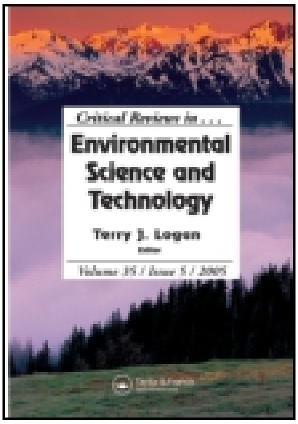

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Phosphorous Cycling in the Greater Everglades Ecosystem: Legacy Phosphorous Implications for Management and Restoration

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Phosphorous Cycling in the Greater Everglades Ecosystem: Legacy Phosphorous Implications for Management and Restoration

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Phosphorus (P) retention in wetlands is an important function of watershed nutrient cycling, particularly in drainage basins with significant nonpoint nutrient contributions from agriculture and urban sources. Phosphorus storage involves complex interrelated physical, chemical, and biological processes that ultimately retain P in organic and inorganic forms. Both short-term storage of P mediated by assimilation into vegetation, translocation within above- and below-ground plant tissues, microorganisms, periphyton, and detritus, and long-term storage (retention by inorganic and organic soil particles and net accretion of organic matter) need to be considered. Here, we review and synthesize recent studies on P cycling and storage in soils and sediments throughout the Greater Everglades Ecosystem and the influence of biotic and abiotic regulation of P reactivity and mobility as related to restoration activities in south Florida. Total P storage in the floc/detrital layer and surface soils (0–10 cm) is estimated to be 400,000 metric tons (mt) within the entire Greater Everglades Ecosystem, of which 40% is present in the Lake Okeechobee Basin (LOB), 11% in sediments of Upper Chain of Lakes, Lake Istokpoga, and Lake Okeechobee, 30% in the

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Everglades Agricultural Area (EAA), and 19% in the Stormwater Treatment Areas (STAs) and the Everglades. Approximately, 35% of the P stored is in chemically nonreactive (not extractable after sequential extraction with acid or alkali) pool and is assumed to be stable. Phosphorus leakage rates from LOB and EAA are approximately 500 and 170 mt P per year, respectively, based on long-term P discharges into adjacent ecosystems. The estimated reactive P in the LOB soils is 65% of the total P, of which only 10–25% is assumed to leak out of the system. Under this scenario, legacy P in LOB would maintain P loads of 500 mt per year to the lake for the next 20–50 years. Similarly, surface soils of the EAA are estimated to release approximately 170 mt P per year for the next 50–120 years. The role of the STAs in reducing loads to downstream regions is critical and requires effective management of P forms to ensure the P is stabilized in these systems by the addition of chemical amendments or by dredging of accumulated soils. Also, additional efforts to minimize leakage of the legacy P from the northern regions should also be evaluated to reduce external P loading loads to the STAs.

KEYWORDS: inorganic phosphorus, internal load, organic phosphorus, phosphorus loads, phosphorus memory, soils and sediments

1 INTRODUCTION

The management of agricultural, forest, range, and urban lands play an integral part in influencing soil and water quality within a watershed, especially the distribution of nutrients and contaminant loads. Wetlands are often the recipient of these nutrient and contaminant loads because of their position in the landscape. Nutrient retention in wetlands is an important function in watershed nutrient cycling, particularly in drainage basins with significant nonpoint nutrient contributions from agriculture and urban sources.

Phosphorus (P) is often a key limiting nutrient in many wetlands and aquatic ecosystems. Unlike carbon (C) and nitrogen (N), most of the P added to an ecosystem accumulates in abiotic and biotic components (Reddy et al., 2005a; Withers and Jarvie, 2008). Biogeochemical processes interact with the P load among various internal storage compartments (soils, vegetation, detritus, periphyton, microorganisms, and fauna) over different time frames. Therefore, when evaluating P retention by wetlands, both short- (assimilation into vegetation, translocation within above- and below-ground plant tissues, microorganisms, periphyton, and detritus) and long-term storage components (retention by inorganic and organic soil particles and net accretion of organic matter) need to be examined (Figure 1).

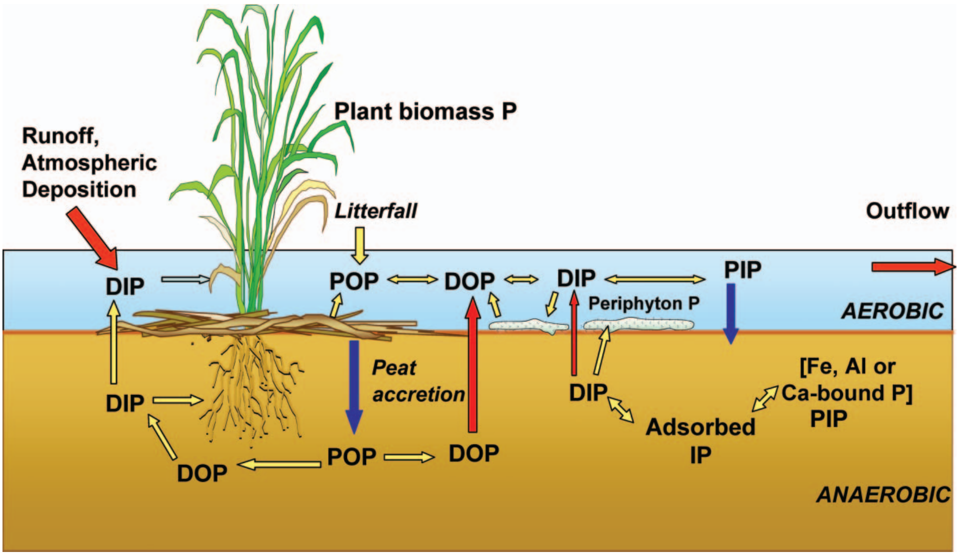

FIGURE 1. Schematic showing phosphorus cycle in wetlands. POP = particulate organic P; PIP = particulate inorganic P; DIP = dissolved inorganic P; DOP = dissolved organic P (Reddy and Delaune, 2008). (This figure is available in color online).

The Greater Everglades Ecosystem can be grouped into two distinct hydrologic units: the Northern Everglades Ecosystem (NEE) and the Southern Everglades Ecosystem (SEE; Figure 2), based on relative locations within the watershed and different restoration goals. The NEE includes the: Upper Chain of Lakes Basin, Lower Kissimmee River Basin, Northern Lake Okeechobee Basin, Lake Okeechobee, and basins associated with the Caloosahatchee and St. Lucie Rivers. The SEE includes the Everglades Agricultural Area (EAA), Stormwater Treatment areas (STAs), Water Conservation Areas (WCAs), Everglades National Park (ENP), Big Cypress National Preserve (BCNP), and Florida Bay.

Historically, the major source of nutrients to the Greater Everglades Ecosystem was from atmospheric deposition, with minimum secondary nutrient inputs through infrequent sheet flow across the northern Everglades wetlands from Lake Okeechobee. Presently, approximately two thirds of the P load from Lake Okeechobee is discharged to the east and west to the St. Lucie and Caloosahatchee estuaries, respectively. Agricultural and urban intensification in the Greater Everglades Ecosystem have led to excessive nutrient loads to natural systems contained within the region. For example, over the past three decades, total P loads to Lake Okeechobee were in excess of 500 mt per year, with the exception of four dry years (McCormick et al., 2010). These loads are approximately 3.6 times the annualized Total Maximum Daily Load (TMDL) of 140 mt per year. Approximately one third of the P load from Lake Okeechobee enters the EAA and other small basins,

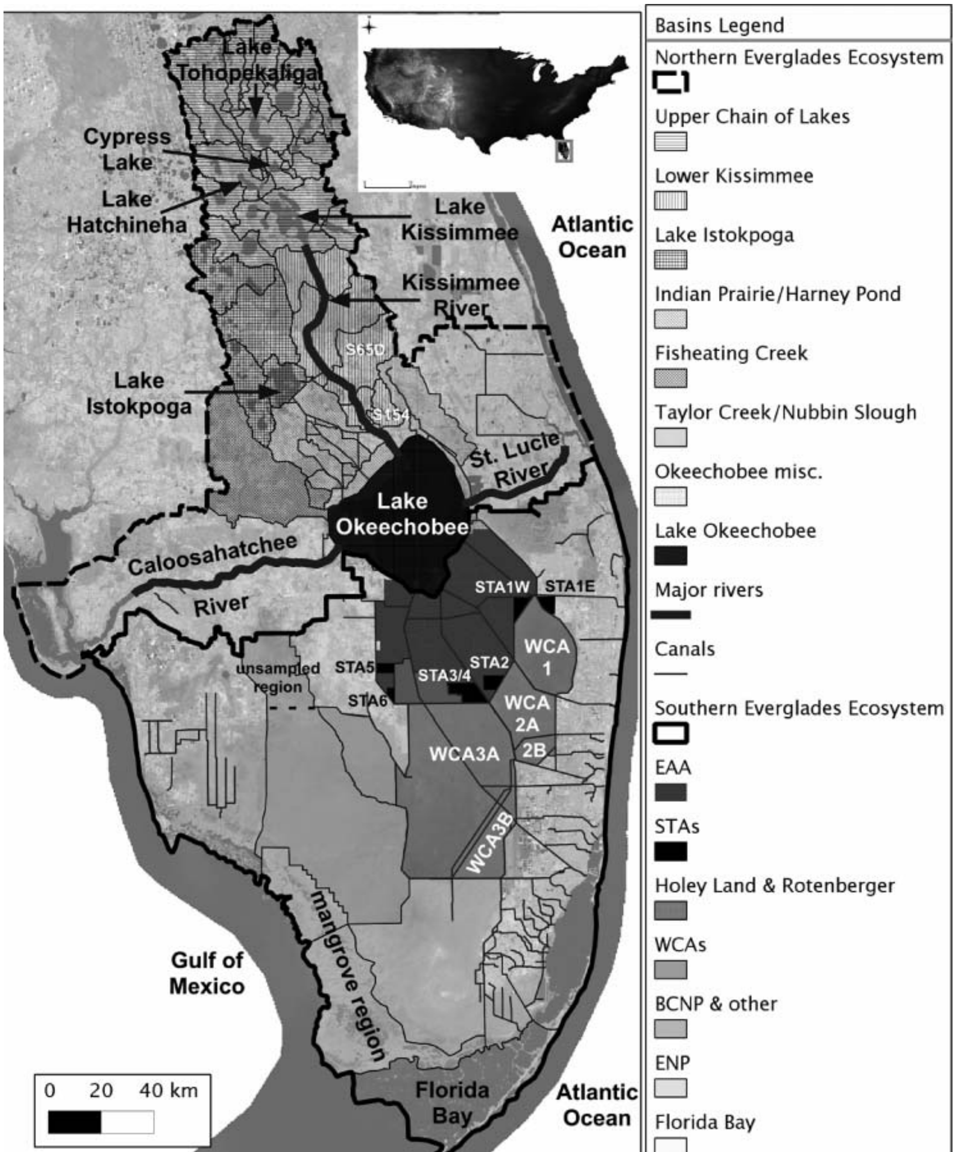

FIGURE 2. Map showing various hydrologic units that were sampled in the Northern Everglades Ecosystem (NEE) and Southern Everglades Ecosystem (SEE). In the NEE, the Lake Okeechobee Basin (LOB) is the sum of the Upper Chain of Lakes Basin, Lake Istokpoga Basin, and the Northern Lake Okeechobee Basin. The larger Northern Lake Okeechobee Basin (Table 1) includes the Lower Kissimmee, Indian Prairie/Harney Pond, Fisheating Creek, Taylor Creek/Nubbin Slough, and Okeechobee misc. Basins. In the SEE, the mangrove region and Florida Bay were not included in the sampling. EAA = Everglades Agricultural Area; STAs = Stormwater Treatment Areas; WCAs = Water Conservation Areas; BCNP & other = Big Cypress National Preserve, including a northern sub-area outside of the Preserve; ENP = Everglades National Park freshwater wetland area.

which contribute P loads downstream to the WCAs. The P load from the EAA basin to the WCAs during the past three decades was estimated as 170 mt per year (Van Horn and Wade, 2010).

Autochthonous nutrient inputs into the WCAs have resulted in significant alterations to the indigenous system with large expansions of cattail (*Typha domingensis*) replacing the predominant plant communities (Craft and Richardson, 1997; Daoust and Childers, 2004; Davis, 1991; Davis, 1994; Noe et al., 2001; Newman et al., 1998; Richardson et al., 2008; Sklar et al., 2005). Extensive documentation of the temporal and spatial distribution of soil nutrients across the northern marshes of the Everglades has delineated areas with highly P-enriched conditions near the source and P-limiting conditions further from these inputs (Bruland et al., 2007; Childers et al., 2003; Corstanje et al., 2006; Craft and Richardson, 1993a, 1993b; DeBusk et al., 1994, 2001; Marchant et al., 2009; Newman et al., 1997; Reddy et al.,1993; Rivero et al., 2007; Scheidt and Kalla, 2007). Between these two extremes there exists a gradient in quality and quantity of organic matter, nutrient accumulation, microbial communities and biogeochemical cycles, resulting in diverse algal/ microbial/plant communities with distinct biogeochemical processes (Noe et al., 2002; Penton and Newman, 2007; Reddy et al., 1999; White and Reddy, 1999, 2001; Richardson, 2008). These biogeochemical gradients and hot spots are frequently observed in the detrital layer, and in the soil and water columns of various hydrologic units of the Everglades.

Soils and sediments serve as long-term sinks for P and store the majority of P in the ecosystem. Storage of P in vegetation and other biotic communities of wetlands and in phytoplankton of lakes tend to be small and short term. Thus, our discussion primarily focuses on P storage in soils and sediments and floc/detrital layer. *Floc* refers to recently accreted material of partially decomposed detrital matter originating from microbes, periphyton, and macrophytes, and particulate inorganic material. In wetlands, during dry periods, dried floc material can become an integral part of surface soils. The genesis of this new material is relatively slow (accretion rates range from 0.1 to 1 cm per year), but can affect the nutrient retention characteristics of wetlands and shallow lakes. Productive wetland systems accrete organic matter over time (ultimately forming peat) that has different physical and biological characteristics than the underlying soil (Craft and Richardson, 1993a, 1993b; Reddy et al., 1993). Eutrophic lakes and nutrient enriched wetlands typically exhibit high rates of floc accumulation. Floc can act as a sink or source of nutrients to the overlying water column and serves as an indicator of the nutrient retention characteristics of a wetland. Floc is often the most biologically active soil fraction and is usually of highest quality with respect to degradability (DeBusk and Reddy, 1998).

Effective P control strategies can only be implemented if the storage, fate, and transport of P in uplands, ditches, canals, wetlands, and streams of the Greater Everglades Ecosystem are understood. Herein, we review and synthesize the results of recent studies conducted in the Greater Everglades Ecosystem on (a) the storage of P in soils and sediments throughout the Northern and Southern Everglades Ecosystems, (b) the effect of land use on P storage, (c) the influence of chemical form in the regulation of P reactivity and mobility, and (d) how the biogeochemical processes influence restoration activities in South Florida.

2 PHOSPHORUS STORAGE IN SOILS AND SEDIMENTS

Extensive spatial sampling and field experimentation has provided a reasonably comprehensive understanding of the P storages and fluxes within the natural areas of the Everglades wetlands (Cohen et al., 2009; Osborne et al., 2010; Reddy et al., 2005b). With the exception of Lake Okeechobee, similar spatial data sets are not available for the NEE, thus making it somewhat difficult to evaluate the total P storage in the system. Nevertheless, sufficient data exist to provide a generalized, regional landscape synthesis of P storages and fluxes in much of south Florida.

Phosphorus stored in surficial (floc and 0–10 cm) wetland soils and lake sediments of various hydrologic units of the Greater Everglades Ecosystem shows distinct north–south gradients, with higher storage in the NEE as compared to the SEE (Figure 3). Areal storage values take into consideration

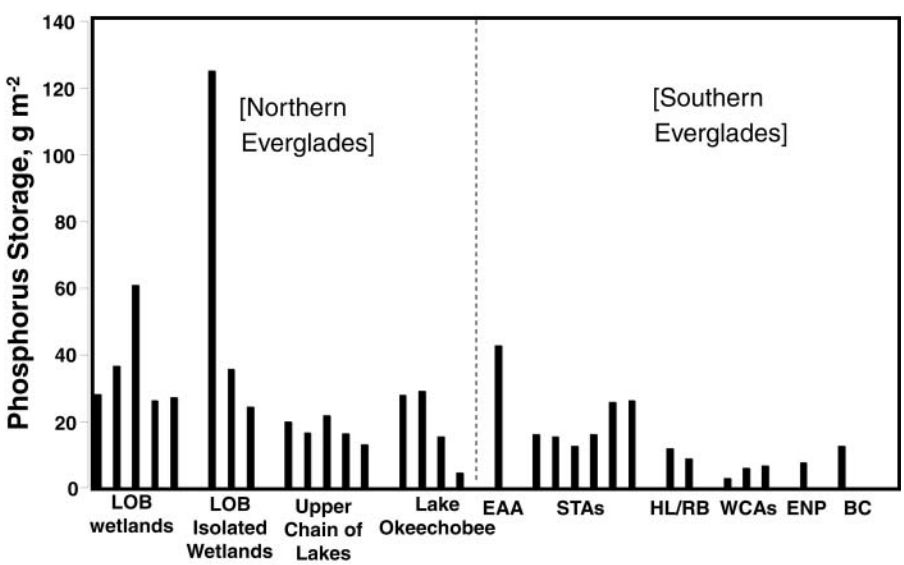

FIGURE 3. Total phosphorus storage in soils/sediments (0–10 cm) of select hydrologic units of the Northern Everglades Ecosystem (NEE). LOB = Lake Okeechobee Basin wetlands; Isolated wetlands includes in various land uses: OK-D = dairy; OK-IP = improved pasture; and OK-UP = unimproved pasture; Lake Okeechobee sediments: LO-M = mud; LO-S = sand; LO-L = littoral; and LO-P = peat.

differences in bulk densities of soils and sediments. On average, P storage per unit area of wetlands of the Everglades wetlands is less than other hydrologic units. High-P storage values were noted in areas of intensive land use, including dairies and other agricultural activities of the NEE. Similarly, the EAA and STAs stored more P in surface soils than the WCAs and other Everglades wetlands. Phosphorus enrichment in surface soils of EAA is due to a combination of peat oxidation (soil subsidence) and long-term P fertilizer application. Estimated P storage values for floc (where present) and surface 0–10 cm soils or sediments are presented in Table 1.

TABLE 1. Phosphorus storage (mt = metric tons) in soils/sediments (for the LOB)

Hydrologic units	Area (km^2)	Soil P storage (mt/km^2)	Soil P storage (mt)	% of total P stored in ecosystem
Northern Everglades Ecosystem				
Upper Chain of Lakes Basin[a]	4,160	11	46,910	21.8
Lake Istokpoga Basin[a]	1,580	13	20,870	9.4
Northern Lake Okeechobee Basin[a]	4,840	21	102,050	47.5
Upper Chain of Lakes–lake sediments[b]	371	16	5,900	2.7
Lake Istokpoga–lake sediments[b]	112	22	2,460	1.1
Lake Okeechobee sediments–Total[c]	1,741	21	36,440	17.0
Lake Okeechobee sediments–Mud[c]	766	28	21,390	10.0
Lake Okeechobee sediments–Sand[c]	296	29	8,620	4.0
Lake Okeechobee sediments–Littoral[c]	296	16	4,610	2.1
Lake Okeechobee sediments–Peat[c]	383	5	1,820	0.8
Total	12,804	19	214,630	
Southern Everglades Ecosystem				
Everglades Agricultural Area (EAA)[d]	2,095	59	123,210	60.6
Stormwater Treatment Areas (STAs)[e]	182	20	3,550	1.7
Water Conservation Area 1 (WCA-1)[f]	566	4	2,380	1.2
Water Conservation Area 2 (WCA-2)[F]	537	9	4,830	2.4
Water Conservation Area 3 (WCA-3)[F]	2,393	7	16,510	8.1
Holey Land Wildlife Management Area[F]	140	14	1,950	1.0
Rotenberger Wildlife Management Area[F]	96	8	730	0.4
Everglades National Park (ENP)[f]	5,560	6	32,250	15.9
Big Cypress National Preserve (BCNP)[F]	2,280	8	18,010	8.9
Total	13,849	15	203,420	100
Greater Everglades Ecosystem	26,183	17	418,050	

Note. The basin surface area values for the Upper Chain of Lakes and Istokpoga Basins do not include the area of the associated lake sediments. P storage includes A, E, and Bh horizons for uplands; soil depth of up to 30 cm for wetlands; 0–10 cm depth for lake sediments and SEE soils, of various hydrologic units of the Everglades ecosystem. * = Phosphorus storage in floc + 10 cm soil. Floc P represents 30% of total P storage. Data sources:

[a]SWET, 2008.

[b]Belmont et al., 2009.

[c]Fisher et al., 2001.

[d]Wright, 2009; WBL, 1998.

[e]WBL, 2009.

[f]Reddy et al., 2005b.

TABLE 2. Selected physicochemical properties of surface and subsurface soils of wetlands as influenced by select land use activities in Lake Okeechobee Basin in the Northern Everglades Ecosystem (Dunne et al., 2010)

Parameter	Units	Soil (0–10 cm depth)	Soil (10–30 cm depth)
Dairy			
Bulk density	g cm^{-3}	1.00 ± 0.1	1.25 ± 0.1
TIP	mg kg^{-1}	717 ± 181	245 ± 80
TP	mg kg^{-1}	1253 ± 230	394 ± 67
TN	g kg^{-1}	12.4 ± 2	8.0 ± 2
TC	g kg^{-1}	190 ± 29	149 ± 36
Improved pasture			
Bulk density	g cm^{-3}	1.01	1.35
TIP	mg kg^{-1}	44 ± 4	18 ± 2
TP	mg kg^{-1}	354 ± 34	147 ± 18
TN	g kg^{-1}	7.3 ± 1	3.3 ± 1
TC	g kg^{-1}	106 ± 11	56 ± 9
Unimproved pasture			
Bulk density	g cm^{-3}	0.78 ± 0.1	1.32 ± 0.1
TIP	mg kg^{-1}	37 ± 4	10 ± 2
TP	mg kg^{-1}	315 ± 33	107 ± 23
TN	g kg^{-1}	8.8 ± 1	2.8 ± 1
TC	g kg^{-1}	151 ± 22	56 ± 17

Note. TIP = total inorganic P; TP = total phosphorus. TN = total nitrogen; TC = total carbon.

2.1 Northern Everglades Ecosystem

Estimated P storage values (Table 1) are based on average total P concentration and bulk density values for each hydrologic unit (Tables 2 and 3). Average TP concentrations for each hydrologic unit can vary with sample size and distribution of sampling locations. Sampling size was relatively small in the Northern LOB and the Upper Chain of Lakes Basin given the total area of these hydrologic units. Nevertheless, these estimates provide a first approximation of P storage. Total P storage in the NEE (including uplands and wetlands in the basins of LOB, Upper Chain of Lakes, Lake Istokpoga, and Lake Okeechobee) is estimated at 215,000 metric tons (Table 1).

TABLE 3. Selected physicochemical properties of surface soils of wetlands in the Northern Lake Okeechobee Basin (Reddy et al., 1995)

Parameter	Units	S-154	S65-D	TC/NS	IPB	FCB
Bulk density	g cm^{-3}	0.46	0.52	0.57	0.78	0.90
TP	mg kg^{-1}	615	702	1079	338	304
TC	g kg^{-1}	110	151	101	105	85

Note. TIP = total inorganic P; TP = total phosphorus; TC = total carbon. TC/NS = Taylor Creek/Nubbin Slough; IPB = Indian Prairie Basin; and FCB = Fisheating Creek Basin.

2.1.1 Wetland and Upland Soils

Approximately 80% of the P imported into the NEE remains in upland soils, while 10% is retained in wetlands and the remaining 10% is transferred through the wetlands downstream into Lake Okeechobee (Reddy et al., 1996; Soil and Water Engineering Technology [SWET], 2008). Isolated wetlands in agriculturally intensive land use areas (e.g., dairy) have accumulated high levels of P compared to improved and unimproved pasture areas (Table 2; Dunne et al., 2010). Wetlands in the Taylor Creek and Nubbin Sloughs have accumulated more P than wetlands in other areas of the drainage basin (Table 3; Reddy et al., 1996; SWET, 2008). Overall, the Northern LOB, Upper Chain of Lakes Basin, and Lake Istokpoga Basin contain approximately 170,000 metric tons of P in surface soils, representing ∼79% of total P storage in the NEE (Table 1). Phosphorus storage estimates in upland soils were based on the whole soil profile, whereas P storage in wetland soils was restricted to the surface 0–10 cm soils (SWET, 2008). In an earlier study, Reddy et al. (1996) estimated a total storage of 190,000 metric tons of P in upland soils (A, E, and Bh horizons) and 33,000 metric tons in wetland soils (0–30 cm depth), suggesting a reduction in P storage. However, this comparison is based on limited data sets during both sampling periods and approximates P storage in the NEE.

2.1.2 Shallow Lakes

Total P storage in surface sediments of lakes was estimated to range from 440 to 36,000 mt of P. High values represent P storage in Lake Okeechobee and low values for storage in Lake Hatchineha, reflecting the relative sizes of the lakes. Accumulation of P in surface sediments represents approximately 30–60 years of P loading to the lakes (Belmont et al., 2009). Phosphorus loading from the LOB to Lake Okeechobee is approximately 500 mt per year (5–year moving average 1981–2009). Except during drought years, P loadings from the drainage basin to the lake have remained consistently high. During the past 30 years (1981–2009), the total P load from the LOB to the lake is estimated to be 14,000 mt P. The external P load represents approximately 40% of the P in the surface sediments of the whole lake and 67% of the P accumulated in the surface 0–10 cm sediments of the mud zone. Lake Okeechobee sediments contains approximately 36,000 mt of P in the surface 10 cm sediments, with approximately 59, 24, 13, and 4% of total storage present in mud, sand, littoral, and peat sediments, respectively (Table 1). Phosphorus budgets for Lake Okeechobee over the last 10 years suggest that P had accumulated in the sediments at the rate 300 mt P per year, representing a net increase of 10 percent in total P mass of surface sediments (Fisher et al., 2001).

2.2 Southern Everglades Ecosystem

Approximately two thirds of the P load from Lake Okeechobee is discharged to the St. Lucie and Caloosahatchee estuaries, respectively. The remaining one third of the P load enters the EAA and other small basins. The EAA is subsequently the primary source of P loads to the downstream STAs and WCAs. Total P storage in surface soils and floc in the entire SEE was estimated to be 200,000 mt (Table 1),

2.2.1 Everglades Agricultural Area

While only 15% of the land area of the SEE, the estimated legacy total P in surface soils of the EAA is 123,000 mt, representing approximately 61% of P stored in the SEE (Table 1). Aggregated to basin-wide values, the mass of P per unit area in the EAA is almost 3 times greater than any of the other NEE or SEE basins reflecting a hot spot of P just upgradient from the Everglades (Table 1). The best management practices (BMPs) presently in place in the EAA have effectively reduced P discharges from the basin (Daroub et al., 2011). The average P load discharged from the EAA (1980–2009) to WCAs and now to STAs is 170 ± 85 mt P, whereas the WY (water year) 2009 load was 129 mt P (Van Horn and Wade, 2010). The BMPs included very little or no P application, suggesting internal P turnover, not P fertilization as the major source of P in the EAA. Consequently, decomposition of soil organic matter and discharge of water from the EAA into STAs and WCAs will continue to dominate the present P loads.

2.2.2 Stormwater Treatment Areas

STAs, large surface water treatment marshes established on former agriculture lands, were strategically established in SEE to capture the P load from the EAA before water enters the WCAs. Thus far, the STAs have been very effective in removing inflow P, with approximately 60–80% of the added P retained in these treatment wetlands (Pietro et al., 2010). Since initial operation, STAs have accumulated 1200 mt P in the floc and surface soils. Total P storage in surface soils and floc sampled in 2007 was estimated to be 3550 mt (Table 1), therefore, P added to STAs accounts for approximately 34% of P stored, while the remaining storage is from native soils and subsurface P mined by vegetation and deposited back into floc as detrital matter (White et al., 2004, 2006).

2.2.3 Freshwater Wetlands

Wetlands outside of the EAA and STAs include the WCAs, Holey Land and Rotenberger Wildlife Management Areas, Big Cypress National Preserve, and Everglades National Park. Combined, the ecosystem contain approximately 77,000 mt P in surface floc and 0–10 cm soil (Table 1). These wetland areas represent 84% of the total area of the SEE, and contain 38% of the stored P. In WCA-1 and WCA-2, sample sites were denser in P enriched areas than P-unenriched areas, because the intent of the sampling was to capture the zone of enrichment. Thus, aggregating the sample point data to a WCA-wide average may slightly overestimate the values calculated for total P concentrations and P storage. However, the differences caused by these factors may be masked by the spatial variability within each unit. Spatial patterns of soil P in WCAs and ENP were recently documented (see Osborne et al., 2011). Total P concentrations in soils and sediments show a distinct gradient from the northern to southern regions of the Everglades wetlands, with low values in soils of the ENP. WCAs have been very effective in accumulating P in floc and soils (Bruland et al., 2006; Corstanje et al., 2006; DeBusk et al., 1994, 2001; Fisher et al., 2001; Newman et al., 1997).

Typically, P accumulation is greater in areas closer to surface water inflow points and decreases exponentially as a function distance from inflow (Reddy et al., 1993). For example, P accumulation rates of 0.11–1.14 g P m^{-2} yr^{-1} have been reported for the WCA-2A of the Everglades (Craft and Richardson, 1993a, 1993b; Reddy et al., 1993). The distinct gradients with distance are noted in areas adjacent to canals and inflow structures, highlighting the connection between hydrologic and nutrient loading. In contrast, in overdrained areas of the system, oxidation of organic matter, resulting from microbial decomposition processes or fire, increases soil inorganic P levels, as observed for the WCA-3A, Holey Land and Rotenberger Wildlife Management Areas (Smith et al., 2001), and EAA soils. Much of the nutrient-loading effects are confined to the shallow soil layers.

Wetlands in the ENP, the final link in the freshwater hydrologic chain from the NEE through the SEE to the estuaries and sea, is not subject to the same high loads as the WCAs. However, the ENP is still experiencing eutrophication via P loading from water conveyance structures. Recent soil monitoring in ENPs Taylor Slough and upper Shark River Slough suggest significant soil P impact (Reddy et al., 2008), as described further in a later section. Approximately, 32,250 mt of P is stored in surface soils of the ENP freshwater wetlands, which accounts for 16% of the P storage in the SEE (Table 1). The freshwater wetlands of the ENP represent 40% of the total area of SEE.

2.3 Greater Everglades Ecosystem—Regional Patterns

When aggregating P storage mass per unit area within each of the large basins considered here (Table 1), it is suggested that the NEE basins contain 15–20 mt P per km^2. The STAs and Holey Land Wildlife Management Area of the SEE have similar landscape P concentrations (14–20 mt per km^2). Downstream of all of these basins, the Everglades wetlands generally exhibit a P mass per unit area that is less than half of those values from the more northern regional basins. Of significant importance to restoration objectives,

TABLE 4. Selected physicochemical properties of surface sediments of Lake Istokpoga and Upper Chain of Lakes in the Northern Everglades Ecosystem (Belmont et al., 2009)

Parameter	Units	Cypress	Hatchineha	Istokpoga	Kissimmee	Tohopekaliga
Bulk density	g cm^{-3}	0.21 ± 0.22	0.21 ± 0.26	0.49 ± 0.52	0.18 ± 0.23	0.70 ± 0.34
TP	mg kg^{-1}	955 ± 753	797 ± 511	449 ± 493	919 ± 722	188 ± 146
TC	g kg^{-1}	120 ± 89	116 ± 74	91 ± 77	154 ± 118	23 ± 22

Note. TIP = total inorganic P; TP = total phosphorus; TC = total carbon.

the EAA, situated between the Lake Okeechobee and Everglades wetland natural systems, has more than triple (approximately 60 mt P per km^2) the mass per area storage of any other Greater Everglades Ecosystem basins. The possibility that internal P loading and redistribution of this legacy P could obviate restoration goals for long periods is a disturbing realization, but one that must be addressed for realistic implementation of Everglades restoration projects. The relative scale of the effects of legacy P depends on land use, which in turn influences the forms of P are stored in or exported from the system.

3 LAND USE EFFECTS ON SOIL PHOSPHORUS

As described previously, in the LOB, the total P content of surface soils of wetlands located in dairy land use was approximately two- to threefold greater than the P content of improved and unimproved pasture wetland soils (Table 2). Similarly, wetland soils in the Taylor Creek/Nubbin Slough Basin were highly enriched compared to other subbasins in LOB (Table 3). Total P concentrations of surface sediments of Lake Istokpoga and Upper Chain of Lakes in the NEE ranged 188 to 955 mg P kg^{-1} (Table 4). Low concentrations of P were found in Lake Tohopekaliga than other lakes in the drainage basin. Lake Okeechobee sediment total P content ranged from 220–1030 mg P kg^{-1}, higher values were measured in mud zone sediments, and lower values were observed in sand and peat sediments (Table 5). The

TABLE 5. Selected physicochemical properties of surface sediments of Lake Okeechobee in the Northern Everglades Ecosystem (Fisher et al., 2001)

Parameter	Units	Mud	Sand	Littoral	Peat
Bulk density	g cm^{-3}	0.27 ± 0.28	1.3 ± 0.3	0.33 ± 0.45	0.19 ± 0.09
TIP	mg kg^{-1}	777 ± 274	233 ± 361	138 ± 117	172 ± 138
TP	mg kg^{-1}	1034 ± 376	224 ± 271	472 ± 493	250 ± 209
TN	g kg^{-1}	9 ± 4	0.37 ± 0.51	18 ± 16	20 ± 6
TC	g kg^{-1}	143 ± 54	10.3 ± 9.9	222 ± 191	358 ± 95

Note. TIP = total inorganic P; TP = total phosphorus. TN = total nitrogen; TC = total carbon.

large differences in total P contents amongst various units in the same basin underscore the effect of land use on soil P enrichment.

In the SEE basin, land use can be compared for agricultural systems (EAA), treatment wetlands (STAs) and natural systems. As expected, the total P content of EAA surface soils were highly enriched, not only due to long-term application of P fertilizers, but also because of oxidation of these highly organic soils. Managing peat soils for crops traditionally grown in this region, vegetables and sugarcane, is accomplished by keeping the soils drained. This has, in turn, resulted in a loss at a rate of 2–3 cm of soil per year and has added to the mineral matter including P enrichment of remnant soil layers through loss of carbon (Wright, 2009).

The runoff from the EAA is passed through STAs, to remove P, before being discharged into the Everglades. Presently six STAs are in full operation and have been in service for variable time periods. During their tenure as treatment systems, STAs have accumulated significant amounts of loosely consolidated floc material on top of the surface soils. Both floc and soil have shown significant P enrichment. The floc layer accounts for approximately 30% of the total P storage in floc + surface 0–10 cm soil, and 100% of water column P retained within the STA (WBL, 2009). Total P contents in the floc ranged from 640 to 1200 mg kg^{-1}, with low values observed in youngest STA and high values recorded the longest running STA (Table 6). Total P contents of STA soils (0–10 cm) ranged from 160 to 600 mg kg^{-1}, reflecting characteristics similar to those of native soils. Low total P values were recorded in STA-1E, which included primarily mineral soils. However, in surface soils of STA-1W, approximately 70% of P was derived from recently accreted material, while the remaining 30% represented native soils. Phosphorus accumulation by STAs varied temporally and among the STAs. Several factors

TABLE 6. Selected physicochemical properties of floc and surface soils of the Stormwater Treatment Areas of the Southern Everglades Ecosystem (data from SFWMD, summarized by WBL, 2009)

Parameter	Units	STA-1E	STA-1W	STA-2	STA-3/4	STA-5	STA-6
Period of record	Years	3	13	8	4	9	8
Floc							
Bulk density	g cm^{-3}	0.26 ± 0	0.1 ± 0.03	0.15 ± 0.04	0.11 ± 0.04	0.11 ± 0.03	0.04 ± 0.03
TP	mg kg^{-1}	644 ± 0*	1192 ± 261	870 ± 167	1072 ± 130	1187 ± 485	1028 ± 520
TN	g kg^{-1}	15 ± 0*	23 ± 2	14 ± 3	18 ± 2	28 ± 2	—
TC	g kg^{-1}	n/a	274 ± 13	242 ± 32	275 ± 22	375 ± 28	—
0–10 cm soil							
Bulk density	g cm^{-3}	1.01 ± 0.37	0.26 ± 0.09	0.25 ± 0.08	0.27 ± 0.09	0.42 ± 0.13	0.58 ± 0.24
TP	mg kg^{-1}	160 ± 135	598 ± 316	511 ± 186	599 ± 175	615 ± 396	455 ± 236
TN	g kg^{-1}	5.6 ± 4.8	26 ± 7	28 ± 2	25 ± 5	21 ± 6	21 ± 6
TC	g kg^{-1}	82 ± 71	398 ± 69	452 ± 38	381 ± 79	297 ± 94	266 ± 79

Note. Soil samples were collected in 2007 for STA-1E, STA1W, STA2, STA3/4, and STA5, and in 2004 for STA6.

influence P removal efficiency of STAs, including antecedent land use, nutrient and hydraulic loading, vegetation composition and condition, soil type, cell topography, cell size and shape, extreme weather conditions, modification activities to improve performance (enhancement activities), and regional operations (Pietro et al., 2010).

In the natural areas, land use P effects are not spatially distributed throughout the entire region, but with the exception of areas that experienced fires and overdrainage, are generally directional, with high values closer to the canals and inflow structures and reaching background levels in the interior (Table 7; DeBusk et al., 1994, 2001; Newman et al., 1997). In WCA-1, total P ranged from 110 to 1050 mg kg^{-1} (0–10 cm) with a mean of 405 mg kg^{-1}, while total P contents in the floc were higher, in the range of 230–1460 mg kg^{-1} with a mean of 630 mg kg^{-1} (Corstanje et al., 2006). In WCA-2, TP ranged from 150 to 1700 mg kg^{-1} (0–10 cm) with a mean of 551 mg kg^{-1}, while TP concentrations in the floc were in the range of 194–1865 mg kg^{-1} (0–10 cm) with a mean of 551 mg kg^{-1} (Rivero et al., 2007; White and Reddy, 2000). DeBusk et al. (2001) observed 48 and 73% of the WCA-2 area was enriched with surface TP values >500 mg kg^{-1},the value above which is considered to indicate P enrichment. In contrast, in 2003, Rivero et al. (2007) estimated that 65% of the floc and 26% surface soils exceeded a value of 500 mg kg^{-1}, suggesting a decrease in P enrichment. However, some of these differences may be due to different soil-sampling methodologies and spatial analysis of the data used during sampling period of 1992, 1998, and 2003. In addition, it is reasonable to speculate that the establishment of STAs has significantly decreased P loads to WCA-2. From 1992 to 2007, approximately 21–30%% of WCA-3 area had total P concentrations of >500 mg kg^{-1} in the 0–10 cm layer indicating P enrichment above historic concentrations levels (Bruland et al., 2006, 2007).

Average total P concentrations in ENP were 140 and 310 mg P kg^{-1} for floc and surface (0–10 cm) soils, respectively (Osborne et al., 2010; Reddy et al., 2005b; Table 7). The relatively low soil total P concentrations found in ENP suggest that this hydrologic unit remains the most pristine of the Everglades system in terms of P enrichment. Most freshwater floc and soil P were observed in the peat accreting areas of ENP, Shark River Slough (mean total P 330 mg kg^{-1}) and to a lesser extent, Taylor Slough (TS; mean total P 190 mg kg^{-1}). These two prominent drainage features within the landscape have extended hydroperiods when compared to the surrounding marl prairies to the east and west (Davis et al., 2005).

A finding of particular interest concerning soil total P, was the lack of an enrichment signature in TS by landscape scale investigations (Osborne et al., 2010; Reddy et al., 2005b). Data from TS showed no samples exceeded the threshold for P impact of 500 mg P kg^{-1}. This observation is supported by Childers et al. (2003) who established soil transects in TS in 1999 and reported

TABLE 7. Selected physicochemical properties of surface floc (detrital matter and benthic periphyton) and soils (0–10 cm depth) in the Southern Everglades Ecosystem

Parameter	Units	Floc	Soil (0–10 cm depth)
EAA			$n = 29$
Bulk density	g cm^{-3}	—	0.42
TIP	mg kg^{-1}	—	334 ± 335
TP	mg kg^{-1}	—	$1,021 \pm 499$
WCA-1		$n = 124$	$n = 131$
Bulk density	g cm^{-3}	0.022 ± 0.02	0.073 ± 0.035
TIP	mg kg^{-1}	159 ± 93	80 ± 50
TP	mg kg^{-1}	634 ± 268	405 ± 156
TN	g kg^{-1}	33 ± 5.5	33 ± 4.8
TC	g kg^{-1}	447 ± 29	473 ± 32
WCA-2		$n = 131$	$n = 131$
Bulk density	g cm^{-3}	0.046 ± 0.032	0.116 ± 0.05
TIP	mg kg^{-1}	232 ± 141	133 ± 140
TP	mg kg^{-1}	776 ± 383	531 ± 311
TN	g kg^{-1}	27 ± 5.3	26 ± 6.2
TC	g kg^{-1}	402 ± 46	420 ± 51
WCA-3		$n = 149$	$n = 389$
Bulk density	g cm^{-3}	0.031 ± 0.025	0.16 ± 0.15
TIP	mg kg^{-1}	165 ± 135	97 ± 90
TP	mg kg^{-1}	544 ± 267	417 ± 171
TN	g kg^{-1}	31 ± 8.7	28 ± 8.2
TC	g kg^{-1}	401 ± 76	391 ± 108
Holeyland		$n = 15$	$n = 54$
Bulk density	g cm^{-3}	0.055 ± 0.022	0.198 ± 0.069
TIP	mg kg^{-1}	307 ± 124	258 ± 311
TP	mg kg^{-1}	905 ± 228	610 ± 281
TN	g kg^{-1}	25 ± 2.3	23 ± 6.7
TC	g kg^{-1}	417 ± 27	368 ± 101
Rotenberger		$n = 43$	$n = 93$
Bulk density	g cm^{-3}	0.11 ± 0.05	0.29 ± 0.15
TIP	mg kg^{-1}	71 ± 79	81 ± 81
TP	mg kg^{-1}	266 ± 313	315 ± 192
TN	g kg^{-1}	14 ± 7.2	17 ± 11
TC	g kg^{-1}	258 ± 29	278 ± 125
ENP		$n = 142$	$n = 310$
Bulk density	g cm^{-3}	0.12 ± 0.09	0.25 ± 0.16
TIP	mg kg^{-1}	40 ± 37	70 ± 51
TP	mg kg^{-1}	143 ± 115	312 ± 182
TN	g kg^{-1}	14 ± 6.6	19 ± 11
TC	g kg^{-1}	230 ± 56	273 ± 119
Big Cypress		$n = 178$	$n = 209$
Bulk density	g cm^{-3}	0.15 ± 0.09	0.64 ± 0.31
TIP	mg kg^{-1}	47 ± 34	45 ± 63
TP	mg kg^{-1}	204 ± 129	198 ± 133
TN	g kg^{-1}	14 ± 5.6	8.0 ± 5.7
TC	g kg^{-1}	208 ± 53	112 ± 73

Note. TIP = total inorganic; TP = total phosphorus (Reddy et al., 2005b).

soil total P ranged from 150 to 250 mg kg^{-1}. However, more recent investigations of TS soils (Reddy et al., 2008) revealed significant P enrichment in the upper reaches of TS, ranging from 450–1200 mg kg^{-1} and an enrichment front extending 7 km downstream of the inflow from the S-332 control structure. Reddy et al. (2008) also reported extensive enrichment along transects from Tamiami Trail southward up to 7 km into SRS. These data suggest that some landscape scale sampling is too coarse to identify localized P enrichment gradients in ENP at this time. Presently, in the ENP, the total P data indicate only 2.3% of floc and 12.5% of surface soils (including mangrove interface regions in southern ENP where marine influence is significant) exceed the enrichment threshold. However, existence of enrichment zones in the northern portion of the ENP, similar to those in the northern Everglades marshes, clearly indicate the potential for future P enrichment of ENP.

4 PHOSPHORUS FORMS

Phosphorus is stored both in organic and inorganic forms in soils. The relative proportion of each of the forms depends on soil types in the landscape (mineral vs. organic) and source and forms of P added to the system. Most inorganic P compounds in soils fall into one of two groups: those containing calcium and those containing iron and aluminum. The availability of P in alkaline soils is determined largely by the solubility of the calcium compounds in which the P is associated. In acid soils, iron and aluminum minerals regulate the solubility of inorganic P. Organic P commonly dominates the total P in wetlands and usually comprises more than half of the soil P (Reddy et al., 2005b). Organic P forms extracted from wetland soils include: inositol phosphates, phospholipids, and nucleic acids (Turner et al., 2006). As much as one third of the inositol P can be complexed with humic and fulvic acids, thereby reducing bioavailability of this organic P.

4.1 Inorganic P Forms

Soils in the NEE are dominated by mineral matter in contrast to the highly organic soils in the SEE. This difference is reflected in a larger proportion of total P in the inorganic pool in soils and sediments in NEE than soils in SEE (Tables 2–7). In LOB, wetlands are dominated by mineral soils (Spodosols) however, surface soils in these systems have a relatively high organic matter content compared to upland soils. Iron and Al-bound P in these soils accounted for 17–43% of total P in wetland soils and 20–70% of total P in stream sediments (Reddy et al., 1995). Organic P accounted for more that 50% of total P, reflecting the high organic matter content of wetland soils. Surface wetland soils located within dairy land use areas contained a larger proportion of P as Fe/Al-bound P, whereas wetland soils within improved and unimproved pasture areas contain a larger proportion of P in organic pools (Dunne et al., 2010). Soils in LOB basin generally have high concentrations of oxalate Fe and Al, and inorganic P retention is governed by these metals.

In Lake Okeechobee, mud, sand, and littoral sediments are dominated by mineral matter, while sediments south of the lake are dominated by peat deposits (Fisher et al., 2001). The mud sediments (occupy 40% of the lake) are dominated by Ca and Mg-bound P (65% of total P) followed by residual P (28% of total P), with low exchangeable (2% of total P) and Fe and Al-bound P (5% of total P; Olila et al., 1995). The peat and littoral sediments of Lake Okeechobee, however, have higher exchangeable P (9–10% of total P) and Fe and Al-bound P (6–18% of total P). Two mechanisms that control exchangeable P have been suggested for Lake Okeechobee mud sediments under different redox conditions. Under oxic conditions, Fe appears to control the amount of exchangeable P, while under anoxic conditions, Ca and Mg seem to control exchangeable P (Moore and Reddy, 1994; Olila et al., 1995).

Similarly, with the exception of WCA1, the predominantly anaerobic soils in the SEE are dominated by Ca and Mg-bound P (Reddy et al., 1998a). In surficial soils, Ca and Mg-bound P accounted for 14–68% of total P, with the highest values observed in the Holeyland Wildlife Management Area soils and lowest values in WCA-1 soils. The inorganic P content in SEE soils is highly variable and ranged from less than 10% to up to 80% of total P. High values were noted in soils subjected to excessive drainage and fire, such as those found in northern part of WCA-3 and Holeyland and Rotenberger Wildlife Management Areas (Smith et al., 2001). Inorganic P concentrations across the Everglades landscape are higher in surface soils and decrease with depth. Iron and Al-bound P accounted for 1–24% of total P, with the highest values measured in EAA soils (Reddy et al., 1998a). Iron and Al-bound P is typically extracted with NaOH, which also extracts humic and fulvic acids from organic soils resulting in dark colored solutions. Analyzing these solutions for P may result in overestimation of inorganic P due to colormetric interference.

In Florida Bay sediments, at the bay–mangrove ecotone, Ca-bound P accounted for approximately 56% of total P and 96% of inorganic P. Calcium-bound P was in the range (34–151 mg P kg^{-1}) reported for coarse-grained low organic sediments, while the organic P associated with this fraction was slightly ($\sim$10%) higher than those reported for other carbonate systems (Koch et al., 2001).

4.2 Organic P Forms

A large proportion of the P in wetland soils, especially in peats, occurs in organic forms, suggesting the importance of organic P sequestration in the long-term stabilization of P in wetlands. The range of organic P forms found in soils include: phospholipids, nucleic acids, inositol phosphates, glucose-6-phosphates, glycerophosphate, phosphoproteins and polymeric organic P of high molecular weight compounds (Stewart and Tiessen, 1987). Organic P forms can be generally grouped into (a) easily decomposable organic P (nucleic acids, phospholipids and sugar phosphates) and (b) slowly decomposable organic P (inositol phosphates or phytin).

Organic P is typically measured only as part of sequential fractionation schemes (e.g., Ivanoff et al., 1998). This is partly due to the analytical difficulties in speciating the multitude of phosphorus compounds present in environmental samples. Recent advances in nuclear magnetic resonance (NMR) techniques, specifically solution ^{31}P-NMR, allow identification of specific organic compounds (Cheesman, 2010; Turner and Newman, 2005; Turner et al., 2006). An example of NMR spectra identifying various organic pools in WCA-2A soils is presented in Figure 4 (Turner et al., 2006).

In LOB isolated wetlands, approximately 73% of the extracted P was organic, with phosphomonoesters constituting the major fraction, ranging from 50 mg P kg^{-1} in the uplands to 130 mg P kg^{-1} in the deep marsh. The remaining organic P forms included phosphodiesters (11–13% total soil P), dominated by identifiable DNA, with the remainder representing various alkali stable phospholipids (Cheesman, 2010). Orthophosphate was the major P compound in sediments of Lake Okeechobee (67–100% of extracted phosphorus). The remaining compounds in the surface layers of the Okeechobee sediment profile were phosphate monoesters (24–27%), and DNA (7–9%), with a trace of pyrophosphate (Torres, 2008).

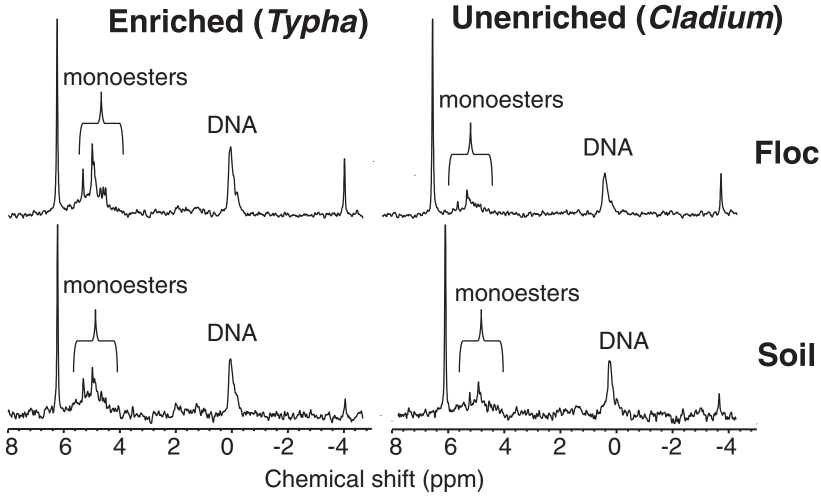

FIGURE 4. Soil organic phosphorus forms in the Water Conservation Area 2A as determined by the ^{31}P-Nuclear Magnetic Resonance Spectroscopy (Turner and Newman, 2005).

Organic P represented up to 70–90% of the total P in deep peat layers in the Florida Everglades, especially in STAs and WCAs, but surface layers contained relative less organic P (Qualls and Richardson, 1995; Reddy et al., 1998a). In recently accreted organic matter in the STAs, the sequestered organic P primarily consisted of phosphate diesters and their degradation products (Turner et al., 2006). These compounds are considered relatively unstable in soils and raises concern about the long-term stability of organic phosphorus sequestered in treatment wetlands (Turner et al., 2006).

Microbial biomass P accounts for approximately 5–30% of the total P of wetland soils. For example, in P-enriched areas of WCAs, approximately 5–10% of total P may be present as microbial biomass P, as compared to 10–20% of total P in soils from P-limited areas (oligotrophic wetlands; Chua, 2000). In P-limited areas, a larger proportion of P is assimilated in the microbial biomass, indicating greater assimilation efficiency of remineralized P.

4.3 Nonreactive Phosphorus

Operationally defined chemical fractionation schemes have been routinely used to identify labile and nonlabile pools (Hieltjes and Lijklema, 1980; Reddy et al., 1998a; Reynolds and Davis, 2001; Ruttenberg, 1992; van Eck, 1982). Key chemical extractants used in identification of organic and inorganic pools are 0.1–0.5 *M* NaOH and 0.5 to 1 *M* HCl. Soil P not extracted by either acid or alkali is considered as residual P or operationally defined nonreactive P, while the remaining P is defined as reactive P. For all practical purposes, nonreactive P is considered essentially unavailable for biotic or abiotic transformations. Approximately 30–40% of soil total P was present in the nonreactive P pool of soils of LOB (Dunne et al., 2010), and 14–48% of total P was in Lake Okeechobee sediments (Olila et al., 1995; Torres, 2008). Similarly, soils in SEE contained 20 to 40% of total P in the nonreactive pool (Reddy et al., 1998a; Wright, 2009). Typically, the P-enriched soil subregions of WCA-1, WCA-2, and WCA-3 contained less total P in the nonreactive pool than in unenriched soils of those basins. In WCA soils, nonreactive P increased with soil depth, with approximately 60–70% of total P contained in subsurface soils (Fisher, 2007; Reddy et al., 1998a).

The relationship between nonreactive P and total P is shown in Figure 5 and represents most hydrologic units of the Greater Everglades Ecosystem. The data suggest that approximately 35% of total P is nonreactive, whereas 65% of total P is biologically available over a range of time scales. Availability depends on a range of environmental factors including hydrology, temperature, nutrient loading, and vegetation (Reddy et al., 2005b). Consideration of P bioavailabilty is critical to understanding the long-term restoration of the oligotrophic nutrient status of ecosystems in the Greater Everglades Ecosystem.

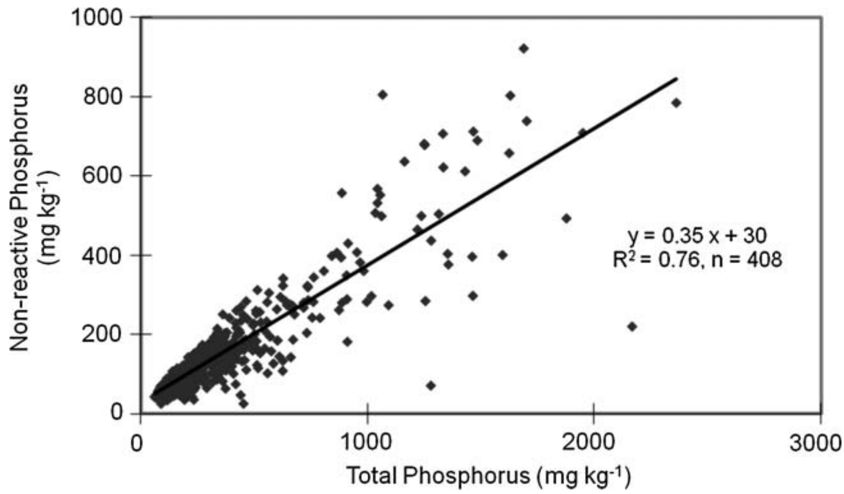

FIGURE 5. Nonreactive phosphorus as a fraction of total phosphorus in surface 0–10 cm soil/sediment of select hydrologic units of the Greater Everglades Ecosystem. Nonreactive phosphorus is defined as soil phosphorus not extracted with alkali and acid.

5 PHOSPHORUS TRANSFORMATIONS

5.1 Biotic Transformations

The cycling of organic P in wetland soils and lake sediments is largely mediated by microbial metabolism. Microbial metabolic activities influence mineralization of organic P in two ways: (a) direct biochemical mobilization by extracellular or periplasmic enzymes, particularly from mono- and diesters; and (b) metabolism of microbes attached to senescent particulate detritus.

Bacteria and algae growing on soil particles are able to utilize exogenous organic P compounds through enzymatic hydrolysis of terminal phosphate groups. Sharma et al. (2005) used a fluorescent-labeled enzyme substrate to examine the location of in situ phosphatase activity in a periphyton mat and explored the potential associations of phosphatase-producing organisms and cyanobacteria within these mats. Phosphatase-producing organisms are concentrated in the lower section of the periphyton mat, and the phosphatase activity appears to be associated with heterotrophic organisms in close proximity to chlorophyll-containing cyanobacteria (Sharma et al., 2005).

Within the SEE, phosphatase activity was found to be higher in the floc and benthic periphyton layer, as compared to the 0–10 cm section of soil, and lowest APA was found in subsurface soils (10–30 cm depth; Wright and Reddy, 2001). There was also a distinct relationship with local P contents. Detrital plant tissue and soil samples collected along the P gradient in WCA-2A was at background levels for samples collected up to 5 km from the inflow, and then increased exponentially between 5 and 10 km, indicating

P limitation in the interior marsh (Wright and Reddy, 2001). These results suggest that APA can be used as an indicator of P enrichment or P limitations in an ecosystem. This was confirmed in a field study in which phosphatase activity in periphyton mats significantly decreased following the initiation of phosphorus loading to unenriched Everglades marsh (Newman et al., 2003).

Phosphomonoesters are by far the most frequently studied enzyme influencing P-cycling in the greater Everglades, but, phosphodiesters can be a significant contributor to the organic P pool. The ratio of monoesters to diesters was close to 1 in the nutrient enriched areas of WCA1 compared to 2 to 4 in the unenriched interior (Turner and Newman, 2005). Relatively high diester contents in the unimpacted sites suggest that a significant source of organic P in the floc is of microbial origin.

Organic P mineralization is governed by microbial metabolic activities functioning in the soil profile, which include aerobic, facultative anaerobic and obligate anaerobic activities. Accordingly, the rate of microbial breakdown of organic P not only depends on substrate characteristics but also on soil redox conditions and availability of electron acceptors. Mineralization of organic P was approximately 3-fold greater under aerobic conditions, than under nitrate, sulfate, and bicarbonate reducing conditions (McLatchey and Reddy, 1998). Phosphatase activity is directly influenced by redox potential, with higher activities found under aerobic conditions than anaerobic conditions (Newman and Reddy, 1993). Under anaerobic conditions, low microbial activity and greater availability of soluble inorganic P results in lower phosphatase activity. Organic P mineralization is directly related to the phosphatase activity in soils.

Labile organic P hydrolysis was measured by adding a substrate (glucose-6-phosphate) to soils collected along the nutrient gradient in northern Everglades wetland soils (Chua, 2000). Phosphorus released as result of hydrolysis of the ester bond can potentially be assimilated by microbial communities as a nutrient source; however, this process is energy intensive and therefore regulated by P availability. Mineralization rates of glucose-6-phosphate decreased as dissolved inorganic P increased (Chua, 2000), indicating organic P turnover was no longer necessary to meet microbial P metabolic requirements. Cheesman (2010) reported that leaf litter decomposition at a P-enriched site in WCA-2A resulted in net sequestration of P in microbial biomass (i.e., phosphodiesters and inorganic polyphosphate), while at low-P concentrations at the unenriched site there was little or no net sequestration of P, as a result of P limitation to microbial communities.

5.2 Abiotic Transformations

Both biotic and abiotic processes regulate the retention of inorganic P added to soils and sediments. Adsorption refers to accumulation of soluble inorganic

P from soil pore water at soil mineral surfaces, and typically increases with soil clay content. Desorption refers to release of adsorbed inorganic P from the mineral surfaces into soil/sediment pore water. Depletion of P from soil/sediment pore water encourages the release of P from mineral surfaces until a new equilibrium is reached. The balance between P adsorption and desorption represents an equilibrium between solid phase and P in soil pore water. Several approaches have been used to assess P retention or release potential of soils and sediments. Many of these studies include addition of known amount of P to soil/sediment slurries maintained either under aerobic or anaerobic conditions, followed by measuring the quantity of P removed from solution after a set time (Reddy et al., 2005b). Three key P retention parameters often reported are EPC_0 (equilibrium P concentration in pore waters where net sorption equals zero, S_{max} (P sorption maxima, which provides an estimate of maximum P retention capacity), and Kd (P sorption coefficient or partition coefficient, which is the ratio between P sorbed to P in solution).

Phosphorus sorption maximum and Kd values measured in various wetland soils and stream sediments in the LOB were highly correlated with amorphous and poorly crystalline forms of Fe and Al, and organic matter content (Reddy et al., 1998b). Soils in the LOB basin are sandy loams with low P sorption capacity. Approximately 78% of the S_{max} variability in the LOB soils was explained by Fe and Al with a P/[Fe + Al] mole ratio of 0.17 (Reddy et al., 1998b).

Sediments from the Upper Chain of Lakes in the Kissimmee River Basin and Lake Istokpoga showed strong correlations between P sorption and total C, total P, Ca, Mg, Fe, and Al (Belmont et al., 2009). Equilibrium P concentration values ranged between 0.001 and 0.192 mg L^{-1} under aerobic conditions. Results suggest that although these sediments have high P sorption capacities, P is released into the water column by desorption under aerobic conditions when water-column P concentrations are low enough ($<$0.036 mg L^{-1} for Lake Tohopekaliga and $<$0.003–0.027 mg L^{-1} for the other four lakes; Belmont et al., 2009).

In Lake Okeechobee sediments, equilibrium P concentration values measured under anaerobic conditions ranged between 0.009 and 0.025 mg L^{-1} for mud sediments and from 0.028 to 0.084 mg L^{-1} for peat sediments (Olila and Reddy, 1994). Phosphorus sorption by Lake Okeechobee sediments was strongly correlated with Fe, Al, and Ca concentrations (Olila and Reddy, 1994). Pore water P concentrations in mud zone sediments of Lake Okeechobee increased over a 10-year period (1988–1998), suggesting a decrease in P sorption capacity of these sediments (Fisher et al., 2001).

5.3 Biotic and Abiotic Interactions

The mobility of P across the soil/sediment water interface is regulated by mechanisms associated with mineral-water equilibria, sorption processes (particularly ion exchange), oxygen and alternate electron acceptor-dependent redox interactions, metabolic activities of microbes, bioturbation by benthic invertebrates, and advective and diffusive flux. Lake Okeechobee pore water P showed increases in all sediment regions, possibly indicating that the surface sediments are limited in their ability to buffer soluble P at lower solution concentrations. This is of concern because it indicates that more soluble P could become available to the water column and increase the eutrophication of Lake Okeechobee (Fisher et al., 2001). Phosphorus flux measured in the mud zone of Lake Okeechobee was 0.4 mg P m^{-2} day^{-1} (Reddy et al., 2007). In studies conducted 10 years ago, maximum P fluxes measured for mud sediments ranged from 0.14 to 1.9 mg P m^{-2} day^{-1} (Fisher et al., 2005; Moore et al., 1998). The data suggests that over the last 10 years the internal P load from sediments has not changed appreciably. Internal dissolved P fluxes, measured in 1988 in Lake Okeechobee, were equivalent to external loads (Moore et al., 1998; Fisher et al., 2005). Similarly, the significance of internal P loads in regulating eutrophication has been demonstrated in other shallow lakes (Anderson and Ring, 1999; Graneli, 1999; Sondergaard et al., 1999; Steinman et al., 2004). Therefore, internal P fluxes from benthic sediments to the water column can offset any water column responses to external P load reductions (Malecki et al., 2004).

In mineral wetland soils, reduction of ferric hydroxides and complexes results in Fe (II) and adsorbed phosphate to be mobilized into soil pore water. This has been shown in soils of the LOB and sediments of Upper Chain of Lakes and Lake Okeechobee (Belmont et al., 2009; Moore et al., 1998; Olila and Reddy, 1997; Reddy et al., 1998a). In wetlands, sulfate reduction to some extent can enhance organic P mineralization. In iron-dominated wetland soils, Fe (II) can react with hydrogen sulfide and form FeS (Figure 6). Iron removal by FeS formation can lead to less Fe (II) available for precipitation with P and potential release of P into the interstitial waters (Caraco et al., 1991; Roden and Edmonds 1997; Wetzel, 2001). Sulfide oxidation in aerobic portions of the floc or benthic periphyton layer can potentially solubilize calcium phosphate associated with calcium carbonate (Figure 7). There is no documented evidence that sulfate loadings will enhance the solubility of inorganic P in wetland soils and lake sediments of the Greater Everglades Ecosystem. Sulfate reduction in these systems can play a significant role in microbial metabolic activities related to organic matter decomposition, and possibly enhance the formation of methyl mercury (Gilmour et al., 1998).

Phosphorus reactivity and mobility in the SEE is regulated by biotic and abiotic reactions related to Ca, mediated by periphyton activities. Periphyton can utilize both organic and inorganic forms of P (Bentzen et al., 1992), and can induce marked changes in pH and dissolved oxygen concentration of the water column and soil-floodwater interface (McCormick and O'Dell,

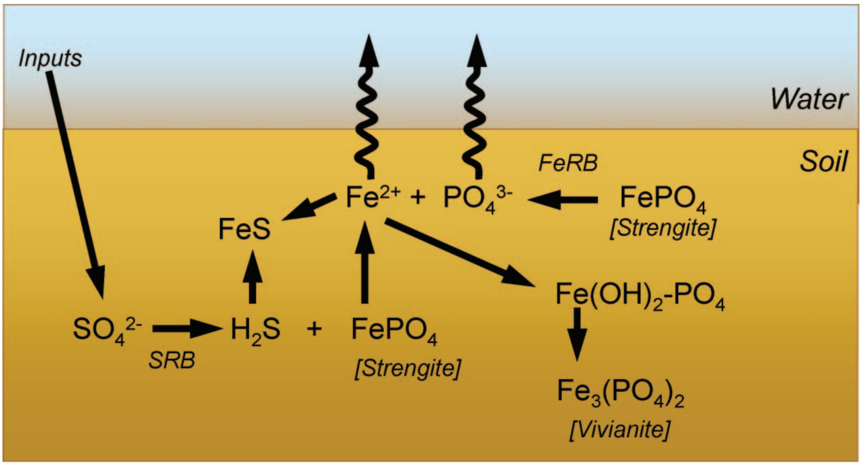

FIGURE 6. Schematic showing the role of ferric iron and sulfate reduction on solubility of inorganic phosphorus in wetland soils. (Reddy and Delaune, 2008) (This figure is available in color online).

1996; McCormick et al., 2002). In the uniquely low mineral content waters of WCA-1 interior oligotrophic sites, periphyton assemblages consist of green algae and diatoms adapted to the extremely low mineral content of the surface waters (McCormick et al., 2002). In contrast, mineral-rich waters, such as those found in WCA-2, WCA-3, and ENP, support a periphyton mat assemblage dominated by a few species of Ca-precipitating cyanobacteria and diatoms (McCormick et al., 2001), that appears to be favored by waters that are both low in P and at or near saturation with respect to $CaCO_3$ (Gleason,

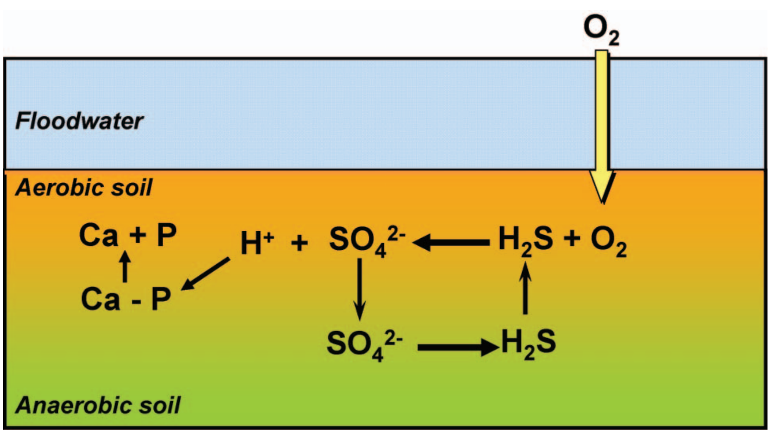

FIGURE 7. Schematic showing oxidation reduction of sulfur on solubility of calcium phosphorus in wetland soils. (Reddy and Delaune, 2008) (This figure is available in color online).

1972). Photosynthesis and respiration can initiate significant changes in water column pH on a diurnal basis. These processes can increase pH to as high as 10, depending upon the buffering capacity of the water column, and can result in the coprecipitation of P with $CaCO_3$ (Otsuki and Wetzel, 1972; Scinto and Reddy, 2003). Chemical analysis of periphyton obtained from the Florida Everglades indicated that <20% of the total P in periphyton was present as P associated with Ca and Mg, whereas the remaining P was in organic forms (Scinto and Reddy, 2003). Tracer studies using ^{32}P showed rapid uptake by periphyton mats in the water column (Noe et al., 2002; Scinto and Reddy, 2003). The biotic compartment contained >83% of the incorporated P after 12 hour incubations, suggesting that biological demand exceeds abiotic adsorption in this P-limited system, but adsorption mechanisms are responsible for a portion (<15%) of water-column P removal (Scinto and Reddy, 2003). It was hypothesized that P added to the water column dominated by calcareous periphyton is initially adsorbed or coprecipitated on the $CaCO_3$, followed by diffusion into biotic component. This mechanism is possibly mediated by a decrease in pH at the interface as a result of respiration by periphyton, followed by solubilization of P and subsequent uptake by biotic component (Scinto and Reddy, 2003). The surface waters in the Everglades (with the exception of WCA-1), are typically characterized by high alkalinity, which may buffer the pH around 8.5. However, Diaz et al. (1994) noted that about 75–90% of the precipitated P was solubilized when pH levels decreased to <8 as a result of an increase in carbon dioxide levels.

Mechanisms regulating abiotic P retention in the Everglades soils are clearly not well understood, especially with respect to microgradients that exist within the periphyton mats and organic matter. However, the dominance of Ca in the Everglades system suggests that it may be one of the main regulators of P dynamics and can influence long-term retention of P. In recent years, decreased Ca loading to Lake Okeechobee and the STAs has been speculated to be one of the reasons for higher levels of P in the water column. Decreased Ca loading to STAs was shown to decrease P removal efficiency, underscoring the importance of Ca in P retention (WBL, 2009). The STAs were designed based, in part, on the P retention observed along the P enrichment gradient in WCA-2A. Long-term Ca accumulation in WCA-2A is significantly related to Ca accumulation in soils (Reddy et al., 1993).

However, the role of Fe and Al in inorganic P retention should not be ruled out, as these metals can play a significant role in soils of some of the hydrologic units (i.e., in the NEE). As noted previously, in Lake Okeechobee sediments, short-term P retention is regulated by redox reactions of iron, while long-term retention in anaerobic sediments is regulated calcium and P interactions (Moore and Reddy, 1994).

6 CARBON–PHOSPHORUS RATIOS

Plant detritus, periphyton, and soil organic matter components function as the major storage pools of organic P. Phosphorus storage is mediated in several ways: (a) direct assimilation of P by microbes and algae colonizing detrital plant tissues in the water column, (b) assimilation of P by plant communities and enriched detritus on the soil surface, and (c) abiotic retention of P on soil components. Microbes are dependent on organic substrates provided by macrophytes, while macrophytes are dependent on microbes to transform organic forms of nutrients into more bioavailable forms. Net release of nutrients is regulated by the microbial nutrient requirement and C/P and N/P ratios of the substrate undergoing decomposition. The mutual dependency between microbes and macrophytes is one of the key regulators of biogeochemical processes in wetlands.

The C/P ratio of water and soils indicates P enrichment and potential limitation of P to biotic communities. Cleveland and Liptzin (2007) estimated that an average C/P ratio of 186 was considered an indicator of P limitation in mineral soils. Soil C and N concentrations are tightly coupled, since both these elements are linked to organic matter accumulation. In contrast, soil P contents are not always linked to organic matter accumulation, and are increasingly decoupled from C. This is due to the fact that as P is added to an ecosystem, it accumulates in both in organic and inorganic forms.

Molar C/P ratios of soils showed distinct gradients with lower values in the LOB wetland soils and lake sediments and greater values in hydrologic units of the SEE (Figure 8). Carbon to P ratios of wetland soils in LOB ranged from 240 to 1200, with low values recorded in Taylor Creek/Nubbin Slough

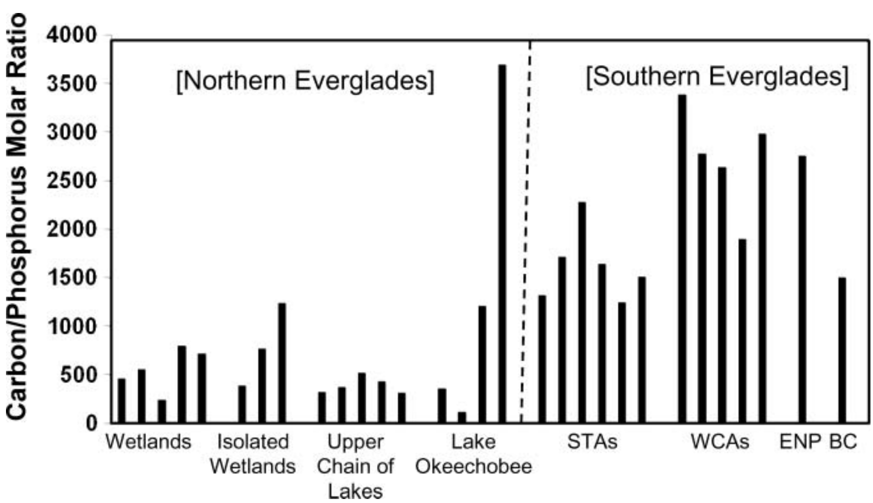

FIGURE 8. Molar C:P distribution in the surface 0–10 cm soil/sediment of select hydrologic units of the Greater Everglades Ecosystem.

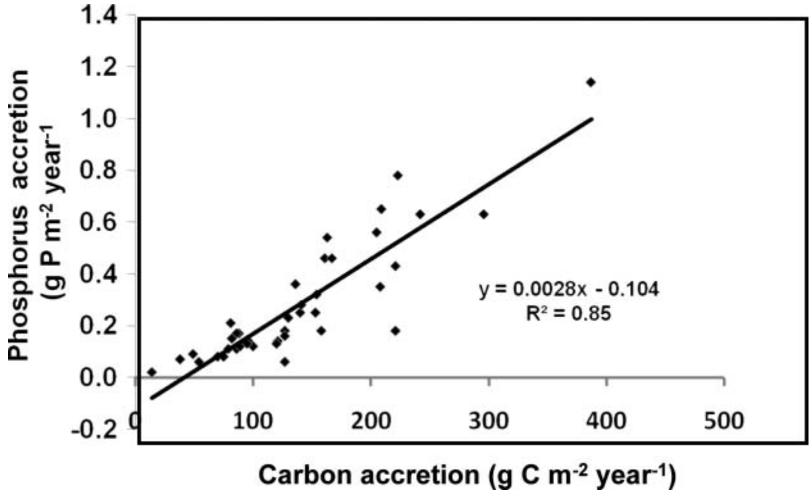

FIGURE 9. Relationship between long-term phosphorus accretion and organic carbon accretion in soils of Water Conservation Area 2A (Reddy et al., 1993).

and high values in wetlands located in unimproved pasture areas. Low C/P ratios reflect high P accumulation in soils. For LOB, wetlands located in unimproved pasture areas are probably the least impacted and high C/P ratios suggest P limitation. In sediments of the Upper Chain of Lakes, the C/P ratios were in the range of 30–520, while in Lake Okeechobee sediments C/P ratios ranged from 120 to 3700. Peat sediments in Lake Okeechobee had the greatest C/P ratios, whereas lower C/P ratios were recorded in sand and mud sediments. The C/P ratios of wetland soils and lake sediments of NEE were lower than soils in WCAs and ENP, reflecting the large amounts of P accumulation per unit of C in the northern basins.

Phosphorus accumulation is coupled tightly to organic matter accumulation in wetland soils and lake sediments rich in organic C. In WCA-2A, long-term organic C accumulation is directly linked to P accumulation (Figure 9). However, P in mineral soils and sediments is decoupled from organic C, since P accumulation in these systems is primarily regulated by inorganic (mineral) P retention mechanism.

7 IMPLICATIONS FOR THE EVERGLADES RESTORATION

Wetlands and aquatic systems in the Greater Everglades Ecosystem are often the final recipients of nutrients discharged from adjacent agricultural and urban ecosystems. Water flows through the multiple hydrologic basins in the Greater Everglades Ecosystem and are presently managed by an extensive infrastructure of canals, levees, and water control structures. Associated with local runoff and interbasin flows are the P loads that are a consequence of the variety of land uses distributed throughout this large region. Thus, landscape position and local/regional water and nutrient management practices are important drivers of P transport and fate in the Greater Everglades Ecosystem. Management practices in the LOB directly affect the eutrophication status of Lake Okeechobee; lake water and nutrient outflows that not only affect the receiving estuaries to the east and west of the lake, but also directly affect the P-removal capabilities of the recipient EAA STAs. Restoration of the downstream Everglades wetlands, and other components of the Greater Everglades Ecosystem, requires the integrated management of water and nutrients throughout this interconnected system.

Understanding the hydrologic interactions within and among the managed basins, and understanding associated ecosystem responses to altered nutrient flows, is a complex problem. A variety of computer simulation models of hydrology, water quality, and other ecological dynamics have been applied to aid in understanding ecosystem dynamics and as part of the planning process for Everglades restoration. For example, the South Florida Water Management Model (2005) has been a useful planning tool in developing alternative water management plans for the south Florida region. Using managed flow data from that hydrologic model, Fitz et al. (2010) used a Multi-Criteria Decision Analysis tool to evaluate scenarios of altered hydrologic flows and wetland P accumulation in the central Everglades, as simulated by a landscape model of integrated ecosystem dynamics. Informed by such simulation experiments, scenario analyses using simple nutrient budgets (such as those described subsequently), and other planning methods, water managers can better understand and refine future plans for restoring the Greater Everglades Ecosystem.

The significant heterogeneity in legacy P distribution (and P bioavailability) is an important factor to consider in ecosystem restoration in south Florida. The NEE contains subbasins of high P concentrations, but the EAA contains the highest (mass per area) concentration of legacy P among the large hydrologic units within the Greater Everglades Ecosystem and is located downstream of Lake Okeechobee and upstream of the Everglades wetlands. Effective surface water and nutrient management in the EAA and LOB, as well as in source areas further upstream in the NEE, is critical in helping to achieve the Everglades restoration goals.

Improved land use management practices in uplands can reduce overall P load to receiving water bodies. While the external P loading from uplands is curtailed through the implementation of BMPs and other improved practices, will the P impacted wetlands and lakes respond to overall P load reduction? The key questions are (a) Will wetlands and aquatic systems respond to P load reduction? (b) If so, how long will it take for the systems to recover and reach background conditions? and (c) What are the economically feasible management options to hasten the recovery process?

Characterizing the P release potential (P memory) from the reactive P pool in soils and sediments of the Greater Everglades Ecosystem requires consideration of both biotic and abiotic processes. Biotic processes in the Everglades wetlands include assimilation by vegetation, periphyton and microorganisms; abiotic processes include sedimentation, adsorption by soils, precipitation, and exchange processes between soil and the overlying water column. This P memory can extend the time required for restoration and recovery to a lower nutrient status that historically supported the native Everglades vegetation with associated biogeochemical processes that dominated under more oligotrophic conditions. This lag time for recovery should be considered in developing restoration and management strategies for reducing P loads (Figure 10).

We used the P storage in surface soils to estimate the potential lag time to recovery resulting from the legacy P presently stored throughout the drainage basin. Based on the chemical fractionation of soil P, we estimate approximately 35% of total P in soils is nonreactive and is not biologically available. The remaining 65% may be available for release at different time scales. Three scenarios are presented that represent the potential ramifications of the mobility of the legacy P in LOB, Lake Okeechobee, and the EAA (Figures 11 and 12). Using present P release rates from each hydrologic unit, and assuming either 10 or 25% of reactive soil P is released, we estimate multidecadal lag times in restoration towards background nutrient status of the recipient hydrologic unit.

In the first scenario (Figure 11), present P release rates from the LOB to Lake Okeechobee are estimated as ~500 mt P per year (based on 30 year

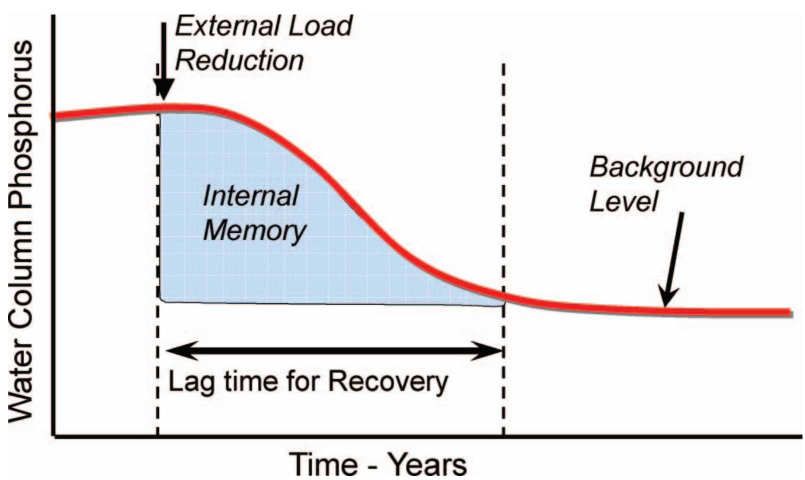

FIGURE 10. Schematic showing the relationship between water column phosphorus and internal memory resulting from legacy phosphorus (Reddy and Delaune, 2008). (This figure is available in color online).

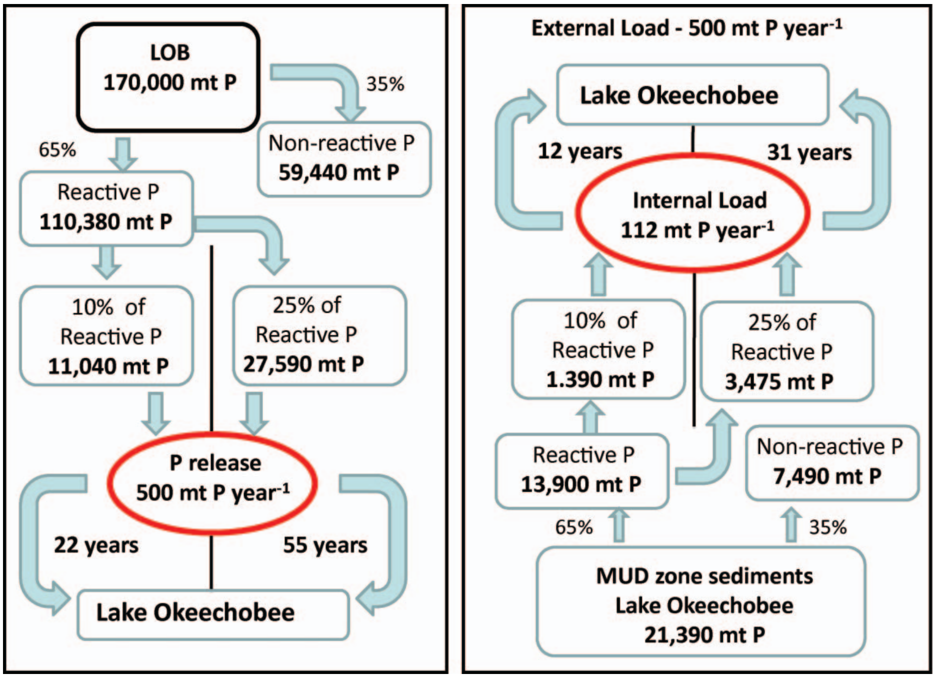

FIGURE 11. Role of legacy phosphorus in the Lake Okeechobee Basin and Lake Okeechobee in determining the lag time for recovery. (This figure is available in color online).

P loading average). A 22-year lag time results if 10% of the reactive P is assumed to be available for release to the downstream receiving basin. The lag time is on the order of 55 years if 25% of the reactive P pool available for release (Figure 11). In other words, legacy P in the LOB would support the present 500 mt P per year load to the lake for the next 22–55 years even if all other sources of P were curtailed. At the same time, the mud zone sediments in Lake Okeechobee support an estimated internal load of approximately 112 mt P per year. Based on the present legacy P in mud sediments and the assumed reactive P (10–25) percentage available, the internal loading supply would continue to provide P over the next 12–31 years.

Similarly, the legacy P in the EAA can be expected to have significant long-term impacts on the nutrient status of the STAs and WCAs. The long-term P load (29-year average) from the EAA was estimated to be 170 mt P per year. Present P loads (WY2009) from the EAA (129 mt P per year; Van Horn and Wade, 2010) are lower than the long-term average load of 170 mt P per year. However, the estimated P load to STAs during the WY2009 was 218 mt P (Pietro et al., 2010), suggesting that the STAs are receiving significant P loads from other sources. STAs removed approximately 82% of this load or 1.4 g P m^{-2} $year^{-1}$ (Pietro et al., 2010). Assuming that 10–25% of reactive P is available for release, it is suggested that legacy P in surface

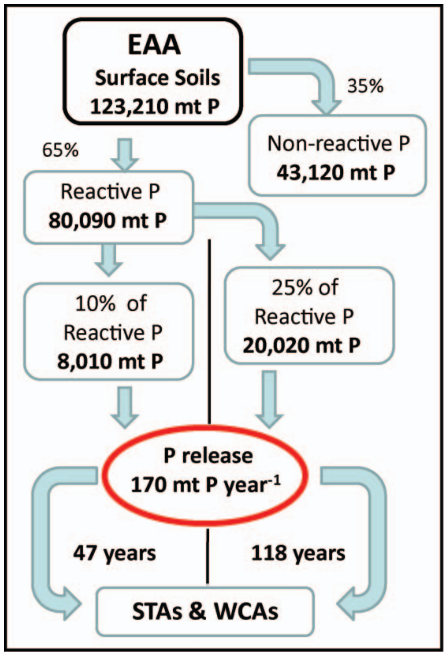

FIGURE 12. Role of legacy phosphorus in the Everglades Agricultural Area in determining lag time for recovery. (This figure is available in color online).

soils of the EAA would support the 170 mt P per year load to the STAs and WCAs for the next 47–118 years (Figure 12).

Even very conservative estimates (i.e., ≤ 25% of reactive P available for downstream release) suggest that the legacy P can sustain P loads for many decades in critical habitats targeted for restoration. For the LOB, effective P control strategies are needed to reduce P loads due to the legacy soil P. The BMPs alone will likely be insufficient to reduce P loads to the necessary levels. Additional P control strategies including the addition of chemical amendments (Malecki-Brown and White, 2009; Malecki-Brown et al., 2007) and intensively managed STAs should be considered in the LOB to reduce P loads to Lake Okeechobee. External P load reduction should be a high priority for environmental managers, because very little can be done to reduce the internal load. Dredging and removing sediment P from a lake the size of Lake Okeechobee would costs billions of dollars and have associated spoil disposal problems and ecological impacts within the lake. In the EAA, decomposition of soil organic matter will continue to release P at steady rate and maintain present P loads to STAs and Everglades wetlands. Thus any management strategies that maintain these organic soils are essential to reduce continual P enrichment of the Florida Everglades.

Clearly, reduction of P loading to the Everglades wetlands depends on the successful management of the EAAs, STAs, and the LOB, given the managed interactions between the NEE and SEE. Without effective management, the STAs are unlikely to maintain sustained performance over the long-term and to provide safeguard in preventing P loading to the Florida Everglades. Further consideration and evaluation of P control strategies in the LOB, EAA and STAs are needed to maintain sustained P load reduction for restoration objectives over the long-term.

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