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Decomposition responses to phosphorus enrichment in an Everglades (USA) slough

S. NEWMAN*, H. KUMPF, J.A. LAING & W.C. KENNEDY
Everglades Department, South Florida Water Management District, P.O. Box 24680, West Palm Beach, FL 33416-4680, U.S.A.
*(*Author for correspondence; e-mail: snewman@sfwmd.gov)*

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Abstract. The effects of phosphorus (P) enrichment on decomposition rates were measured in a P loading experiment conducted in an oligotrophic marsh in the northern Everglades, USA. In this study, eighteen 2.5 m^2 enclosures (mesocosms) were placed in a pristine open-water (slough) wetland and subjected weekly to 6 inorganic P loads; 0, 0.2, 0.4, 0.8, 1.6 and 3.2 $g{\cdot}m^{-2}g{\cdot}yr^{-1}$. Phosphorus accumulated rapidly in the benthic periphyton and unconsolidated detrital (benthic floc) layer and significantly higher P concentrations were recorded after 1 yr of P addition. In contrast, a significant increase in surface soil (0–3 cm) TP concentrations was measured in the surface soil layer only after 3 yr of loading at the highest dose. Plant litter and benthic floc/soil decomposition rates were measured using litter bags, containing sawgrass (*Cladium jamaicense* Crantz) leaves, and cotton (cellulose) strips, respectively. Litter bag weight losses were similar among treatments and averaged 30% at the end of the 3 yr study period. Litter N concentrations increased over time by an average of 80% at P loads < 1.6 $g{\cdot}m^{-2}{\cdot}yr^{-1}$, and by $> 120\%$ at P loads ≥ 1.6 $g{\cdot}m^{-2}{\cdot}yr^{-1}$. In contrast, litter P concentrations declined up to 50% in the first 6 months in all P loads and only subsequently increased in the two highest P-loaded mesocosms. Cotton strip decay demonstrated that benthic floc and soil microbial activity increased within 5 mo of P addition with more significant treatment effects in the benthic than the soil layer. The influence of soil microbial transformations was shown in porewater chemistry changes. While porewater P levels remained close to background concentrations throughout the study, porewater NH_4^+ and Ca^{2+} increased in response to P enrichment, suggesting that one significant effect of P enrichment in this oligotrophic peat system is enhanced nutrient regeneration.

Introduction

Organic matter decomposition is an important process controlling internal nutrient cycling and soil accumulation/loss. Nutrients are considered a primary regulator of this complex process. In general, nutrient enrichment in the soil or water tends to increase decomposition rates; however, several studies have shown that increased nutrient input may cause either no change in decomposition, or a variable response (Brinson et al. 1981; Webster & Benfield 1986; Rybczyk et al. 1996). Nitrogen (N) limitation of decomposition in many ecosystems has been well-documented (Brinson et al. 1981; Webster & Benfield 1986; Rybczyk et al. 1996). In contrast, although phosphorus (P) is a primary limiting factor in some systems and can increase decomposition once N limitation has been eliminated, studies have frequently shown P addition has little or no effect on decomposition rates (Howarth & Fisher 1976; Coulson & Butterfield 1978; Federle et al. 1982; Brock et al. 1985). However, in P-limited systems, P enrichment has resulted in increased decomposition (Maltby 1985; Qualls & Richardson 2000).

The Everglades (USA) is an oligotrophic wetland ecosystem that historically encompassed approximately 1 million ha from Lake Okeechobee to Florida Bay (Figure 1). The remnant system, approximately 0.5 million ha, is fragmented into several hydrologic units; Water Conservation Areas 1, 2, and 3 (WCAs), and Everglades National Park. Approximately 65–70% of the vegetation community was sawgrass (*Cladium jamaicense* Crantz) marsh, interspersed with wet prairies and deeper-water sloughs (Loveless 1959). Historically water and nutrients were provided primarily through rainfall (Parker 1984) and macrophyte and periphyton growth were P-limited (Steward & Ornes 1983; Davis 1994; McCormick & O'Dell 1996; Miao & DeBusk 1999). Over the last three decades, the WCAs were exposed to significant P enrichment, primarily from agricultural runoff. In most regions, highly P impacted areas are confined to a distance of 0–3 km from canals and inflow structures (Reddy et al. 1998); although in the most nutrient impacted area, WCA-2A, elevated TP concentrations extend 7 km downstream from inflow (McCormick et al. 2000). In nutrient enriched areas, periphyton and macrophyte communities adapted to low nutrient environments were replaced by communities competitive under P-enriched conditions (Davis 1994; McCormick & O'Dell 1996; McCormick et al. 1996; Newman et al. 1996; Miao & Sklar 1998; Miao & DeBusk 1999; Richardson et al. 1999). This, in turn, has had a significant effect on the internal nutrient recycling within the ecosystem. Studies suggested that decomposition rates increased in areas impacted by nutrient enrichment (Davis 1991; DeBusk & Reddy 1998). However, these comparisons along existing nutrient gradients were confounded by changes in hydrology and the concentration of other nutrients. In addition to nutrients, decomposition is influenced by a number of environmental conditions including temperature, oxygen, and pH (Brinson et al. 1981; Webster & Benfield 1986). Thus, in field studies where environmental conditions change in concert with nutrients the influence of nutrient enrichment may be masked.

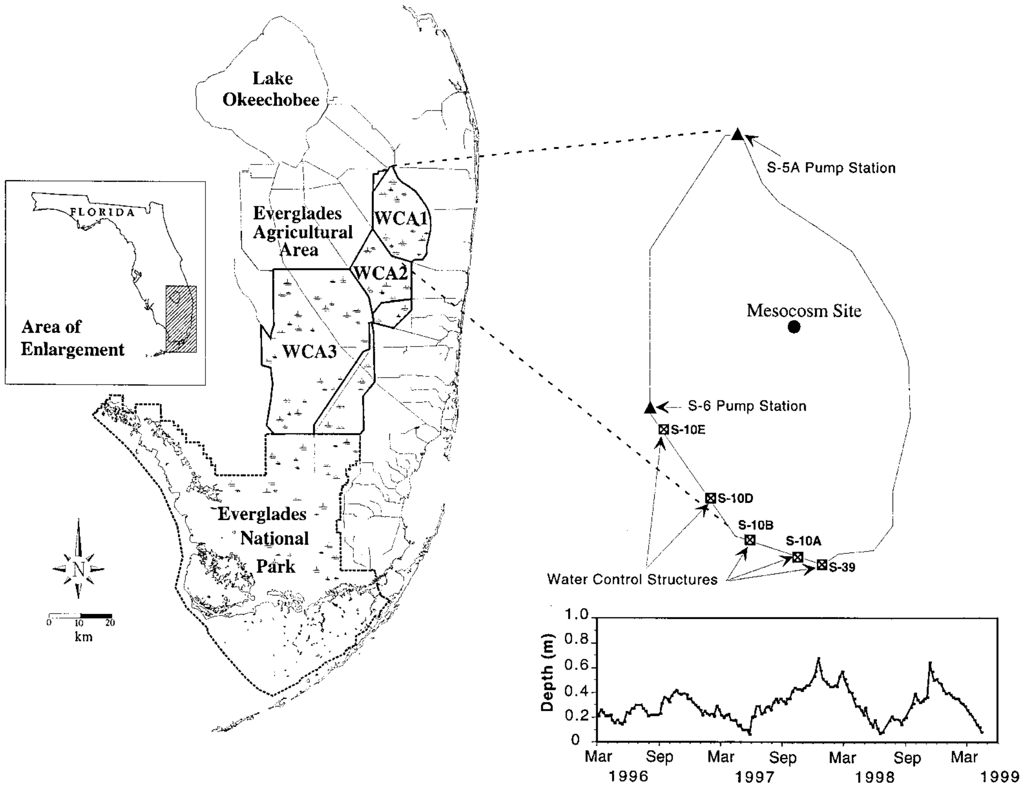

Figure 1. Location of study site in WCA1 and weekly water depths throughout the study period.

We conducted a controlled P enrichment experiment to quantify the responses of periphyton, macrophytes and nutrient chemistry to increased P loading in the Everglades. As part of this larger experiment, we measured the effect of P enrichment on decomposition processes using litter bag and cotton strip techniques. In addition, the concurrent measurement of porewater nutrients allowed us to assess how P enrichment influenced the regeneration of nutrients. Previous studies have demonstrated that the benthic detrital/flocculent layer in the Everglades (Reddy et al. 1999) and other wetlands (Richardson & Marshall 1986) is one of the most active zones in nutrient accumulation and cycling. Thus, we focussed our measurements in this layer to capture the most rapid response to P enrichment. We hypothesized that 1) P enrichment would result in increased decomposition rates; and 2) decomposition rates would be greater in the benthic layer than the underlying soil. Phosphorus enrichment was recently linked to an increase in potentially mineralizable N in the detritus and soil along a nutrient enrichment gradient in the northern Everglades (White & Reddy 2000). Thus, our third hypothesis was increased decomposition rates would increase nutrient regeneration in the soil.

Methods

Site description

The WCAs are wetlands impounded within a series of canals and levees, initially established for flood protection and water supply for the surrounding agricultural and urban areas. Water Conservation Area 1 encompasses 590 km^2 of the northern-most remnant of Everglades habitat (Figure 1). Rain represents the major water inflow into the area and nutrient-enriched agricultural runoff enters the area via pump stations S-5A and S-6. The majority of water exits the area through a series of water control structures, the S-10's, at the south end of WCA1.

This experiment was conducted in a slough; a predominantly openwater area with low macrophyte biomass, surrounded by sawgrass in the interior of WCA1 (Figure 1). The slough vegetation consisted of the macrophytes fragrant water lily (*Nymphaea odorata* Ait.), spikerush (*Eleocharis* spp.), and bladderwort (*Utricularia* spp.).

Experiment description

Twenty-one plots, with vegetation and water depth conditions typical of the surrounding slough, were selected for experimentation. A circular mesocosm enclosure (1 m height × 1.8 m diameter) constructed from UV-resistant polycarbonate, Lexan^{TM}, was installed in each of 18 plots. Treatments were assigned using a completely randomized design. The remaining 3 plots were left unenclosed to determine the effects of enclosure.

During installation, mesocosms were pushed 10 cm into the soil and then bolted to six 5-cm polyvinyl chloride (PVC) poles pounded to bedrock. Each mesocosm had 24 10-cm diameter equally spaced holes in the sidewalls to allow water exchange with the surrounding marsh. An identically perforated 0.5 m high sliding collar, made of the same polycarbonate material, girdled each mesocosm. This sliding collar could be placed in an open position (holes on the collar aligned with holes on the mesocosm) to allow water exchange with the surrounding slough, or closed (holes on collar and mesocosm out of alignment) to prevent such exchange. Although water flow rates in WCA1 are variable and often low, there is significant turnover during rainfall events. Water exchange between mesocosms and the surrounding marsh was assumed critical to maintaining ambient water quality and biological conditions in the enclosures. Therefore, a partially closed system that retained P, but allowed water depth fluctuations and minimized changes other than P, was considered a good compromise. Unenclosed controls were bordered with 6 PVC poles to delineate the same 2.5 m^2 area as that enclosed by mesocosms. The plots were accessed by a walkway to minimize disturbance to the experimental site.

Mesocosms were loaded weekly with orthophosphate (NaH_2PO_4) beginning 14 March 1996, except for 2 weeks in July 1998 when no surface water was present. This manuscript discusses the first 3 yr of sampling (March 1996 through April 1999). Six loading rates, 0, 0.2, 0.4, 0.8, 1.6 and 3.2 g $P \cdot m^{-2} \cdot yr^{-1}$, subsequently referred to as loads 0, 0.2, 0.4, 0.8, 1.6 and 3.2, were applied to triplicate mesocosms. Using peat accumulation data, surface water chemical composition and atmospheric deposition data, background P loads to the Everglades have been estimated at < 0.1 $g \cdot m^{-2} \cdot yr^{-1}$ (Walker 1995). There are no estimates of P loads to nutrient enriched areas, however, peat accumulation data collected within highly enriched areas of the Everglades show P accumulation rates of 1.14 g $P \cdot m^{-2} \cdot yr^{-1}$ (Reddy et al. 1993). Therefore, loading rates used in this experiment are similar to the range of P loads likely experienced by enriched areas over the last three decades.

The P load was mixed with slough water and dispensed by gravity through a 2-cm (outside diameter) perforated PVC pipe. The pipe was moved slowly throughout the water column of each mesocosm to disperse the solution as evenly as possible with minimal disturbance to the plant and periphyton communities. Phosphorus treatments were added as a load, therefore instantaneous concentrations were a function of water depth. Calculated instantaneous water column P concentrations for loads 0.2 and 3.2 loads were 0.02 and 0.31 mg L^{-1}, respectively at a water depth of 20 cm. While at 100 cm, concentrations were 0.004 and 0.02 mg L^{-1} for loads 0.2 and 3.2, respectively. Unenriched (control) mesocosms were dosed in an identical manner as enriched treatments, except that only slough water was used. Mesocosms were closed just prior to dosing and opened 24 hr later, by which time all the added SRP typically had been removed from the water column. Mesocosms remained open between weekly dosing events to allow free exchange of water with the slough.

Water quality sampling

Water-column samples, integrated across the entire water volume within the plot, were obtained monthly during the first 12 months and quarterly thereafter. All water samples were analyzed using standard methods (U.S. Environmental Protection Agency 1983). Samples collected from control plots (enclosed and unenclosed) were analyzed for several parameters including soluble reactive P (SRP; EPA 365.1), total dissolved P (TDP), total P (TP; EPA 365.1, 365.4), total Kjeldahl nitrogen (TKN), total dissolved Kjeldahl N (TDKN; EPA 351.2), ammoniacal-N (NH_4^+; EPA 350.1), nitrate + nitrite-N (NO_x; EPA 353.2), calcium (Ca^{2+}), magnesium (Mg^{2+}), iron (Fe), potassium (K^+; EPA 200.7), silica (SiO_2; EPA 370.1) and dissolved organic carbon (DOC; EPA 415.1). Water samples, obtained at the same frequency as described above, were collected just prior to opening the mesocosms and analyzed for TP and SRP, to estimate P uptake efficiency, i.e., percent P removed over the 24 hr period, and to support the assumption that background conditions were similar among treatments. All water quality and porewater samples were collected in plastic containers, acidified (with the exception of SRP), and stored at 4 °C until analyzed within holding times specified in standard methods (U.S. Environmental Protection Agency 1983). Samples for SRP analysis were stored at 4 °C and analyzed within 48 h. Water depth in the slough was recorded weekly from a stage gauge located on site.

Soil sampling

Soil cores were collected from each plot using a 5-cm thin-walled butyrate-tube piston corer, encased in a thin-walled stainless-steel housing. The tube were pushed 15 cm into the soil and removed with the core intact. A flocculent layer of living and dead algal and material, as well as bacteria and decaying plant matter overlies the soil in the slough. The core was sectioned in the field by first collecting this benthic periphyton and unconsolidated detrital (benthic floc) layer by pouring, and then collecting the surface 0–3 cm soil depth. Benthic floc and soil samples were placed in plastic bags on ice and stored at 4 °C until analyzed for TP, total nitrogen (TN), total carbon (TC), and Ca^{2+}. Total P and Ca^{2+} were determined from acid-digested samples (U.S. Environmental Protection Agency 1983; U.S. Environmental Protection Agency 1986). Total N and TC were determined from finely-ground soil samples using a Carlo-Erba NA 1500 C-N-S analyzer (Haak-Buchler Instruments, Saddlebrook, NJ).

Decomposition bag sampling

In the Everglades, 65–70% of the vegetation was comprised of sawgrass marsh (Loveless 1959); therefore, air-dried standing dead sawgrass leaves were considered an appropriate indicator of decomposition in this ecosystem. Five g of air-dried sawgrass, with initial mass C:N and C:P ratios of 100 and 3700, respectively, were placed in litter bags, made using 30 × 30 cm squares of 1.6 mm fiberglass window screening. The bags were tied at the top using fishing line. Three bags were loosely tied to a stainless steel rod and inserted into each plot, allowing the bags to sink to the top of the soil surface. Upon retrieval, epiphytes were removed using forceps and litter material was gently rinsed using a water bottle containing deionized water. Tissue TC, TN and TP concentrations were determined using the same methods as described for soil. Total C, TN and TP contents of the litter were calculated by multiplying the dry mass by tissue TC, TN and TP concentrations, respectively.

Cotton strip sampling

Cotton strip decomposition rates were obtained using a similar technique to Maltby (1985), with the follow exceptions. Two 12 cm (wide) by 31 cm (long) cotton strips (Shirley Institute, Manchester, England) were attached to a stainless steel frame (6 mm thick), to support the cotton strips vertically across the benthic floc/soil profile. The frame and strips were pushed into the soil to a depth of 15 cm and incubated for 2 weeks. Upon analysis, the strips were cut into 2-cm increments encompassing 10 cm above (i.e., predominantly within the benthic floc layer) and 10 cm below the soil surface. The cut edges were frayed using a wire brush or by hand until a single string could be removed intact along the length of the cut edge. Prior to tearing, each strip was soaked in water for at least 5 min and excess water was blotted from the strip using a paper towel, thus simulating 100% humidity. Tensile strength was tested by inserting the strip width-wise into the grips of a Chatillon TCD-200 tensiometer equipped with a digital force gauge (DFIS 200, Chatillon, Greensboro, North Carolina, USA) and applying force to the strip until it tore. In August 1996, 3-cm depth increment samples were frayed to 2-cm increments and analyzed in a similar fashion using a Monsanto Type W tensometer (Royal Holloway Institute for Environmental Research, Surrey, UK). All cotton strip data were linearized and presented as annual cotton rotting rates (CRR) as follows to correct for non-linear changes in tensile strength over time (Hill et al. 1985),

$$\text{CR (cotton rottenness)} = \sqrt[3]{(y_o - y/y)}$$

$$\text{CRR (cotton rottenness expressed as an annual rate)} = (CR/t) \bullet 365$$

where y_0 = mean tensile strength of control strip; y = mean tensile strength of the test strip at a given depth; and t = duration of burial.

Interstitial water sampling

Porewater samples were collected every two months for the first 12 mo and quarterly thereafter. Polyvinyl chloride wells with a 5-cm well screen were placed within the soil column in each mesocosm and unenclosed control to encompass a depth of 2–7 cm. Prior to sampling, the wells were evacuated using a peristaltic pump and immediately recharged. Porewater was then sampled by pumping through a 0.45-μm inline filter, which minimized exposure to air prior to filtering. Porewater was analyzed for several parameters including TDP, SRP, TDKN, NO_x, NH_4^+ and Ca^{2+} using the same methods as for water-column samples. Porewater pH was determined immediately upon sampling. Platinum redox rods were placed in close proximity to the wells, at a depth of 5 cm to provide supporting redox data. Redox rods were equilibrated for at least one day prior to measurement. All redox values were corrected by +244 mv to account for the contribution of the calomel reference electrode to the reading (Faulkner et al. 1989).

Statistical analyses

All analyses were conducted using SAS® ver. 6.12 (SAS Institute Inc 1989), all results are significant at α = 0.05 unless specified otherwise. A t-test was used to compare significant differences in the response variables between unenriched mesocosms (0 load) and unenclosed controls for each sampling date. Porewater NH_4^+ concentrations in unenclosed and unenriched mesocosms were significantly different for three sampling events. However, these differences were small compared to the changes observed in the high doses. In general, there were no significant differences between the unenriched mesocosms and unenclosed controls; therefore, unenclosed controls were not included in subsequent statistical analyses.

With the exception of litter bag weight data, treatment comparisons were made using Dunnett's multiple comparison test, which compared the response caused by each load to the response observed in the unenriched mesocosms. This test was considered conservative because the experiment-wise error rate was fixed at $\alpha = 0.05$. Litter weight loss was compared using analysis of covariance. Preplanned comparisons between responses from P loaded mesocosms and unenriched mesocosms were made using the least square means (LS means) procedure (SAS Institute Inc 1989). All residuals were examined for normality and heteroscedascity and data transformed to meet the assumptions of analysis of variance.

Results

Water depth and quality

Water depths were seasonal and ranged from 6–68 cm. Maximum water levels occurred between November and January, and minimum water levels occurred between May and July (Figure 1). Water-column concentrations of Ca^{2+}, Mg^{2+}, K^+ and P were low, which is characteristic of a rainfall driven system (Table 1). The average molar ratio of TN:TP in unenriched and unenclosed mesocosms was 440, indicating the extremely P-limited nature of this ecosystem. All added P was removed from the water column within 24 hours, as prior to opening SRP concentrations in all P loaded mesocosms were the same as the unenriched controls (< 0.004 mg L^{-1}).

Soil sampling

Elevated TP concentrations in the floc layer were detected within 6 mo of P loading and significant differences were determined 1 yr after experiment initiation (Figure 2(a)). In general, soil TP concentrations in mesocosms receiving loads 1.6 and 3.2 were elevated above background concentrations, and after 3 yr, TP concentrations were 2.2 and 2.9-fold higher, respectively, than the unenriched mesocosms. A significant increase in surface soil TP concentrations was measured in the surface soil layer only after 3 yr of loading at the highest dose (Figure 2(b)).

Initial mass C:N and C:P ratios were 11 and 1600, respectively for benthic floc. While soil initial mass C:N and C:P ratios were slightly higher at 13 and 2200, respectively. Neither TN nor TC concentrations changed in response to P additions, in either the benthic floc or the soil. However, as observed for TP, there was some seasonal variation in the data. Total N concentrations averaged 40 g kg^{-1} (range 32.8–50.8 g kg^{-1}) and 38.6 g kg^{-1} (range 31.2–43.8

Table 1. Select chemical characteristics of water samples collected from unenriched plots between March 1996 and February 1999. All values mg L^{-1} except where noted

Variable	N	Mean	±	1 S.E.
Soluble reactive P	126	0.004*	±	<0.001
Total dissolved P	135	0.004*	±	<0.001
Total P	134	0.008	±	<0.001
Dissolved NO_x	66	0.005*	±	<0.001
Dissolved NH_4^+	66	0.051	±	0.018
Dissolved TKN	69	1.2	±	0.04
TKN	68	1.4	±	0.04
Dissolved K^+	69	0.42	±	0.03
Dissolved Ca^{2+}	69	4.76	±	0.15
Dissolved Mg^{2+}	69	1.44	±	0.04
Dissolved Fe (μg L^{-1})	69	52	±	3
Dissolved Silicate	69	1.78	±	0.25
DOC	69	20	±	<1

*Most values were at or below detection; therefore, reported values are upper estimates of ambient concentrations

g kg^{-1}) for benthic floc and soil layers, respectively. Total C concentrations averaged 450 g kg^{-1} (range 400–549 g kg^{-1}) and 484 g kg^{-1} (range 431–533 g kg^{-1}) for benthic floc and soil layers, respectively. Redox values averaged 210 ± 8 mv and did not respond significantly to P enrichment.

Decomposition bags

Initial weight loss observed during the first 6 mo in the decomposition bags was highly variable, ranging from 5 to 16% with no response to P addition (Figure 3(a)). While a trend of increasing decomposition, as shown by weight and carbon loss, appeared in the highest loaded mesocosms, there was no significant response to P enrichment at $\alpha = 0.05$. Initially there was a loss in TP concentrations as P was leached from the litter. Only the highest dose had a significantly higher TP concentration than the control (Figure 3(b)). After 21 mo all treatments had higher TP concentrations than the control, which averaged only 0.051 g kg^{-1}. While TP concentrations increased, there was no net accumulation of P in any of the treatments. After 3 yr, the final P contents in the litter bags averaged 32, 36, 32, 33, 35, 63 and 86% of the initial P content in P loads 0–3.2, respectively. Total N concentrations in litter material also increased over time in the highest loaded treatments, exhibiting a clear hierarchy in response to P addition (Figure 3(c)). Nitrogen was also

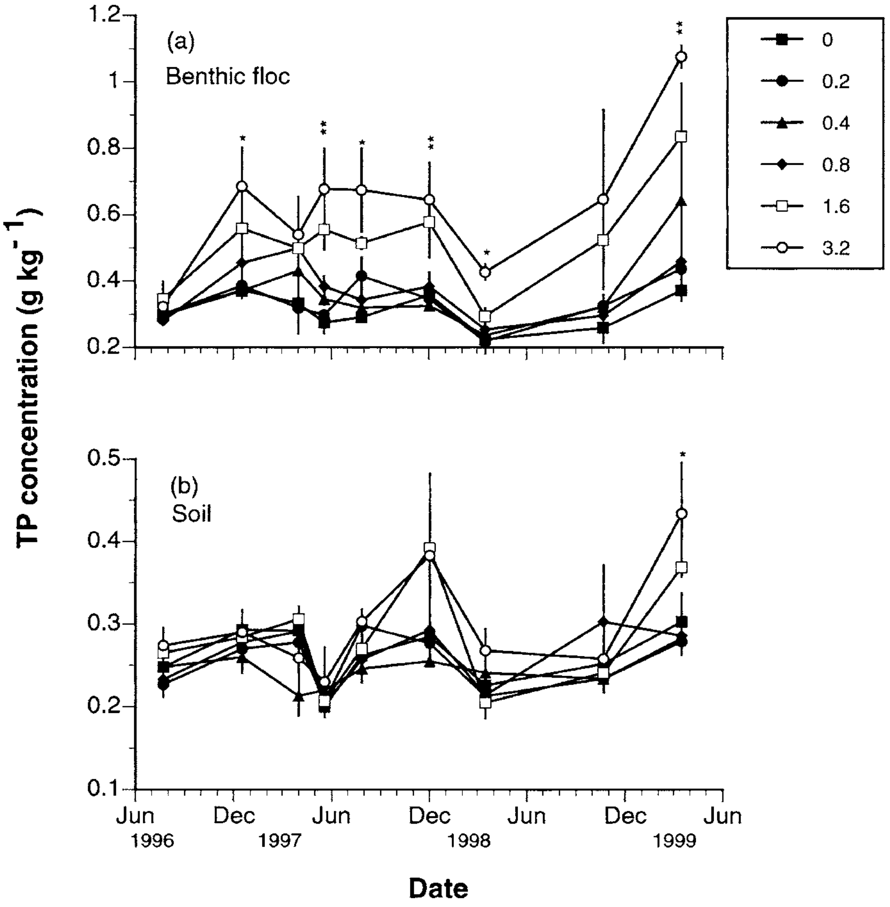

Figure 2. TP concentrations (mean ± 1 S.E.) in the (a) benthic flocculent layer and (b) surface 0–3 cm soil depth in the mesocosms. Number within graph indicates P loading rate ($g{\cdot}m^{-2}{\cdot}yr^{-1}$). Note the soil depth increment was 0–5 cm in December 1996. *indicates treatment 3.2 is significantly different from the unenriched mesocosm, **indicates treatments 1.6 and 3.2 $g{\cdot}m^{-2}{\cdot}yr^{-1}$ are significantly different from the unenriched mesocosm. See text for statistics.

accumulated by the litter as shown by the increased TN content. After 3 yr, the final N contents in the litter bags averaged 131, 136, 134, 115, 155 and 162% of the initial N content in P loads 0–3.2, respectively.

Cotton strip sampling

In 1997 and 1998 there was some evidence of increased CRR at the benthic floc-soil interface. However, in general, there were no distinct CRR depth profiles (Figure 4) and, therefore, decomposition rates were averaged for

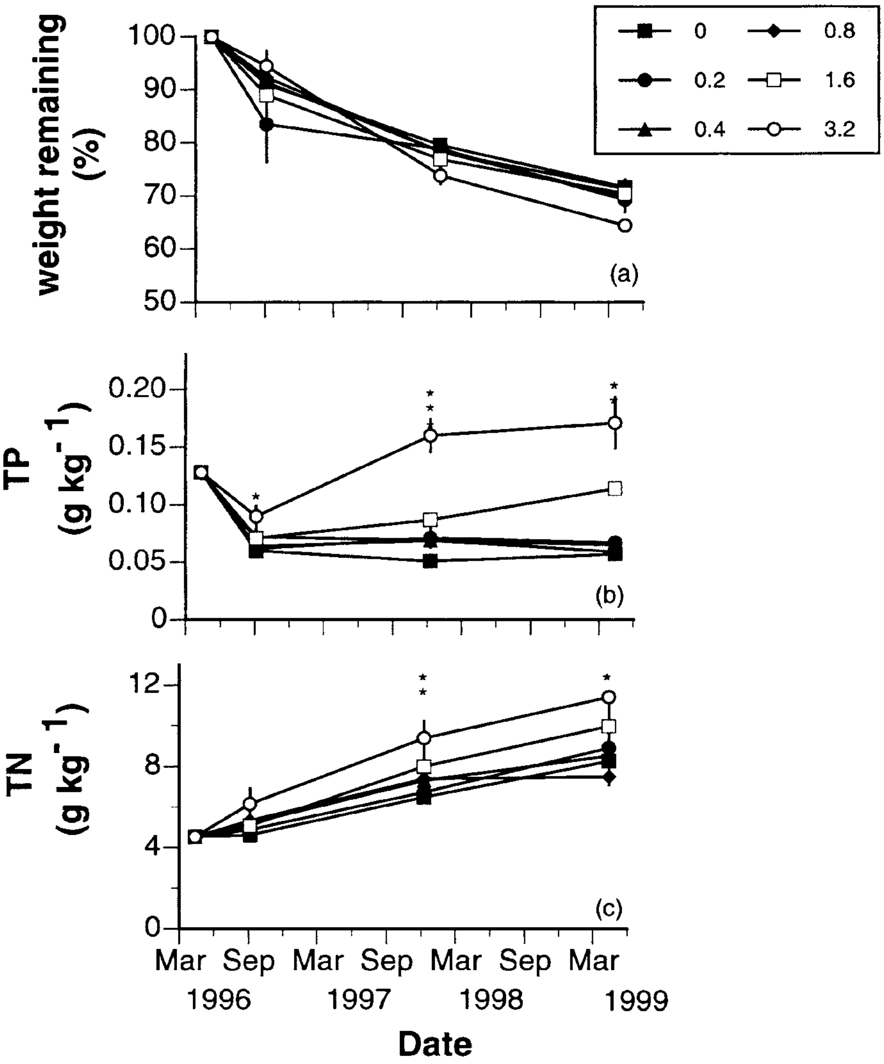

Figure 3. (a) Percent weight loss, (b) TP concentration and (c) TN concentration in litter bags incubated in mesocosms for 3 yr. *indicates treatment 3.2 g·m^{-2}·yr^{-1} is significantly different from the unenriched mesocosm, **indicates treatments 1.6 and 3.2 g·m^{-2}·yr^{-1} are significantly different from the unenriched mesocosm, ***indicates all P loads are significantly different from the unenriched mesocosms. See text for statistics.

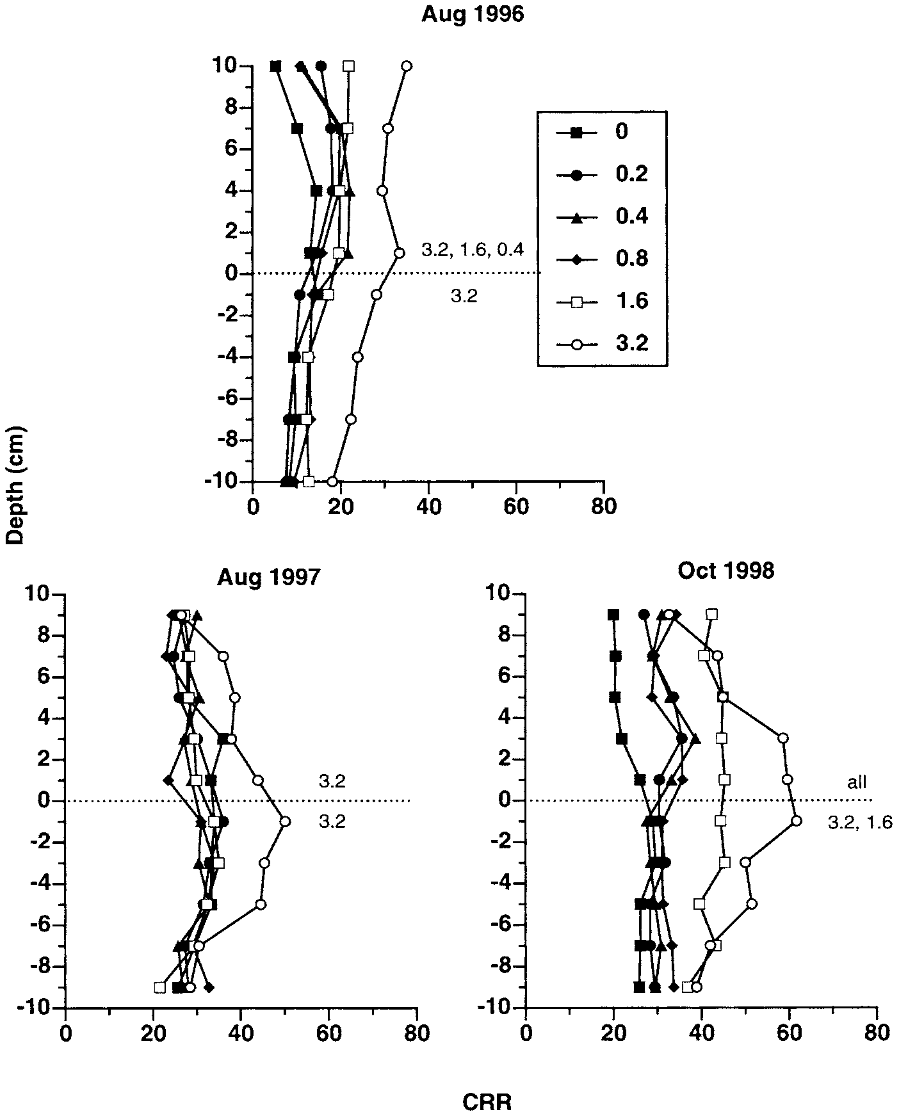

Figure 4. Cotton rotting rate (CRR) measured following 2 week incubations of cellulose strips. Numbers above and below the dashed lines show the treatments that are significantly different from the control for above or below CRR averages.

depths above and below the benthic floc-soil interface. After 6 months of P loading, mesocosms receiving P loads 0.4, 1.6, and 3.2 had a higher CRR above the soil than unenriched mesocosms. Trends were similar in the soil, but only the highest load produced a statistically significant response. After 17 mo only the highest load had higher CRR rates in both benthic floc and soil samples. After 31 mo of P loading, all P loads produced significantly higher CRR in above-soil samples with increases ranging from 40 to 120% higher than controls. Soil CRR were 50 and 80% higher than unenriched mesocosms at the two highest loads, 1.6 and 3.2, respectively.

Interstitial water

No detectable increase in P concentrations occurred in porewater well samples after more than 3 yr of P loading (data not shown). Total P and SRP concentrations were close to detection limits (0.004 mg L^{-1}) for all treatments. In contrast, increased NH_4^+ concentrations were observed within 4 mo of P addition at the two highest loads and within 18 mo at loads 0.4–0.8 (Figure 5). NH_4^+ concentrations in mesocosms loaded at 0.4–1.6 remained higher than unenriched mesocosms throughout the sampling period. However, after 2 yr, NH_4^+ concentrations in the highest loaded mesocosms decreased relative to unenriched controls. Similar relationships were observed for TDKN, of which over 70% was present as NH_4^+ (data not shown).

Other cation concentrations also increased significantly in response to P loads. Calcium concentrations were over 1.5 times higher than unenriched mesocosms within 4 mo in the two highest loads (1.6 and 3.2), and after 1 yr at a load of 0.8 (Figure 6). The same trends also were observed for Mg^{2+} concentrations over time (data not shown) with concentrations averaging from 1.7 mg L^{-1} in unenriched mesocosms to 2.1 and 2.2 mg L^{-1} in 1.6 and 3.2 loaded mesocosms, respectively. None of the changes in nutrient chemistry caused a significant change in pH, which averaged 5.79 (range 5.55–6.23).

Discussion

Decomposition

In this study, the effects of P enrichment on the decomposition of organic matter (litter bags and cotton strips) and the subsequent regeneration of nutrients (porewater chemistry) were examined. Approximately 30% of litter weight was lost over the 3 year period, producing calculated first-order exponential decay rates averaging 0.1 to 0.15 yr^{-1}. These rates are considerably

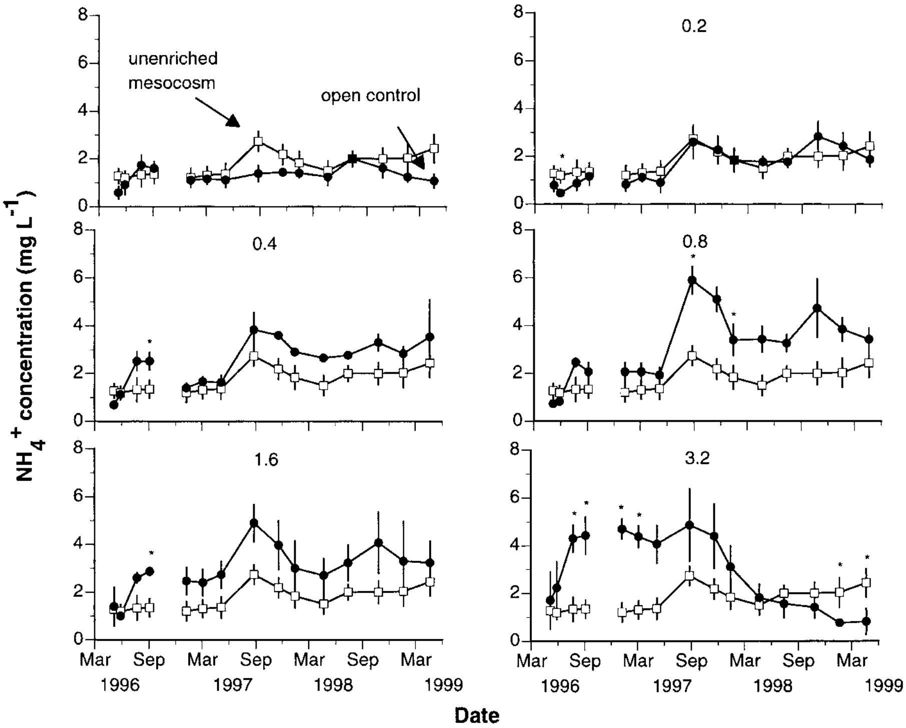

Figure 5. NH_4^+ concentrations (mean ± 1 S.E.) in the porewater in the mesocosms. Open squares = response of unenriched controls, circles = response of P loaded mesocosms. Number within each plot indicates P loading rate ($g \cdot m^{-2} \cdot yr^{-1}$). ∗indicates P load response is significantly different to that of the unenriched control.

lower than the average of 1.02 yr^{-1} reported for Cyperaceae by Webster and Benfield (1986) and the range 0.46 to 1.11 yr^{-1} recently reported for sawgrass litter in a northern Everglades marsh; WCA-2A (DeBusk & Reddy 1998; Qualls & Richardson 2000). Decomposition rates are influenced by a number of factors including the chemical and physical composition of the organic matter, microbial community composition and production, and external nutrient concentrations (Brinson et al. 1981; Webster & Benfield 1986; Rybczyk et al. 1996). Although no structural comparisons can be made between sawgrass litter from WCA-2A and WCA1, in many systems substrate C:N ratios are a good predictor of decay rate (Webster & Benfield 1986; Taylor et al. 1989). In the Everglades, substrate P concentrations had a significant influence on decomposition rates (DeBusk & Reddy 1998). The initial mass C:N and C:P ratios of sawgrass litter in the WCA-2A study were 161 and 11,800, respectively and 100 and 3,700, respectively in this study. Mass ratios of C:N < 30 and C:P < 200 are generally used to indicate that

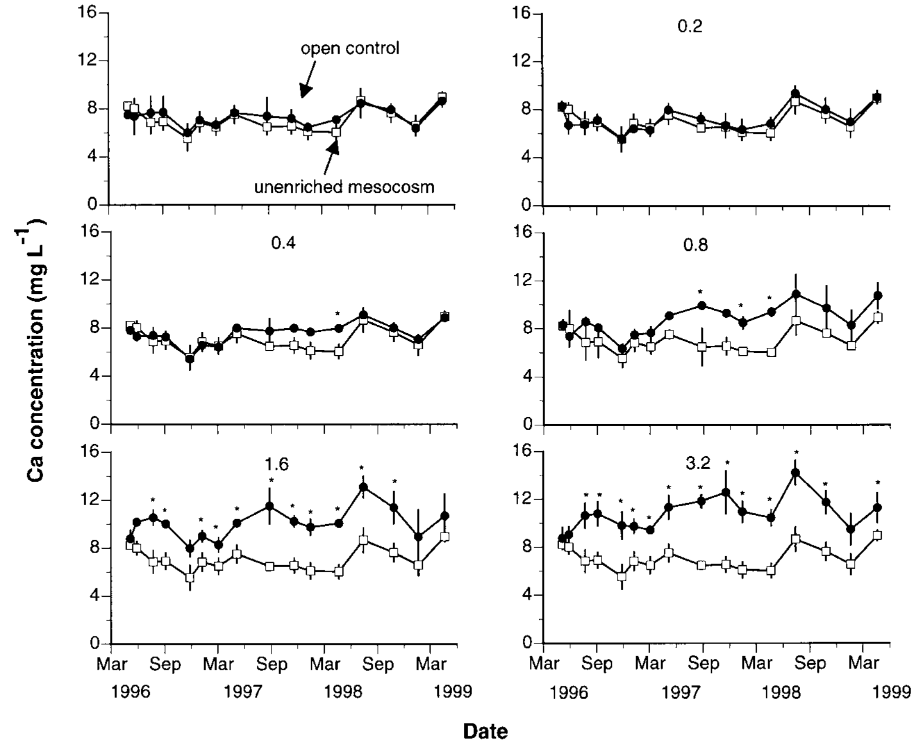

Figure 6. Ca^{2+} concentrations (mean ± 1 S.E.) in the porewater in the mesocosms. Open squares = response of unenriched controls, circles = response of P loaded mesocosms. Number within each plot indicates P loading rate ($g{\cdot}m^{-2}{\cdot}yr^{-1}$). $*$indicates P load response is significantly different to that of the unenriched control.

net mineralization of N and P are likely to occur (Stevenson 1986; Fenchel et al. 1998). Using these ratios, decomposition in both WCA-2A and WCA1 would be predicted to be limited by N and P availability. Based on the similar concentrations of available N and P in surface water and porewater in unenriched areas of WCA-2A and WCA1 (Davis 1991; DeBusk et al. 1994; Qualls & Richardson 1995; Newman et al. 1997; Vaithiyanathan & Richardson 1998; Qualls & Richardson 2000), nutrient limitation would be expected to be similar in both regions. Lower decomposition rates in WCA1 might therefore, be attributable to lower microbial biomass and activity, which were not measured in this study.

Alternatively, although primary productivity in WCA1 is P-limited (McCormick et al. 2000), litter decomposition rates in WCA1 may be controlled by other nutrients in addition to P. The key distinguishing characteristics between WCA1 and WCA-2A appear to be the metal ion concentrations. WCA1 is a softwater site and WCA-2A is a hardwater site. Low concentrations of cations, such as Ca^{2+}, may affect decomposition rates by influencing substrate quality. Litter with a high Ca^{2+} content has been observed to decay faster than Ca^{2+} poor litter (Smith et al. 1993). Additionally, the initial microbial decomposition of complex plant material is catalyzed by extracellular enzymes. Enzyme hydrolysis of organic matter, considered the rate-limiting step in decomposition (Meyer-Reil 1991; Sinsabaugh et al. 1993), is influenced by several factors, including ionic strength and metal ion concentrations (Jansson et al. 1988). For example, phosphatase enzymes, which hydrolyze the degradation of organic P, are inhibited in softwater systems due to the reversible binding of enzymes with humic acid (Wetzel 1991). In hardwater systems divalent cations, such as Ca^{2+}, bind with the humic acids, thereby suppressing the inhibition of enzyme activity by humic compounds (Wetzel 1991). Thus, in this highly organic system low cation concentrations may influence decomposition rates through their potential effect on substrate quality and enzyme activity. It is unknown whether low cation concentrations within WCA1 had a significant influence on decomposition rates. Low decay rates may be attributable to other factors not measured in this study including structural composition of the litter and microbial activities. However, canal water entering WCA1 is enriched in minerals as well as P (McCormick et al. 2000), therefore the relative importance of this mechanism warrants further evaluation.

While the litter data provided insights into the interrelationship of nutrients, nutrient uptake, and decomposition, the results are dependent on the composition of the litter material and its pretreatment (Boulton & Boon 1991). Due to the low nutrient content and labile nature of cellulose, the cotton strip assay can be used to assess the effects of environmental change on microbial decomposition rates, independent of the substrate quality of the litter material (Harrison et al. 1988). Both CRR and nutrient content changed more rapidly in the benthic floc layer than in the soil in response to P enrichment. Cotton strip decomposition has been proposed as an index of soil biological activity (Smith et al. 1993) and as a potential bioindicator of soil health in response to agricultural management practices (Pankhurst et al. 1995). In this study, CRR increased significantly in response to P enrichment before a P concentration response was observed in either benthic floc or surface soil layers. In a P-limited system, added P is likely to be cycled rapidly leading to little or slow changes in static nutrient concentrations. Thus, CRR is a more sensitive indicator of microbial response than decomposition determined by weight loss of litter bags, and may be a useful bioindicator. This has significant implications for systems such as the Everglades where water resource agencies are trying to establish criteria that can be used to protect the resource. Once seasonal variability is established, CRR could be used to provide an indication of wetland benthic and soil recovery or decline in response to P enrichment.

Nutrient regeneration

In organic-rich systems, internal nutrient regeneration from organic matter mineralization has been suggested to be as important as external (*de novo*) inputs in providing nutrients to a system (Verhoeven et al. 1988). Multiplying the amount of P lost per gram of unenriched litter during the first year of the study by the average annual production of unenriched sawgrass (894 g m^{-2} yr^{-1}; Davis 1989) suggests that decomposing litter releases approximately 80 mg P m^{-2} yr^{-1}. In contrast, in rural areas, P loading from atmospheric deposition, the primary nutrient source in the marsh interior, has been estimated at 27 mg m^{-2} yr^{-1} (Brezonik & Pollman 1999). Therefore, while decomposition rates may be low, the internal regeneration of P from litter decomposition is substantially higher than P inputs from rainfall.

While P enrichment reduced net nutrient regeneration from the litter, it increased nutrient regeneration in the soil. The initial mass C:N ratio of the soil was 13, suggesting that net N mineralization was likely to occur (Stevenson 1986; Fenchel et al. 1998). Thus, once P limitation of microbial activity is alleviated by the addition of P, microbial breakdown of organic matter and the associated release of NH_4^+ is possible. White and Reddy (2000) recently determined that microbial activity, microbial biomass, and potentially mineralizable N increased in P enriched Everglades soils and suggested this would increase inorganic N availability. In this study, the increase in porewater NH_4^+ in association with increased CRR confirms that organic matter mineralization caused by P enrichment results in enhanced porewater NH_4^+ regeneration. Of all the parameters measured in this study, porewater NH_4^+ accumulation appeared the most sensitive indicator of P loading. The subsequent decrease in NH_4^+ concentrations at the highest load is likely due to increased uptake by water lily, spikerush and the microbial community (McCormick et al. 2000).

In addition to NH_4^+, Ca^{2+} concentrations also increased as a function of P load. There was no apparent decrease in pH, and, thus, Ca^{2+} increase was not a function of the solubilization of Ca^{2+} mineralization under acidic conditions, but more likely a release of Ca^{2+} from organic matter. Alternatively, while no distinct pH changes were observed, Ca^{2+} could be locally released in response to the release of organic acids from actively growing macrophytes.

In summary, the addition of P enriched runoff to a P-limited system such as the Everglades resulted in increased decomposition and increased microbial activity in both the benthic layer and surface soils. The benthic floc layer responded more rapidly than the soils, indicating the important role this layer plays in this wetland system. A comparison of decomposition data and porewater chemistry suggests that one of the significant impacts of P enrichment in the Everglades is the regeneration of nutrients in the porewater.

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