotracer. In contrast, the rank (in decreasing order) of mean ^{32}P specific activities after day 18 was (i) epiphyton on live stems, (ii) water, (iii) epiphyton on dead stems, (iv) metaphyton, (v) consumers (mean of all species), (vi) dead macrophytes, (vii) floc, (viii) soil and (ix) live emergent macrophytes.

Discussion

In general microorganisms dominate short-term P cycling in aquatic and wetland ecosystems, but not necessarily short-term P storage or long-term cycling. Others have also found that heterotrophic bacteria and fungi, algae, and small sediments and particulates (and associated microbes) control short-term cycling through their fast rates of phosphate uptake in freshwater wetlands (Barsdate, Prentki & Fenchel, 1974; Howard-Williams, 1985; Richardson & Marshall, 1986; Wetzel, 1990) and estuaries (Correll, Faust & Severn, 1975). Although uptake rates are fast, microbes are thought to store only a small proportion of total wetland ecosystem P standing stocks (Richardson, 1999). For example, bacterioplankton had higher uptake rates but stored much less P than other ecosystem components in the littoral zone of Lake Okeechobee (Hwang, Havens & Steinman, 1998). In addition, soil adsorption regulates wetland P cycling in the long-term (Richardson, 1985).

Our results suggest that microbial components dominate short-term P cycling in oligotrophic Everglades freshwater wetland ecosystems. Small particles (0.45–88 μm) in the water column captured radioactively labeled, carrier-free orthophosphate in the first 5 min following radiotracer addition (Fig. 1). The ^{32}P in these particles, which were probably strongly microbial, then cycled into the microbe-rich periphyton and floc within 10 days (Fig. 4). The mechanisms for this transfer probably include a combination of particle settling and filtration, and particle mineralisation followed by uptake by floc and periphyton. By

day 18, large amounts of ^{32}P began to enter the soil (Table 3; Fig. 4). Parts of the ecosystem that were likely to have a large microbial pool (water-column particulates, periphyton, macrophyte detritus, floc and soil) stored 85% of the radiotracer in oligotrophic wet prairie marshes by the end of the 18 day incubations.

Soluble ^{32}P activity decreased quickly to <5% of total water column activity within 5 min after dosing in Everglades marshes (Fig. 1). Similarly, Jones (2001) found short $^{32}PO_4^{3-}$ turnover times (7.5 min) in Everglades water samples. McCormick *et al.* (2001) added large amounts of $NaH_2^{31}PO_4$ to mesocosms in an unenriched Everglades slough and also found that 100% of SRP was removed from the water column and that *ca.* 25% of the added P remained as TP in the water column. Thus, water column particulates appear to be an important regulator of short-term Everglades wetland P cycling. Other researchers have found that water column P cycling is strongly regulated by fungi and yeast in temperate wetlands (Richardson & Marshall, 1986), by bacteria in estuaries (Correll *et al.*, 1975), and by bacterivorous picoplankton in oligotrophic lakes (Lyche *et al.*, 1996). In Everglades wet prairies, water column particles appear to be fine, particulate detrital organic matter (personal observation); phytoplankton is not abundant (E. Gaiser, FIU, personal communication). However, very little is known about the content and function of this particulate fraction. The identity, fate and transport of water-column particulates in the Everglades need further attention.

Periphyton, both floating (metaphyton) and attached to emergent macrophytes (epiphyton), had the highest affinity (specific activity) for P among the ecosystem components (Fig. 2; Table 2). Periphyton also accumulated a significant proportion of the recovered ^{32}P relative to other ecosystem components (Fig. 4; Table 3). Periphyton greatly influences nutrient cycling and storage in wetlands of the Everglades (this study; McCormick & Scinto, 1999; Pan *et al.*, 2000; McCormick *et al.*, 2001), the littoral zone of Lake Okeechobee in south Florida (Havens *et al.*, 1999), and other parts of the world (Howard-Williams & Allanson, 1981; Wetzel, 1990; Rejmánková & Komárková, 2000).

The specific activity of ^{32}P (Bq μg^{-1} ^{31}P) decreased in periphyton types with greater biomass. Epiphyton growing on live macrophyte stems incorporated the greatest concentration of radiotracer relative to its internal ^{31}P pool, but had the lowest mass among the periphyton components. Conversely, metaphyton had the largest mass but lowest ^{32}P activity. Epiphyton on dead macrophyte stems had intermediate mass and ^{32}P activity. Presumably, the smaller mass of epiphyton on live stems than dead stems was because of the age of the substratum. The negative relationship between periphyton mass and radiotracer activity suggests that the thickness of periphyton mats limits P uptake; smaller periphyton mats have a larger proportion of their cells exposed to a source of P in the water column than larger periphyton mats (which have a smaller surface area to volume ratio). Similarly, Riber & Wetzel (1987) found that diffusion across the boundary layer of periphyton mats limits P uptake and that mat thickness influences the relative importance of internal vs. external sources of P. Finally, the low activity of ^{32}P in the emergent macrophytes and the relatively high activity of epiphytes on these stems suggest that macrophytes are probably not a significant source of P to these epiphytes in the short term (but see Burkholder & Wetzel, 1990).

Four-fifths of the initial (60 min) ^{32}P uptake by the floating, calcareous metaphyton was associated with Ca. Photosynthetic activity in periphyton mats decreases pCO_2, stimulating the precipitation of $CaCO_3$ in waters with high Ca concentration (such as the Everglades; Gleason & Spackman, 1974). Phosphate may precipitate as Ca-P compounds, co-precipitate with $CaCO_3$, or adsorb to a $CaCO_3$ matrix (Otsuki & Wetzel, 1972; House, 1990; Diaz, Reddy & Moore, 1994). Following the initial Ca-associated uptake of ^{32}P (81% of total uptake), the abiotic fraction of P in metaphyton decreased to about 15% of total activity after 1 day, then remained at this level for the duration of the incubations. Scinto (1997) also found that ^{32}P cycled from abiotic to biotic fractions in benthic periphyton mats from the northern Everglades, where the abiotic component decreased from 20 to 8% of total from 1 to 12 h. Thus, calcareous periphyton mats appear initially to sequester a large amount of P in association with Ca, and this P is eventually incorporated into organic matter within the periphyton mat. Night-time respiration and release of CO_2, and the potential decrease in pH leading to dissolution of $CaCO_3$ (Gleason & Spackman,

1974), may release P internally for biotic uptake within the periphyton mat.

Floc (which is thought to originate from senescing periphyton and macrophytes) stored 38% of total ecosystem ^{32}P 18 day after dosing in this study. Other studies confirm the importance of floc to Everglades P biogeochemistry. The floc ^{31}P pool increased from 20 to 35% of total ecosystem storage following 6 months of dosing 30 μg L^{-1} orthophosphate above ambient TP (*ca.* 10 μg L^{-1}) in oligotrophic wet prairies of the Everglades (Noe *et al.*, 2002). The floc layer in the northern Everglades is also responsive to P enrichment and important to P cycling and storage (Reddy *et al.*, 1999; Newman *et al.*, 2001). Thus, detrital organic matter appears to be a strong regulator of P cycling in Everglades wetlands.

We found that aquatic consumers also exhibited a high affinity for P. Our laboratory experiment demonstrated that fish did not obtain P through incorporation of orthophosphate, indicating that their body activity load was a result of consumption of organic ^{32}P in our mesocosms. ^{32}P activity peaked at day 10 and then decreased at day 18 in both *G. holbrooki* and *H. formosa* individuals (Fig. 2), suggesting high turnover rates or low incorporation efficiency of P by fish. Many ecosystem components had incorporated ^{32}P prior to or concurrent with the appearance of ^{32}P in consumers, and thus we were unable to resolve the food source of consumers. Not surprisingly, radiotracer levels were variable among the fish and invertebrate species present in the mesocosms (Table 2). However, most fish and macroinvertebrates had ^{32}P activities an order of magnitude higher than floc, macrophytes or soil, indicating the ability of consumers to rapidly sequester and process P.

Despite the high affinity of consumers for P, the Everglades is characterised by extremely low fish and aquatic invertebrate biomass (Turner *et al.*, 1999) that stores relatively little ^{31}P compared with other ecosystem components (except water, Noe *et al.*, 2002). Aquatic consumers held only 3.1% of total ecosystem ^{32}P after 18 days. However, in addition to the direct uptake and release of P (Schaus *et al.*, 1997), consumers can indirectly influence wetland and lake P cycling (Everest & Davis, 1979; Schindler *et al.*, 1993; Elser & Urabe, 1999; Carpenter *et al.*, 2001). Therefore, it is possible that aquatic consumers in the Everglades have a disproportionately greater effect on P cycling relative to their biomass or P storage. Possible mechanisms for this include physical disturbance of periphyton mats, mineralisation of organic P and excretion of inorganic P, and translocation of P in the ecosystem and landscape.

Macrophytes respond relatively slowly to increases in P availability in wetlands (Howard-Williams, 1985; Richardson & Marshall, 1986) and in the Everglades in particular (Daoust, 1998; McCormick & Scinto, 1999; Chiang *et al.*, 2000). This is supported by the relatively little ^{32}P activity and storage found in live aboveground macrophyte tissues and belowground roots in this study (Table 3; Fig. 2). However, adventitious roots of *P. hemitomon* appeared to be sites of rapid P uptake compared with belowground roots, as has been observed for macrophytes in other wetlands (Howard-Williams, 1985). Aquatic macrophytes had greater ^{32}P uptake than emergent species, but this was confounded by the microbial biomass that could not be removed from the aquatic macrophytes before measurement. We suggest that future studies of wetland plant responses to added nutrients focus on adventitious roots as a locus of nutrient uptake.

Davis (1982) conducted a similar *in situ* ^{32}P partitioning study in unenriched habitats of both *Cladium jamaicense* Crantz and *Typha* spp. communities of the northern Everglades (Water Conservation Area 2A). Davis (1982) sampled once, 10 days after radiotracer addition; to compare the two studies we refer only to our day 10 sampling. We found a much greater proportion of ^{32}P in the water column and periphyton, and a smaller amount in the soil and macrophyte detritus, at our oligotrophic wet prairie sites compared with the unenriched *Cladium* and *Typha* sites studied by Davis (1982). Although our study occurred in a different month (October) than Davis (1982) (June and July), both radiotracer additions occurred during periods of high water levels at the two locations. It is unlikely that lower temperatures during our study would increase the importance of water column relative to benthic nutrient cycling compared with a ^{32}P addition in summer. Thus, we hypothesise that the increased importance of water-column components to P cycling in wet prairies relative to *Cladium* and *Typha* marshes might be because of the deeper, faster water and greater abundance of floating periphyton in oligotrophic wet prairies. This comparison of P uptake

among different Everglades marsh types suggests that wet prairie marshes are more likely to export P downstream because of the location of P uptake in the water column and greater water velocity.

The oligotrophic wet prairie marshes of the Everglades exhibited a pattern of ecosystem P cycling qualitatively similar to other freshwater wetlands. Our Everglades wetland sites were similar to both a Michigan fen (Richardson & Marshall, 1986) and a littoral marsh of Lake Okeechobee, FL, U.S.A. (Hwang *et al*., 1998), in that water-column particulates dominated very short-term P cycling. However, SRP uptake from the water column of oligotrophic Everglades wetlands was faster than in a mesotrophic, P-limited Michigan fen (Richardson & Marshall, 1986). In lakes, particulates and microbes also control the cycling of P (Lean, 1973; Lyche *et al*., 1996; Hwang *et al*., 1998), with turnover of SRP regulated by bacteria (Rigler, 1956; Lean, Abbott & Pick, 1987). In a warm, shallow, South African oligotrophic lake, detritus stored most P, but epiphytic algae were important for P uptake and cycling (Howard-Williams & Allanson, 1981). In addition, floc dominated P uptake in a temperate, deep oligotrophic lake in NY, U.S.A. compared with sediment or water interactions (Doremus & Clesceri, 1982). Finally, suspended fine particulates and benthic coarse particulates also controlled P uptake, cycling and downstream transport in temperate streams (Newbold *et al*., 1983). These similarities among different systems suggest the general importance of water-column particles, periphyton and detritus to P cycling in wetland and shallow aquatic ecosystems.

In conclusion, microbial components dominated short-term P cycling in an Everglades wetland ecosystem. Particles in the water column, periphyton and floc dominated short-term P cycling and partitioning. Additionally, biota in these oligotrophic wetlands quickly removed labile P from the water column and floc layer. However, a large of amount of 'new' P remained as particulates in the relatively clear water column. This particular finding could have important implications for the management and restoration of the Everglades and other wetland and shallow aquatic ecosystems. Specifically, anthropogenic P could be transported large distances downstream as particulates in the flowing Everglades ecosystem. This suggests that the restoration of greater water flow velocities in the Everglades could result in greater loads of P to downstream estuaries.

Acknowledgments

Comments by members of the Wetland Ecosystems Ecology Lab, Quan Dong, Aga Pinowska and Joel Trexler improved the quality of the manuscript. Meghan Fellows and Joel Trexler assisted with the design of the study. Eudel Cepero, Robin Gray, Mac Kobza and Shawn Liston helped with sample collection and laboratory analyses, and Meghan Fellows and David Jones managed the database. This work was made possible through funding to the Southeast Environmental Research Center from the United States Department of the Interior, Everglades National Park, Arthur R. Marshall Loxahatchee National Wildlife Refuge, and the South Florida Water Management District. Additional support was provided by the Florida Coastal Everglades Long-Term Ecological Research (FCE LTER) Program under National Science Foundation Grant number DEB-991051. This is SERC publication series contribution 208.

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(Manuscript accepted 1 August 2003)