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Phosphorus budgets in Everglades wetland ecosystems: the effects of hydrology and nutrient enrichment

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Abstract The Florida Everglades is a naturally oligotrophic hydroscape that has experienced large changes in ecosystem structure and function as the result of increased anthropogenic phosphorus (P) loading and hydrologic changes. We present whole-ecosystem models of P cycling for Everglades wetlands with differing hydrology and P enrichment with the goal of synthesizing existing information into ecosystem P budgets. Budgets were developed for deeper water oligotrophic wet prairie/slough ('Slough'), shallower water oligotrophic *Cladium jamaicense* ('Cladium'), partially enriched *C. jamaicense*/*Typha* spp. mixture ('Cladium/Typha'), and enriched *Typha* spp. ('Typha') marshes. The majority of ecosystem P was stored in the soil in all four ecosystem types, with the flocculent detrital organic matter (floc) layer at the bottom of the water column storing the next largest proportion of ecosystem P pools. However, most P cycling involved ecosystem components in the water column (periphyton, floc, and consumers) in deeper water,

oligotrophic Slough marsh. Fluxes of P associated with macrophytes were more important in the shallower water, oligotrophic Cladium marsh. The two oligotrophic ecosystem types had similar total ecosystem P stocks and cycling rates, and low rates of P cycling associated with soils. Phosphorus flux rates cannot be estimated for ecosystem components residing in the water column in Cladium/Typha or Typha marshes due to insufficient data. Enrichment caused a large increase in the importance of macrophytes to P cycling in Everglades wetlands. The flux of P from soil to the water column, via roots to live aboveground tissues to macrophyte detritus, increased from 0.03 and 0.2 g P m^{-2} yr^{-1} in oligotrophic Slough and Cladium marsh, respectively, to 1.1 g P m^{-2} yr^{-1} in partially enriched Cladium/Typha, and 1.6 g P m^{-2} yr^{-1} in enriched Typha marsh. This macrophyte translocation P flux represents a large source of internal eutrophication to surface waters in P-enriched areas of the Everglades.

Keywords Budget · Enrichment · Everglades · Hydrology · Phosphorus · Wetland

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Introduction

The impacts of anthropogenic nutrient enrichment on the biota and biogeochemistry of aquatic

and wetland ecosystems are an important global issue (National Research Council 1992; Carpenter et al. 1998; Downing et al. 1999; Howarth et al. 2000). Nutrient enrichment has especially large impacts on oligotrophic ecosystems, which generally respond more quickly and dramatically to increased nutrient availability due to a greater ratio of external inputs to internal stores of nutrients compared to more eutrophic systems. For example, increased nutrient loading has a proportionally larger effect on phytoplankton (Smith 1998) and macrophyte biomass (Morris 1991) in oligotrophic compared to enriched aquatic and wetland ecosystems. Thus, oligotrophic systems are excellent end-members for eutrophication synthesis (Childers et al. 2006a). In addition, multiple components of ecosystems interact to influence the resilience of an ecosystem to increased nutrient inputs (Carpenter and Cottingham 1997). Valuable insight on the impacts of eutrophication can be gained by examining whole-system nutrient cycling in oligotrophic ecosystems that are receiving anthropogenic nutrient enrichment.

The Florida Everglades provides a case study for examining the effects of nutrient enrichment on oligotrophic ecosystems. Anthropogenic phosphorus (P) loading to the Everglades has caused large changes in the structure and function of its wetland ecosystems (Davis 1994; Noe et al. 2001; McCormick et al. 2002). Additions of P to this P-limited, oligotrophic ecosystem result in a cascade of ecological changes, starting with changes to periphyton, followed by detritus, consumers, soils, and macrophytes (Gaiser et al. 2005). Characteristic P-induced alterations include the loss of calcareous periphyton mats (McCormick et al., 2001; Gaiser et al. 2006) and proliferation of *Typha domingensis* (Davis 1994; Childers et al. 2003). Phosphorus enrichment has also been shown to alter a large number of biogeochemical processes in the Everglades, such as decomposition (Newman et al. 2001), water-column metabolism (McCormick et al. 1997), DOC production and loss (Qualls and Richardson 2003), nitrogen fixation (Inglett et al. 2004), nitrogen mineralization (White and Reddy 2000), and denitrification (White and Reddy 1999). Similar responses to P enrichment have been observed in other limestone-based marshes of Central America (Rejmánková, 2001).

Many of these studies have sampled along P-enrichment gradients or experimentally dosed P to understand the effects of P additions on individual components of the Everglades ecosystem, e.g. macrophytes, periphyton, or soil (see review in Noe et al. 2001). Despite this body of research, whole-ecosystem P budgets for the Everglades are lacking. In addition, hydrology is the most important factor that differentiates the oligotrophic wetland ecosystems in the Everglades (Gunderson 1994). Changes in surface water stage, velocity, and hydroperiod have resulted in the conversion of deeper water sloughs to shallower water *Cladium jamaicense* marsh across large parts of the Everglades (Sklar et al. 2001). The effect of this conversion of oligotrophic ecosystems types on P cycling is not known. The synthesis that ecosystem budgeting and modeling provides can identify gaps in our understanding of how enrichment and hydrology affect P cycling in the Everglades, and thereby aid efforts to conserve and restore Everglades ecosystems.

Phosphorus budgets developed for other wetlands have proven useful for identifying the ecosystem components most important to P cycling. These studies found that soils (Richardson and Marshall 1986), soil microbes (Chapin et al. 1978), algae (Yarbro 1983, Hwang et al. 1998), or aquatic macrophytes (Mitsch et al. 1979) can dominate ambient P fluxes in a variety of wetland types (Howard-Williams 1985). With P enrichment, most of the added P enters wetland soils (Dolan et al. 1981; Brinson et al. 1984; Richardson and Marshall 1986; Wang and Mitsch 2000) and detritus (Wang and Mitsch 2000). In addition, the general importance of macrophytes to ecosystem P cycling increases with wetland nutrient enrichment, while microorganisms and litter decrease in importance (Richardson and Marshall 1986). Specifically, macrophyte removal of P from sediment increases in importance (Wang and Mitsch 2000), macrophyte litterfall P increases as a proportion of ecosystem P fluxes (Brown 1978), and macrophyte belowground biomass P storage greatly increases (Dolan et al. 1981) following P enrichment to wetlands.

Thus, nutrient budgets provide a synthetic understanding of nutrient cycling in ecosystems and changes in nutrient cycling in response to disturbance. To our knowledge, detailed P budgets have not been developed for an ecosystem as nutrient-poor as the Everglades. Development of P budgets for Everglades wetlands along a continuum from very oligotrophic to P-enriched, and along a water depth gradient, provides an opportunity to generate insight on the effects of nutrient and hydrologic disturbances on whole-ecosystem nutrient cycling. The goals of the present study were to identify 1) key fluxes and stores of P in oligotrophic Everglades wetland ecosystems, 2) differences in P cycling due to hydrology, 3) changes in whole-ecosystem patterns of P cycling in response to P enrichment, and 4) poorly understood or poorly parameterized P-cycling processes.

Ecosystem descriptions

We included four ecosystem types, each with contrasting water depth or P enrichment, in our analysis of Everglades wetlands. The two ecosystem types that dominate in the naturally oligotrophic Everglades are *C. jamaicense* marsh (hereafter Cladium) and wet prairies/sloughs (hereafter Slough). Cladium occurs at shallower water depths and shorter hydroperiod than Slough marshes. Mean water depth in one region of the Everglades has previously been reported to be 25 cm in Cladium marsh and roughly 35–45 cm in Slough marsh, and annual inundation duration ranges from 32% to 85% in Cladium marsh and 61 to 96% in Slough marsh (David 1996). Slough marsh is distinct from the other ecosystem types with its relatively low biomass of macrophytes and abundant periphyton. In areas where P enrichment is occurring, a mixture of *C. jamaicense* and *Typha domingensis* (hereafter Cladium/Typha) is common. With further P enrichment, a monoculture of *T. domingensis* (hereafter Typha) dominates (Miao and DeBusk 1999).

Methods

Budgeting approach

The major stocks and fluxes of P in Everglades wetland ecosystems were included in the budgets

(Fig. 1). Our budgets modeled a representative 1-m² of Everglades wetland with surface water flowing in and out and P cycling among the ecosystem components within this area of marsh. Each budget included the water column, periphyton, aquatic consumers, flocculent detrital organic matter (floc), soil, belowground live macrophytes, and aboveground live and dead macrophytes. Other ecosystem components were either lumped into represented components or considered to be relatively unimportant to ecosystem P dynamics. The included components were also aggregates of individual smaller ecosystem components. For example, the water column included all P fractions, and consumers included aquatic invertebrates and fish. The same budget structure was used for all four ecosystem types. Although P enrichment alters ecosystem structure in the Everglades, the same components are present and are important for P uptake (Davis 1982). In addition, the fluxes were presented as net fluxes between components (with the exception of above- and below-ground macrophyte tissues). Differences in hydroperiod among the four ecosystem types were accounted for by assuming that P cycling by components located in the surface water (water column, periphyton, floc, and consumers) occurred only when surface water was present. The drying and wetting of wetland ecosystems can stimulate large nutrient fluxes (Baldwin and Mitchell 2000). However, insufficient information exists on this process in the Everglades to include in these budgets, likely resulting in an underestimate of annual P cycling rates. Finally, the budget for each ecosystem type was in steady state and was a snapshot in time of ecosystems responding to P enrichment. The assumption of steady state was necessary to estimate unknown fluxes by mass balance. The most P enriched ecosystem type, Typha monoculture, is thought to be saturated with P (DeBusk et al. 2001; Childers et al. 2003), suggesting that steady-state analysis is appropriate for P budgeting in this case. It was beyond the scope of this work to create a dynamic simulation model of ecological feedbacks in response to P enrichment, which already exists for the Everglades (Fitz and Sklar 1999).

The budgets were parameterized with a combination of literature meta-analysis and published and unpublished data. Standing stocks of P in

Fig. 1 Phosphorus budgets for Everglades wetland ecosystems: **a**) oligotrophic wet prairie/slough, **b**) oligotrophic *Cladium jamaicense*, **c**) partially enriched *Cladium jamaicense*/*Typha* spp. mixture, and **d**) enriched *Typha* spp. Standing stocks (g P m^{-2}) in individual ecosystem components are shown in boxes, and net directional fluxes (g P m^{-2} yr^{-1}) between components are shown with arrows. Measured fluxes are shown with solid black arrows, fluxes estimated using data from other ecosystems or estimated indirectly are shown with solid gray arrows, fluxes estimated by mass balance are shown with dashed gray arrows, and fluxes with insufficient information are shown with double gray arrows. Phosphorus concentrations in inflowing and outflowing surface water are also shown. AG = aboveground
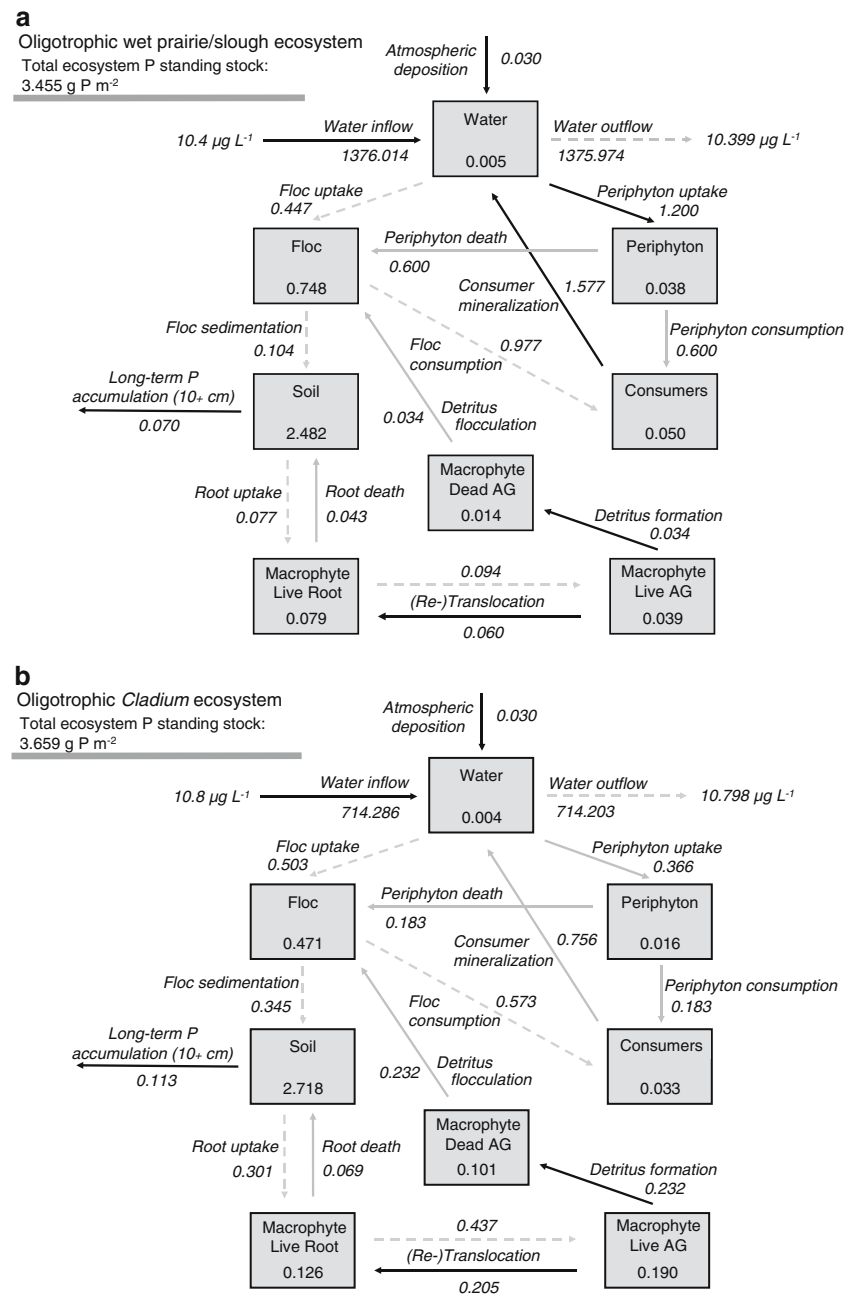
different components were estimated primarily from the published literature with some use of unpublished data from a transect-based sampling along P-enrichment gradients throughout the Everglades (Childers et al. 2003) for relatively poorly studied components (e.g. consumers). Average values of component masses, water depth, and soil bulk density (Appendix 1) and P

concentrations (Appendix 2) were used to calculate P standing stocks (g P m^{-2}). Fluxes of P (g P m^{-2} yr^{-1}) between components were estimated by 1) measured fluxes determined from ^{32}P turnover rates in a field mesocosm dosing experiment (Noe et al. 2003); 2) turnover rates of biomass with known P concentration; or 3) mass balance, in descending order of priority.
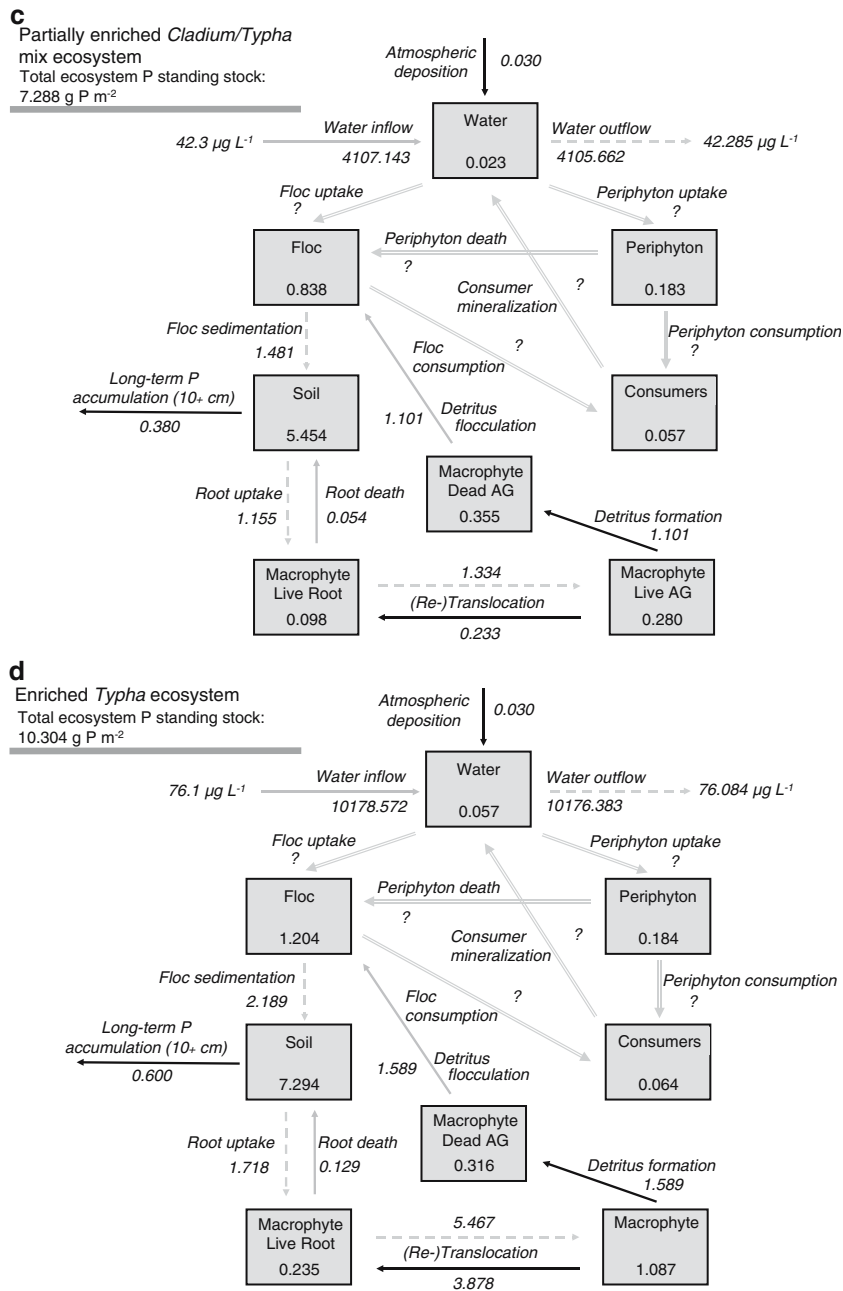
c

Partially enriched *Cladium/Typha*
mix ecosystem
Total ecosystem P standing stock:
7.288 g P m⁻²

Atmospheric deposition   0.030

42.3 µg L⁻¹   Water inflow   Water   Water outflow   42.285 µg L⁻¹
             4107.143   0.023   4105.662

Floc uptake ?   Periphyton uptake ?

Floc   Periphyton death ?   Periphyton
0.838   0.183

Floc sedimentation   Consumer mineralization ?
1.481

Long-term P accumulation (10₊ cm)   Soil   Floc consumption ?   Consumers
0.380   5.454   1.101   Detritus flocculation   0.057

Root uptake   Root death   Macrophyte Dead AG
1.155   0.054   0.355   Detritus formation 1.101

Macrophyte Live Root   1.334   Macrophyte Live AG
0.098   (Re-)Translocation   0.280
         0.233

d

Enriched *Typha* ecosystem
Total ecosystem P standing stock:
10.304 g P m⁻²

Atmospheric deposition   0.030

76.1 µg L⁻¹   Water inflow   Water   Water outflow   76.084 µg L⁻¹
             10178.572   0.057   10176.383

Floc uptake ?   Periphyton uptake ?

Floc   Periphyton death ?   Periphyton
1.204   0.184

Floc sedimentation   Consumer mineralization ?
2.189

Long-term P accumulation (10₊ cm)   Soil   Floc consumption ?   Consumers
0.600   7.294   1.589   Detritus flocculation   0.064

Root uptake   Root death   Macrophyte Dead AG
1.718   0.129   0.316   Detritus formation 1.589

Macrophyte Live Root   5.467   Macrophyte
0.235   (Re-)Translocation   1.087
         3.878

Fig. 1 continued

Ecosystem component fluxes

Water column

The total (wet + dry) atmospheric deposition rate of P in the Everglades was estimated from the median value of previously published rates (reviewed by Noe et al. 2001). Concentrations of total P in inflowing surface water were from Noe et al. (2001). Outflowing concentrations of P were adjusted to account for the annual net ecosystem uptake of P as determined for each budget. The turnover rate of P standing stock in the water column was calculated from the typical

mean annual surface–water velocity, water volume (depth) during the wet season, and hydroperiod. Mean water velocity has been estimated at 0.9 cm sec^{-1} in Slough marsh (ranging from 0.6 cm sec^{-1} to 1.7 cm sec^{-1} among sites; Schaffranek, 2004; E. Gaiser, Florida International University, unpublished data) and 0.8 cm sec^{-1} in Cladium marsh (Schaffranek 2004). We could find no information on water velocity in Cladium/ Typha and Typha marshes; thus, we assumed velocities were the same as in Cladium marsh because of similarity in the volume of submerged stems (G. Noe, personal observation). Estimates of P fluxes through the water column derived from these data are likely overestimates given that water velocity decreases, and solutes and particles are entrained, at the bottom and top of the water column relative to the middle of the water column where velocity is most often measured (Saiers et al. 2003; Harvey et al. 2005). Mean hydroperiods in Slough (surface water present 95% of the year) and Cladium marsh (69%) were estimated from measurements of water depths in a region with intact ridge and slough landscape in the central Everglades, Water Conservation Area 3A, in relation to 14 years of data from a nearby USGS water depth gauge (G. Noe, unpublished data). Mean annual water depth is similar in Typha and Cladium marshes (Urban et al. 1993), supporting our assumption that hydroperiod is the same in Cladium, Cladium/Typha, and Typha marshes.

Periphyton

Periphyton P turnover rates were determined from a ^{32}P field mesocosm dosing study in Slough marsh with calcareous periphyton in which peak radiotracer content occurred at 11 days following dosing (Noe et al., 2003). We extrapolated this P turnover rate to periphyton in oligotrophic Cladium marsh. Although Davis (1982) also added P radiotracer to Everglades wetlands, we could not estimate turnover rates from this study because sampling only occurred once. Fluxes removing P from periphyton were assumed to be evenly split between detrital and consumer pathways (Buzzelli et al., 2000). Fluxes involving periphyton were assumed to be zero during periods of the year when surface water was not present in each ecosystem type. Periphyton P turnover rates in enriched Everglades wetlands have not been measured. However, research in other wetlands has shown that P enrichment strongly influences P uptake rates by periphyton (Vymazal 1995). Therefore, we did not attempt to extrapolate P fluxes by periphyton to Cladium/Typha or Typha marshes.

Floc

Reliable estimates of P fluxes for floc are not available (data in Noe et al. 2003, is too temporally variable). Therefore, unknown P fluxes into and out of floc were estimated by mass balance after known fluxes had been determined.

Consumers

Peak ^{32}P content in fish occurred at 11 days after dosing in Everglades Slough marsh (Noe et al., 2003). Macroinvertebrates, which comprise half of Everglades aquatic consumer biomass (Turner et al. 1999), were only sampled at the completion of the ^{32}P-dosing study. At that time, no consistent differences in ^{32}P content were found between fish and macroinvertebrates. Therefore, we assumed that the two consumer groups had similar ^{32}P turnover rates, and the fish ^{32}P turnover rate was applied to all aquatic consumers in this budget. Lacking data from the other ecosystem types, we assumed turnover rates are the same in Cladium, but we provide no estimate for P-enriched Cladium/ Typha or Typha marsh. Consumer fluxes of P were assumed to be zero during periods of the year when surface water was not present in each ecosystem type. Biomass and P fluxes from fish and aquatic macroinvertebrates to higher trophic levels are insufficiently documented to include in the P budget.

Soil

Only the top 10 cm of soil were modeled in the budgets. This depth was chosen due to the prevalence of Everglades soil cores taken to this depth and low root biomass observed below

10 cm (G. Noe, personal observation). We modeled soil P accumulation as the downward movement of annual soil deposition increments to below 10 cm. Average soil P-accumulation rates for each ecosystem type were taken from ^{210}Pb and ^{137}Cs studies (Craft and Richardson 1993a, b; Reddy et al. 1993; Scinto 1997; Craft and Richardson 1998; W. Orem, U.S. Geological Survey, unpublished data [Slough marsh from Taylor Slough]). It was assumed that the most likely source of accreting soil P is the deposition or mineralization of floc P, as opposed to the advection of water column P into soil or macrophyte uptake of P from the water column followed by translocation into roots or rhizomes in the soil.

Macrophytes

Macrophyte fluxes of P were modeled to include belowground tissue uptake and death, translocation and retranslocation between live belowground and live aboveground tissues, and death of aboveground tissues. Leaf turnover rates were calculated from measurements of leaf longevity and used to estimate the production of dead aboveground biomass. Culms of *Eleocharis cellulosa*, the dominant macrophyte in Slough marsh, have a 4.9-month average life span (Daoust and Childers 2004). Average *C. jamaicense* leaf longevity in oligotrophic areas is 5.3 months (Childers et al. 2006b; Davis 1991). Average *C. jamaicense* leaf longevity decreases to 5.0 months in Cladium/Typha marsh (Davis 1991). Average *T. domingensis* leaf longevity decreases from 3.1 months to 2.4 months in Cladium/Typha and Typha marsh, respectively (Davis 1991). We were unable to find any estimates of root turnover for Everglades macrophytes. Instead, we used the global average for fine root turnover in wetlands (55% annually, Gill and Jackson 2000). The herbaceous macrophytes of the Everglades do not have long-term aboveground storage tissues. Therefore, retranslocation of P from aboveground to belowground tissues was calculated as the difference between live and dead aboveground P standing stocks multiplied by the leaf turnover rate.

Results and discussion

General patterns

Soil is the dominant factor in P storage in Everglades wetland ecosystems. In all four ecosystem types, ranging from shallow to deeper water and from oligotrophic to P-enriched, the top 10 cm of soil stored roughly 70% of total ecosystem P (Fig. 1). However, not all of this soil P is a biogeochemically active pool. Labile inorganic and microbial P are usually small but active fractions relative to larger but less available fractions such as refractory organic P (Reddy et al. 1998). Thus, most soil P serves as a long-term sink for the limiting nutrient in the Everglades. This pattern is also found in most wetland ecosystems (Johnston 1991), treatment wetlands (Kadlec and Knight 1996), and terrestrial ecosystems (Richey 1983).

The importance of soil to P storage under steady-state conditions differs from the findings of P dosing studies in the Everglades. Short-term pulses of P in Slough marsh accumulated in the floc layer at the end of a 18-day ^{32}P-phosphate dosing study (Noe et al. 2003) and a 6-month addition of phosphate to experimental flumes (Noe et al. 2002). In contrast, floc stored much less P than soil in the P budgets, although floc was the 2nd-largest pool of P (Fig. 1). Floc stored 21% of ecosystem P in Slough marsh and 11–13% of ecosystem P in Cladium, Cladium/Typha, and Typha marshes. This P stored in the floc layer can move to the soil by diffusive flux (P concentrations in floc are greater than in soil), particle settling, consolidation during dry down, and transpiration-driven flux (Kadlec 1999). It is also possible for floc P to enter the water column through diffusion or particle suspension, but most P appeared to move from the floc to the soil in the [32]P- (Noe et al. 2003) and phosphate-dosing studies (Noe et al. 2002). Microbes are also more abundant and metabolically active in floc than soil of the Everglades (Reddy et al. 1999). Therefore, floc appears to function as an important transient pool of P in the ecosystem before P enters the soil for long-term storage.

The largest fluxes of P in a 1-m^2 patch of Everglades marsh involved the water column.

The dominant flux, by far, is P in surface water flowing into and out of the 1-m^2 patch of marsh. Not all of the P in surface water is readily available for biotic uptake. Dissolved reactive P, the most biologically available fraction, is a small fraction of total P; refractory organic P is the dominant form of dissolved P in surface waters of the Everglades (Noe et al., in press). Particulate P can hold 20 to 51% of total P in surface water with unattached bacteria cells being the major component (Noe et al., in press). It should be noted, however, that attached and unattached microbes could mineralize some organic P being transported through the marsh by the production of the extracellular enzyme phosphatase (Wright and Reddy 2001). Most of the P transported in surface water through a 1-m^2 patch of Everglades

wetland likely does not participate in P cycling within that patch.

The total annual flux of P entering an ecosystem component (identical to the flux leaving that component in these steady-state budgets; "through-flux") is a measure of the importance of that component to whole-ecosystem P dynamics. In oligotrophic Everglades wetlands, the through-fluxes of P were greater for ecosystem components residing in the water column. Periphyton, consumers, and floc had much larger P through-fluxes than did soil (Table 1). Periphyton and consumers cycled large amounts of P due to their high P turnover rates (Table 2), whereas floc had lower turnover rates but larger stores of P (Table 2, Fig. 1). Both periphyton and floc also have very active microbial communities. In

Table 1 Calculated phosphorus through-flux (sum of fluxes entering a component, g P m^{-2} yr^{-1}) for the different ecosystem components and summation for the whole ecosystem in each ecosystem type

Component	Slough	Cladium	Cladium/Typha	Typha
Water	1,377.621	715.072	4,107.173	10,178.602
Periphyton	1.200	0.366	no data	no data
Floc	1.081	0.918	no data	no data
Consumers	1.577	0.756	no data	no data
Macrophyte live AG	0.094	0.437	1.334	5.467
Macrophyte dead AG	0.034	0.232	1.101	1.589
Macrophyte live BG	0.137	0.506	1.388	5.596
Soil	0.147	0.414	1.535	2.318
Total ecosystem	1,381.891	718.701	4,112.531[a]	10,193.572[a]
Total ecosystem (not including water)	4.270	3.629	5.358[a]	14.970[a]
Total macrophyte	0.265	1.175	3.823	12.652

AG = aboveground, BG=belowground

[a] Includes components with no flux data

Table 2 Calculated phosphorus turnover rate (P through-flux/standing stock; yr^{-1}) for the different ecosystem components and the whole ecosystem in each ecosystem type

Component	Slough	Cladium	Cladium/Typha	Typha
Water	276,000	179,000	179,000	179,000
Periphyton	31.6	22.9	no data	no data
Floc	1.4	1.9	no data	no data
Consumers	31.5	22.9	no data	no data
Macrophyte live AG	2.4	2.3	4.8	5.0
Macrophyte dead AG	2.4	2.3	3.1	5.0
Macrophyte live BG	1.7	4.0	14.2	57.1
Soil	0.1	0.2	0.3	0.3
Total ecosystem	400	196	564[a]	989[a]
Total ecosystem (not including water)	1.236	0.992	0.735[a]	1.453[a]

AG = aboveground, BG = belowground

[a] Includes components with no flux data

contrast, soil had very low P turnover rates and through-flux despite its very large P stores. As previously discussed, a large proportion of soil P resides in refractory pools (Reddy et al. 1998), resulting in lower total turnover rates. Through-fluxes of P for macrophytes were intermediate between the water column components and soil and varied greatly among the different ecosystem types. The finding that most P cycling occurs among components residing in the water column was confirmed by a 5-yr experimental dosing of P in flow-through flumes in the Everglades. In that experiment, responses to P enrichment were first observed in periphyton, then floc, consumers, macrophytes, and finally soil (Gaiser et al. 2005). Other P-dosing experiments in the Everglades have shown similar patterns (Newman et al. 2004).

Influences of water depth

Hydrology is the primary environmental forcing factor that differentiates the oligotrophic wetland ecosystems in the Everglades (Gunderson 1994). The shallower water in Cladium marsh compared to Slough marsh promotes the growth of the less inundation-tolerant *C. jamaicense* (Urban et al. 1993). The whole-ecosystem P budgets revealed both similarities and significant differences in P storage and cycling between these two oligotrophic ecosystem types. Both Slough and Cladium marsh stored very similar total amounts of P in the ecosystem and in the soil component (Fig. 1a, b). However, it should be noted that Cladium marsh has deeper peat above the limestone bedrock compared to Slough marsh (Science Coordination Team 2003) and therefore stores more P in deep peat (>10 cm deep). Furthermore, the components of both ecosystem types also cycled similar amounts of P (Table 1). The sums of P through-fluxes in all ecosystem components, not including the water component, were estimated to be 4.3 and 3.6 g P m^{-2} yr^{-1} in Slough and Cladium marsh, respectively. Both Slough and Cladium ecosystem types are very oligotrophic and occur in a landscape with historically small external P inputs, which are mostly from rainfall (Davis 1994; Noe et al. 2001). This functional convergence of ecosystem attributes is perhaps not surprising given that both ecosystem types have the same atmospheric P inputs, and similar soil P outputs and surface-water P concentrations. However, Slough and Cladium marsh did differ in where much of their P cycling occurred. The water column (periphyton, floc, and consumers) was the dominant location for P cycling in the Slough ecosystem type (Table 1), which has more water, sparse macrophytes, and abundant periphyton compared to Cladium marsh (Appendix 1). In contrast, aboveground macrophyte tissues and detritus were much more important to P cycling in Cladium marsh. The slightly faster surface-water velocity, deeper water, and longer hydroperiod in Slough marsh also resulted in twice the total P through-flux for the water component compared to Cladium marsh (Table 1). Thus, sloughs are important locations for downstream water and P transport in the Everglades hydroscape compared to the same area of Cladium marsh. To summarize, both oligotrophic ecosystem types stored very similar amounts of P and had similar internal P cycling rates, but had different ecosystem components that dominated the P cycling.

One goal for Everglades restoration is to increase surface water flow into sloughs and restore the historic ridge and slough landscape (Science Coordination Team 2003). It is likely that these hydrologic changes will cause a reduction in *C. jamaicense* productivity and cover in some places (Childers et al. 2006b). Our budgets suggest that such an increase in Slough and decrease in Cladium marsh ecosystem types will have at least two effects on P cycling in the Everglades. First, the importance of periphyton and consumers to P cycling may increase while the importance of macrophytes may decrease. This switch in the spatial focus of P cycling could result in greater downstream P transport during high flow events and greater P transfer to higher trophic levels because of the reduced anchoring, higher P turnover rates, and greater importance to food webs (Heymans et al. 2002) of microbe-dominated periphyton than macrophytes. Second, downstream transport of P may increase with hydrologic restoration as more water (with its associated P load) flows through increasing areas of slough. However, we predict that the effect of

this potential increase in P loading on downstream ecosystems is not likely to be great because the freshwater Everglades is a small source of P to Everglades estuaries (Sutula et al. 2003; Childers et al. 2006a).

Effects of P enrichment

Phosphorus enrichment causes large changes to P dynamics in Everglades wetland ecosystems (Davis 1994; Noe et al. 2001; McCormick et al. 2002). Not surprisingly, the ecosystem components in P-enriched ecosystem types all stored more P than their counterparts in the oligotrophic ecosystem types (Fig. 1). Aquatic consumers, however, stored only marginally more P in Cladium/Typha or Typha marsh due to the only slight increase in biomass in these P-enriched ecosystem types (Appendix 1). The total amount of P stored by the ecosystems doubled in the initial stage of P enrichment (Cladium/Typha marsh) and tripled at the most enriched state (Typha marsh) relative to the oligotrophic systems (Slough and Cladium marsh; Fig. 1).

The largest documented changes to P storage and cycling in the enriched ecosystems involved macrophytes. Plant P storage (Fig. 1), fluxes (Table 1), and turnover (Table 2) all were greater in Cladium/Typha and Typha marsh. The total standing stock of P in live aboveground, standing dead aboveground, and live belowground plant tissues in Typha marsh were 4-fold and 13-fold greater relative to Cladium and Slough marsh, respectively (Fig. 1). The proportion of total ecosystem P stored in live aboveground macrophyte tissues also increased from 1% in Slough marsh and 5% in Cladium marsh to 11% in Typha marsh. Therefore, the relative importance of macrophytes to P storage increased with P enrichment. Furthermore, the sum of P fluxes involving macrophytes drastically increased following P enrichment. Phosphorus through-fluxes involving macrophytes increased in Typha marsh 48-fold and 11-fold compared to Slough and Cladium marsh, respectively (Table 1). Similarly, Davis (1982) showed that P uptake associated with macrophyte detritus tripled with P enrichment in the Everglades.

This state change in P cycling involving macrophytes is due to the characteristics of the species that dominates regions of the Everglades that receive P enrichment. *Typha domingensis*, which is native to the Everglades but only occurred in small areas in the historically oligotrophic hydroscape, has greater P concentrations, biomass, and biomass turnover rates than the vegetation of the oligotrophic Everglades (Kadlec 1999; Miao and DeBusk 1999). These traits are ultimately a result of the P-uptake kinetics and growth strategy of *T. domingensis*. The growth rates of *T. domingensis* increase with P enrichment, whereas *C. jamaicense*'s does not (Newman et al. 1996; Lorenzen et al. 2001). This is a result of greater P-uptake rates at enriched P concentrations, greater maximum P-uptake rate, and a lower half-saturation constant by roots of *T. domingensis* compared to *C. jamaicense*, but not a result of a difference in P use efficiency (Lorenzen et al. 2001). To summarize, P enrichment in the Everglades promotes the rapid growth of P-rich *T. domingensis*, resulting in drastically increased rates of P cycling by higher plants.

Nutrient enrichment has increased the importance of macrophytes to nutrient cycling in other ecosystems as well. For example, P storage in aboveground and belowground macrophyte tissues increased 7-fold in a marsh receiving treated sewage (Dolan et al. 1981). Fluxes of P involving macrophytes also have been found to increase greatly with P enrichment in other wetlands. Macrophytes incorporated a larger proportion of soil N and P standing stocks in more productive, nutrient-enriched wetlands compared to more oligotrophic wetlands (Olde Venterink et al. 2002). Plants annually removed up to 7% of soil P standing stock (0–10 cm) in the most nutrient enriched of these marshes (Olde Venterink et al. 2002), whereas *T. domingensis* in this study annually removed 22% of soil P stores in Everglades marshes with greater levels of P enrichment. Similarly, macrophyte litterfall fluxes increased greatly in cypress swamps receiving sewage (Brown 1978) or floodplain forests receiving greater nutrient inputs than other forests (Brinson et al. 1984). Phosphorus uptake by *Typha* spp. also increased from 0.3 g P m^{-2} yr^{-1} to 1.7 g P m^{-2} yr^{-1} in temperate riverine marshes

receiving greater nutrient inputs (Wang and Mitsch 2000). In moist tussock tundra, long-term nutrient additions resulted in changes in plant community composition that had large feedbacks on ecosystem biogeochemistry (Shaver et al. 2001). All of these examples point to the greater importance of plants to nutrient cycling after nutrient enrichment than before. Changes in species composition due to nutrient enrichment can also result in large changes to ecosystem biogeochemistry (Wedin and Tilman 1996; Chapin et al. 1997; Jobbágy and Jackson 2004).

Macrophyte translocation of P from soils in the Everglades is a large source of internal P loading. Decades of P loading from canals draining the Everglades Agricultural Area and urban development have left a legacy of P enrichment in the Everglades (Davis 1994). This accumulation of anthropogenic P has occurred over wide areas of the Everglades, particularly in Water Conservation Area 2A (WCA–2A), where 73% of the wetland area in 1998 had soil and floc P concentrations above what is considered P-enriched (DeBusk et al. 2001). In P-enriched Everglades marsh, *T. domingensis* removes 1.6 g P m^{-2} yr^{-1} from the soil and deposits this P in surface-water as dead aboveground tissues (Fig. 1d). In comparison, upward fluxes due to diffusion (Fisher and Reddy 2001) and downward fluxes by transpiration flux (Kadlec 1999) are each estimated to be roughly 1.0 g P m^{-2} yr^{-1} in Everglades *T. domingensis* marsh, resulting in no net annual flux due to these two processes. Extrapolating the macrophyte translocation flux rates for Typha and Cladium/Typha ecosystems over the entire area of WCA–2A invaded by *T. domingensis* (1646 ha monoculture and 7666 ha mixed community in 1995 out of a total of 41998 ha; Rutchey and Vilchek 1999) results in an estimated 110×10^6 g P yr^{-1} entering the water column by macrophytes compared to 18×10^6 g P yr^{-1} entering externally from canals in 2002 (SFWMD, 2003). Better quantification of the fate of macrophyte detrital P is needed to predict its transport rate to downstream ecosystems. Leaching of P from freshly dead leaves has been shown to be a quantitatively important process in oligotrophic Everglades wetlands (Davis et al. 2006). The P content of macrophyte detritus in P-enriched marshes

eventually increases due to microbial uptake of P from the water column (Davis 1991). This P-rich *T. domingensis* detritus could eventually fragment into particles that advect downstream or incorporate into the soil. Translocation of P from sediments to the water column by rooted macrophytes has also been shown to be an important process in shallow lakes (Carpenter 1981), where internal loading can delay ecosystem recovery following reductions in external P loading (Søndergaard et al. 2001).

Conclusions

Creating whole-ecosystem P budgets was a useful tool for comparing different ecosystems and understanding P-enrichment effects. The budgets identified similar whole-ecosystem P-storage pools and cycling rates between the two oligotrophic Everglades wetland ecosystem types with differing hydrology. However, the locations of P cycling within the ecosystems differed. Most P fluxes occurred among ecosystem components residing in the water column or the sediment in the deeper water Slough and shallower water Cladium marsh ecosystems, respectively. Microbes were most likely responsible for the larger P cycling rates among some ecosystem components of the oligotrophic marshes (periphyton, floc, and water column). Anthropogenic P loading to Everglades wetlands resulted in greater P storage in all ecosystem components. Enriched ecosystem types had large increases in the importance of macrophytes to P storage and cycling relative to oligotrophic ecosystem types. Macrophytes were also a large source of internal eutrophication in P enriched areas, moving large amounts of P from the large storage pool in soils into the water column. The P budgets also identified key gaps in our understanding of P cycling in wetlands. In particular, knowledge of the transport rates for different P fractions is lacking, as are flux rates for components residing in the water column of enriched marshes, hindering predictions of the spread of eutrophication.

Appendix

Appendix 1 Observed mean masses of ecosystem components (AG = aboveground, BG = belowground), water depth, and soil bulk density used to parameterize the budgets for each ecosystem type. Floc depth is included in parentheses. References not included in the Literature Cited are presented in Appendix 3

Component	Slough	Cladium	Cladium/Typha	Typha
Periphyton (g dw m^{-2})	263[a,c,e]	84[f,g]	141[f]	65[f,g]
Floc (g dw m^{-2})	1686[a,c] (9.5 cm)	863[c] (6.1 cm)	795[d]	726[c] (6.9 cm)
Consumers (g dw m^{-2})	2.3[a,h,i,j,k,l]	1.3[h,i]	1.8[k]	2.2[h,i,k]
Macrophyte live AG (g dw m^{-2})	117[a,m,n,o,p]	790[e,n,o,p,q,r,s]	480[m,r,s,t]	681[p,r,s]
Macrophyte dead AG (g dw m^{-2})	85[p]	1269[p,q]	1121[d]	973[p]
Macrophyte live BG (g dw m^{-2})	520[l,o]	900[m,o,s]	183[s,t]	248[s]
Water depth (m)	0.52[a,b,c]	0.35[c]	0.55[d]	0.75[c]
Soil bulk density (g cm^{-3})	0.096[a,c]	0.069[c,u,v]	0.068[u]	0.064[c,u,v]

[a] Noe et al. (2002)

[b] Noe et al. (2003)

[c] L. Scinto, Florida International University, unpublished data (WCA-1, -2A, -3B, Shark River Slough)

[d] Assumed to be mean of Cladium and Typha ecosystem values

[e] Chiang et al. (2000)

[f] E. Gaiser, Florida International University, unpublished data (WCA-1, -2A, -3B, Shark River Slough)

[g] McCormick et al. (1998)

[h] Turner and Trexler (1997)

[i] Turner et al. (1999)

[j] Loftus and Eklund (1994)

[k] J. Trexler, Florida International University, unpublished data (WCA-1, -2A, -3B, Shark River Slough)

[l] G. Noe, United States Geological Survey, unpublished data (Shark River Slough)

[m] Craft et al. (1995)

[n] Daoust and Childers (1999)

[o] Daoust and Childers (2004)

[p] Childers et al. (2003)

[q] Stewart and Ornes (1975)

[r] Davis (1989)

[s] Miao and Sklar (1998)

[t] Assumed to be mean of Cladium and Typha biomass in Cladium/Typha ecosystem type

[u] DeBusk et al. (1994)

[v] Newman et al. (1997)

Appendix 2 Observed mean phosphorus concentrations in the different ecosystem components used to parameterize the budgets for each ecosystem type. AG = aboveground, BG = belowground. References not included in the Literature Cited are presented in Appendix 3

Component	Slough	Cladium	Cladium/Typha	Typha
Water (μg l^{-1})	10.4[a]	10.8[a]	42.3[a]	76.1[a]
Periphyton (μg g^{-1})	185[b,c,d]	211[d,e,f,g]	1031[d,e,f,h,i]	2264[d,f]
Floc (μg g^{-1})	444[c,j]	546[j]	1103[k]	1659[j]
Consumers (μg g^{-1})	Fish: 32,400[l,m]; Invertebrates: 12,100[n,o,p,q,r]			
Macrophyte live AG (μg g^{-1})	332[c,j,s,t,u]	240[s,u,v,w,x,y,z]	649[s,w,x,y,!,@]	1597[u,w,x,y]
Macrophyte dead AG (μg g^{-1})	98[#]	79[w,z,$]	307[w,z,$,@]	325[w,$]
Macrophyte live BG (μg g^{-1})	152[j]	141[x,y]	550[x,y]	950[x,y]
Soil (μg g^{-1})	248[c,j]	397[j,%,^]	802[%]	1127[j,%,^]

[a] Noe et al. (2001)

[b] Chiang et al. (2000)

[c] Noe et al. (2002)

[d] E. Gaiser, Florida International University, unpublished data (WCA–1, –2A, –3B, Shark River Slough)

[e] Grimshaw et al. (1993)

[f] McCormick and O'Dell (1996)

[g] Scinto (1997)

[h] Vymazal et al. (1994)

[i] Pan et al. (2000)

[j] L. Scinto, Florida International University, unpublished data (WCA–1, –2A, –3B, Shark River Slough)

[k] assumed to be mean of Cladium and Typha ecosystem values

[l] J. Trexler, Florida International University, unpublished data (Shark River Slough)

[m] Stevenson and Childers (2004)

[n] Nakashima and Leggett (1980)

[o] Andersen and Hessen (1991)

[p] Briggs and Funge-Smith (1994)

[q] Boyd and Teichert-Coddington (1995)

[r] Penaflorida (1999)

[s] Craft et al. (1995)

[t] Vaithiyanathan and Richardson (1998)

[u] Childers et al. (2003)

[v] Steward and Ornes (1975)

[w] Davis (1991)

[x] Koch and Reddy (1992)

[y] Miao and Sklar (1998)

[z] Richardson et al. (1999)

[!] Richardson et al. (1997)

[@] Asumed to be mean of Cladium and Typha biomass in Cladium/Typha ecosystem type

[#] A. Edwards, Illinois Natural History Survey, unpublished data (Shark River Slough)

[$] Miao and DeBusk (1999)

[%] DeBusk et al. (1994)

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