Biogeochemistry (2005) 75: 217–240
DOI 10.1007/s10533-004-7113-0

Litter decomposition and nutrient dynamics in a phosphorus enriched everglades marsh

WILLIAM F. DEBUSK[1,*] and K. RAMESH REDDY[2]
[1]*West Florida Research and Education Center, University of Florida, 5988 Hwy. 90, Bldg. 4900, Milton, FL 32583;* [2]*Soil and Water Science Department, University of Florida, 106 Newell Hall, PO Box 110510, Gainesville, FL 32611-0510, USA; *Author for correspondence (e-mail: wdebusk@ufl.edu; phone: +1-850-983-5216; fax: +1-850-983-5774)*

Received 30 November 2004; accepted in revised form 2 December 2004

Key words: Decomposition, Detritus, Everglades, Litter, Phosphorus, Wetland

Abstract. A field study was conducted in a nutrient-impacted marsh in Water Conservation Area 2A (WCA-2A) of the Everglades in southern Florida, USA, to evaluate early stages of plant litter (detritus) decomposition along a well-documented trophic gradient, and to determine the relative importance of environmental factors and substrate composition in governing decomposition rate. Vertically stratified decomposition chambers containing native plant litter (cattail and sawgrass leaves) were placed in the soil and water column along a 10-km transect coinciding with a gradient of soil phosphorus (P) enrichment. Decomposition rate varied significantly along the vertical water–soil profile, with rates typically higher in the water column and litter layer than below the soil surface, presumably in response to vertical gradients of such environmental factors as O_2 and nutrient availability. An overall decrease in decomposition rate occurred along the soil P gradient (from high- to low-impact). First-order rate constant (k) values for decomposition ranged from 1.0 to 9.2×10^{-3} day^{-1} (mean = 2.8×10^{-3} day^{-1}) for cattails, and from 6.7×10^{-4} to 3.0×10^{-3} day^{-1} (mean = 1.7×10^{-3} day^{-1}) for sawgrass. Substantial N and P immobilization occurred within the litter layer, being most pronounced at nutrient-impacted sites. Nutrient content of the decomposing plant tissue was more strongly correlated to decomposition rate than was the nutrient content of the surrounding soil and water. Our experimental results suggest that, although decomposition rate was significantly affected by initial substrate composition, the external supply or availability of nutrients probably played a greater role in controlling decomposition rate. It was also evident that nutrient availability for litter decomposition was not accurately reflected by ambient nutrient concentration, e.g., water and soil porewater nutrient concentration.

Abbreviations: WCA – Water Conservation Area

Introduction

Decomposition of plant litter has been widely studied in terrestrial and aquatic ecosystems. Numerous factors related to the chemical properties of the litter ('substrate quality') as well as external, or environmental, factors have been shown to significantly affect decomposition rate. Among the more important environmental factors are temperature, moisture content and availability of

nutrients and electron acceptors (Swift et al. 1979; Heal et al. 1981; Webster and Benfield 1986; Reddy and D'Angelo 1994).

The decomposition (mineralization) process in wetlands differs from that in upland ecosystems in a number of ways (D'Angelo and Reddy 1999; Bridgham et al. 2001). The predominance of aerobic conditions in upland soils generally results in rapid decomposition of organic matter such as plant and animal debris. Net gain of organic matter in upland soils is thus relatively slow, and represents accumulation of highly resistant compounds that are relatively stable even under favorable conditions for decomposition (Jenkinson and Rayner 1977; Paul 1984). Decomposition occurs at a significantly lower rate in wetland soils, due to frequent-to-occasional anaerobic conditions throughout the soil profile resulting from flooding. Consequently, significant accumulation of moderately labile organic matter can occur in wetlands, in addition to lignin and other recalcitrant fractions (Clymo 1983).

Our study is focused on the dynamics of organic C, N and P in plant litter along a nutrient-enrichment gradient in a northern Everglades (Florida) marsh. Phosphorus enrichment has been a major concern in the Everglades, having been implicated, along with altered hydroperiod, in the encroachment of cattail (*Typha domingensis* Pers.) and other rapidly growing vegetation into the native sawgrass (*Cladium jamaicense* Crantz) marsh (Davis 1991; Jensen et al. 1995; Miao and DeBusk 1999). In Water Conservation Area 2A, one of the focal points of Everglades ecological research, P loading has been linked to widespread soil P enrichment (DeBusk et al. 1994, 2001), productivity and community structure of macrophytes (Miao and Sklar 1998; Newman et al. 1998; Miao and DeBusk 1999; Richardson et al. 1999; Vaithiyanathan and Richardson 1999) and periphyton (McCormick and Stevenson 1998; McCormick et al. 1998), organic carbon turnover (DeBusk and Reddy 1998; Wright and Reddy 2001), nitrogen cycling (White and Reddy 2000), microbial community structure (Drake et al. 1996) and diatom assemblages (Cooper et al. 1999).

The objectives of this research were to (1) determine the influence of soil and water nutrient enrichment on plant litter decomposition and nutrient dynamics, (2) evaluate within-site variability in decomposition rate and nutrient immobilization along the vertical water–soil profile, and (3) assess the relative significance of substrate composition vs. environmental factors in controlling decomposition rate. Our study incorporated a litter decomposition assay, conducted *in situ* in Everglades WCA-2A, along a P enrichment and trophic gradient characterized by a transition from sawgrass to cattail marsh.

Materials and methods

Site description

Field study sites were located in Water Conservation Area 2A in the northern Everglades (Figure 1). The WCAs are vast hydrology-managed impoundments

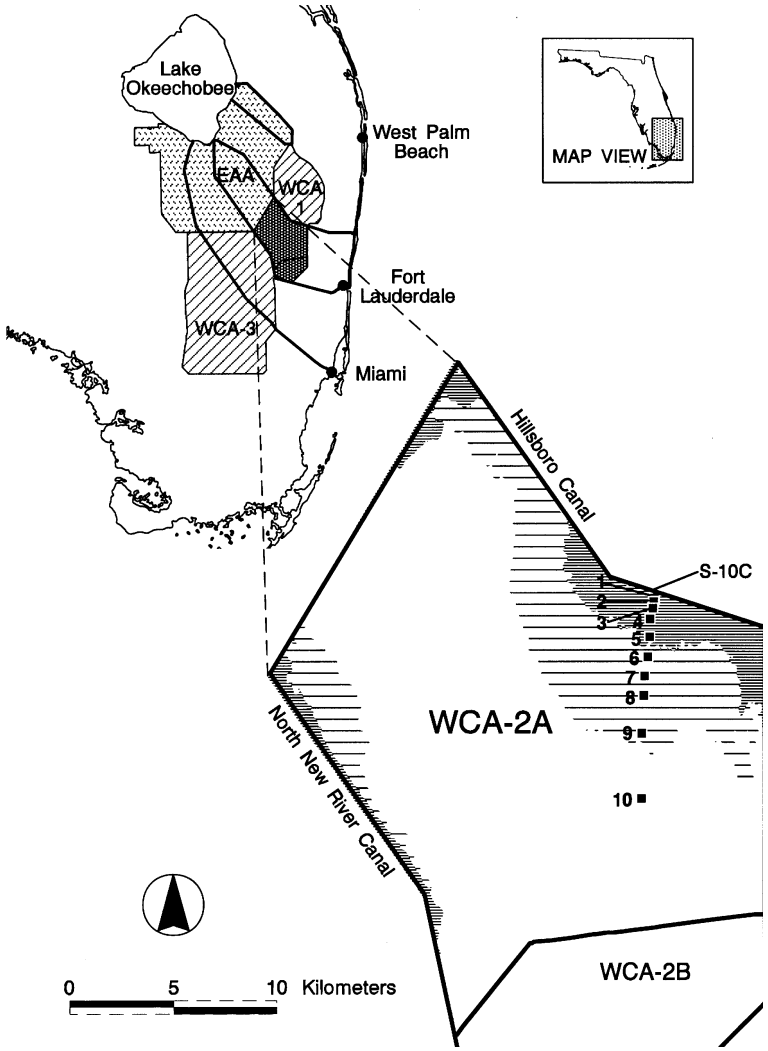

Figure 1. Site map for Everglades WCA-2A study area, with locations of sampling sites along a nutrient-enrichment gradient originating at surface inflow S-10C. The approximate coverage of sawgrass, mixed sawgrass/cattail, and cattail marsh communities within WCA-2A are denoted by open, hatched and finely hatched areas, respectively.

created during the mid-20th century from a network of levees and canals in the northern and central Everglades marshes. Water Conservation Area 2A is situated immediately downstream (via the Hillsboro and North New River Canals) from the Everglades Agricultural Area, a broad expanse of drained Everglades marshland, primarily utilized for production of sugar cane, vegetables and sod. Surface water flows into WCA-2A primarily through the S-10 inflow structures (Figure 1). The general direction of sheet flow through the

WCA-2A marsh is from the S-10 inflows at the northern boundary toward the south. However, actual flowpaths through WCA-2A are believed to be relatively complex and tortuous, due to the influence of an interior perimeter canal and a maze of airboat trails that cut through the emergent marsh.

Dominant ecological communities in the low-nutrient interior region of WCA-2A are sawgrass (*Cladium jamaicense* Crantz) marsh, scattered aquatic sloughs and remnant tree islands. Cattails (*Typha domingensis* Pers.) and mixed emergents (herbaceous and woody) dominate near the inflows, where nutrient-rich water has entered WCA-2A from the nearby Everglades Agricultural Areas over a period of about four decades. The soils of WCA-2A are exclusively Histosols, generally characterized as Everglades and Loxahatchee peats (Gleason et al. 1974). These soils typically display circumneutral pH, high Ca content and low Fe and Al content. Peat in WCA-2A is about 1 to 2 m deep and is underlain by areas of a calcitic 'mud', sandy clay and sand, and a bedrock of Pleistocene limestone (Gleason et al. 1974).

As a consequence of long-term nutrient loading to WCA-2A, a steep gradient of nutrient enrichment (primarily P) of water, plants and soil exists between the region adjacent to the inflows (high-nutrient) and the interior marsh (low-nutrient) of WCA-2A (Koch and Reddy 1992; DeBusk et al. 1994, 2001). Changes in species composition of periphyton and macrophyte communities, as well as an overall increase in net primary productivity, have been well-documented along the P enrichment gradient (Swift and Nicholas 1987; Davis 1991; McCormick and Stevenson 1998; Miao and Sklar 1998; Newman et al. 1998; Vaithiyanathan and Richardson 1999). The most visible change in the marsh ecosystem has been the transition from sawgrass to cattail/shrub marsh along the soil and water P gradient in the northern portion of WCA-2A.

For the current study, 10 field sampling sites were established in WCA-2A along a 10-km north-to-south transect extending from the S-10C inflow on the Hillsboro Canal into the interior marsh (Figure 1). The transect was aligned with the nutrient gradient, in the general direction of surface water flow. The sampling sites, numbered 1–10, were located at distances of 0.1, 0.3, 0.6, 1.2, 2.0, 2.9, 3.9, 4.8, 6.6 and 9.8 km, respectively, from the inflow.

Field decomposition study

Decomposition of plant litter was measured *in situ* in a vertical profile at each of the 10 sampling sites using a modified version of a multi-celled decomposition chamber described in Schipper and Reddy (1995). Decomposition chambers were constructed from 2.5 cm-thick sheets of ultra-high molecular weight (UHMW) polyethylene (60 cm tall × 10 cm wide). Slots were machined through the plastic sheets to create sample cells, open on each side of the apparatus (Figure 2). Spacing of sample cells was 2 cm on center, providing a separate sample chamber within each 2-cm increment of the soil profile. The entire array of sample cells was covered on both sides by screening consisting

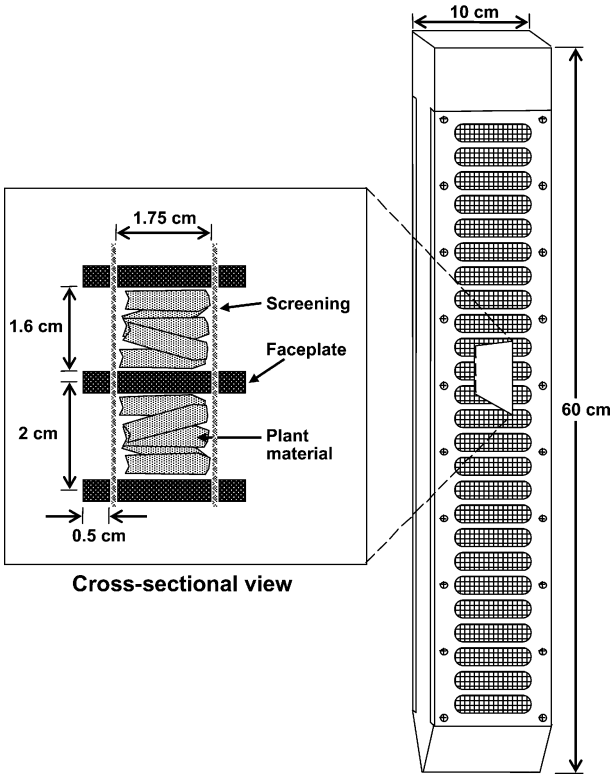

Figure 2. Multi-cell decomposition chamber used for *in situ* determination of litter decomposition rate along the vertical water–soil profile. Adapted from Schipper and Reddy (1995).

of plastic open-cell foam material, commonly sold as air conditioning filter. This material is approximately 3 mm thick, compressible and elastic, with a convoluted porous structure (pore size on the order of 1 mm) similar to a sponge. This type of screening material is well-suited for effective retention of plant litter, while allowing passage of ambient water and associated nutrients, as well as microorganisms and smaller macroinvertebrates, from the surrounding water and soil. Faceplates with matching slots were fastened to both sides of the apparatus to hold the filter material in place.

Standing dead (attached to the plant) leaf tissue was collected from each of the 10 sampling sites for use as the organic substrate for evaluating *in situ* decomposition at the respective sites. Dead leaves were collected from cattail plants at sites 1–8, and from sawgrass plants at sites 6–10. Sites 6, 7 and 8 were located within a transitional zone dominated by a mixed cattail–sawgrass marsh community (Figure 1). In all cases, a composite sample of dead leaves from five plants was collected, dried in a forced-air drying oven at 40°, then chopped into 2-cm pieces. From each composite sample, subsamples were obtained for initial chemical analysis. Total C and N analysis was performed

on dried, finely ground (< 0.2 mm) samples using a Carlo-Erba NA-1500 CNS Analyzer (Haak-Buchler Instruments, Saddlebrook, NJ). Total P analysis was performed on additional subsamples by combustion (ashing) at 550 °C for 4 h in a muffle furnace and dissolution of the ash in 6 M HCl (Anderson 1976). The digestate was analyzed for P using the automated ascorbic acid method (Method 365.4, USEPA 1983). Ash weights were recorded for calculating sample ash content.

For each sample site along the experimental transect, a 0.5 g (dry weight) portion of site-native dead plant material was placed in adjacent cells of the decomposition chambers. The chambers were installed vertically in the peat, with approximately 13 cells (26 cm) situated above the peat surface in the detrital layer and overlying water, and 10 (20 cm) within the peat itself. Decomposition chambers containing cattail litter were installed at sites 1 and 8 in triplicate, while one chamber each was placed at sites 2–7. For sawgrass litter, triplicate chambers were placed at sites 6 and 10, and single chambers at sites 7–9. The chambers were placed in the field in March 22, 1995 and removed after approximately 6.5 months of field incubation on October 11. The plant litter samples were removed from each cell and processed separately. Samples were dried in a forced-air drying oven at 40 °C, then weighed to determine mass loss. Samples from selected sites (1, 4, 6, 9 and 10) were analyzed for total N, total P and ash weight, according to the procedures described above for initial analysis of plant litter. Concentrations of tissue N and P were calculated based on total dry mass of the tissue sample.

Sample decomposition rates were calculated from mass loss (ash-free dry weight) and expressed as a first-order decay constant. Decomposition of cattail and sawgrass leaves was assumed to follow simple first-order kinetics, based on results of previous decomposition studies in WCA-2A (Davis 1991). The rate constant for each sample was calculated as

$$k = \frac{\ln[C_0/C(t)]}{t}, \tag{1}$$

where k is the first-order rate constant (day^{-1}), $C(t)$ is ash-free dry mass as a function of time, and C_0 is the initial mass of the sample. Thus, k for the entire incubation period was calculated from initial and final ($t = 204$ days) ash-free dry mass of the sample.

Air and soil temperature was monitored continuously at site 7, the approximate mid-point of the sampling transect, during the greater part of the decomposition study, from June 7 through October 11. Thermocouples connected to a data logger were placed in the peat at depths of 0 (peat surface), 5, 10 and 20 cm. Hourly readings were averaged for each 24-h period, and stored as the daily mean temperature for each depth. Prior to June 7, air temperature data from the nearby Everglades Nutrient Removal (ENR) experimental field site (SFWMD 1996) was substituted. Soil temperatures prior to June 7 were estimated from air temperatures, based on regressions of air vs. soil temperatures during June 7–October 11 time period.

Mean water depth at sites 1–10 during the study period was calculated from daily mean stage data for nearby WCA-2A field site 2–17 (SFWMD 1996). Water depth was calibrated using depth data from individual sites during two different sampling events.

Soil porewater – surface water nutrient analysis

Soil and surface water ammonium and soluble reactive P (SRP) were measured at 1-cm depth increments along the vertical surface water – soil porewater profile at each of the 10 sampling sites. Measurements were made twice during the study, in March and October, using porewater samplers designed after Hesslein (1976). Porewater samplers were constructed from Plexiglas stock (60 cm H × 7 cm W × 2 cm D), with an array of horizontally oriented sample cells (approximately 8 ml volume) at 1-cm depth increments. Prior to deployment in the field, sample cells were filled with deoxygenated deionized water, then covered with a sheet of 0.2-μm pore size membrane filter (Supor-200, Gelman Sciences – Pall Corp., Ann Arbor, MI) and a protective fiberglass screen. A Plexiglas faceplate (0.3 cm thick) with slots matching the cell openings was used to hold the filter and screen firmly in place.

Porewater samplers were installed vertically into the soil, so that a minimum of 30 cells (30 cm) were embedded in the peat and at least 10 cells remained above the peat surface, in the litter layer and/or water column. For the initial sampling event in March, one sampler was installed at each of the 10 sites and two additional samplers were installed at sites 4 and 10 as replicates for high- and low-nutrient sites, respectively. One sampler was deployed at each site for the final (October) sampling event. The porewater samplers were retrieved following a 13-day equilibration period in the field. Sampling was performed in the field upon retrieval of the porewater samplers, using 10-ml disposable plastic syringes. Samples were analyzed for ammonium and SRP using automated methods (EPA Methods 351.2 and 365.1; USEPA 1983).

Soil nutrient analysis

Soil cores were obtained from the 10 sampling sites during June 1995. The plant litter layer overlying the peat was sampled by inserting a short section of 15-cm diameter PVC pipe and manually collecting the loosely packed litter contained within the 177 cm^2 sample area. Next, a simple coring apparatus consisting of 7.6 cm-diameter aluminum irrigation pipe was used to obtain intact samples of the top 30 cm of the peat profile. The coring tube was pushed into the peat where litter had been previously removed, and extracted with the soil core intact. The intact peat was extruded from the coring tube using a plunger apparatus, and the upper 10 cm and the 10–30 cm layers of the peat profile were collected separately.

Soil coring was performed in quadruplicate at each sampling site, within a radius of approximately 5 m. Samples were processed in the laboratory, by removing live roots from the samples, then combining replicate samples to create a single composite sample for each soil depth and sampling site. The composited samples were stored in leak-proof polypropylene jars in a refrigerator at 4 °C. All soil samples (litter and peat) were prepared and analyzed for total N and P using the procedures described above for plant tissue analysis.

Results

Environmental factors

Flooded conditions persisted at all sites for the duration of the study, although water depth fluctuated within a range of approximately 20 cm to 1 m. Water depth reached a minimum of approximately 20 cm during the period May 18–June 22. Periodic measurements taken at the 10 sampling sites indicated that water depth typically varied among sites less than 10 cm from the mean depth for all sites.

Daily mean air and soil temperatures (measured at site 7 near the midpoint of the transect) varied within a range of approximately 10 °C during the course of the study. The mean daily air temperature for the study period was 27.2 °C. Differences among mean soil temperatures in the detrital layer and peat (to 20 cm depth) were less than one degree. Mean temperatures for the study period were 27.0, 27.0, 26.8 and 26.4 °C at depths of 0 (detrital layer), 5, 10 and 20 cm. During the period June 6–October 11, the difference in daily mean temperature among soil depths averaged 0.8° (standard deviation = 0.7°), and never exceeded 2.5°. Because of the small variation in temperature with depth, decomposition rates were not temperature-corrected.

Soil chemistry

Analysis of ammonium-N and SRP in porewater samplers revealed substantial variability among sites along the transect, and along the surface water–litter–peat profile (Figures 3 and 4). Ammonium concentrations in surface water, measured at 10 cm above the peat surface (and above the dense litter layer), ranged from less than 100 μg N l^{-1} at sites ≥4 km from the S-10C inflow (sites 7–10) to approximately 100–1600 μg N l^{-1} at the sites < 3 km from the inflow (sites 1–6). For all sites, ammonium concentration was typically higher in the litter layer, and generally increased with soil depth, although at some sites (e.g., sites 4–8) the maximum porewater ammonium concentration occurred near the peat surface. This may be related to a high level of recent peat accumulation and subsequent mineralization of organic N in the peat. Maximum concentrations of soil porewater ammonium, in the 5–7 mg N l^{-1} range, were found

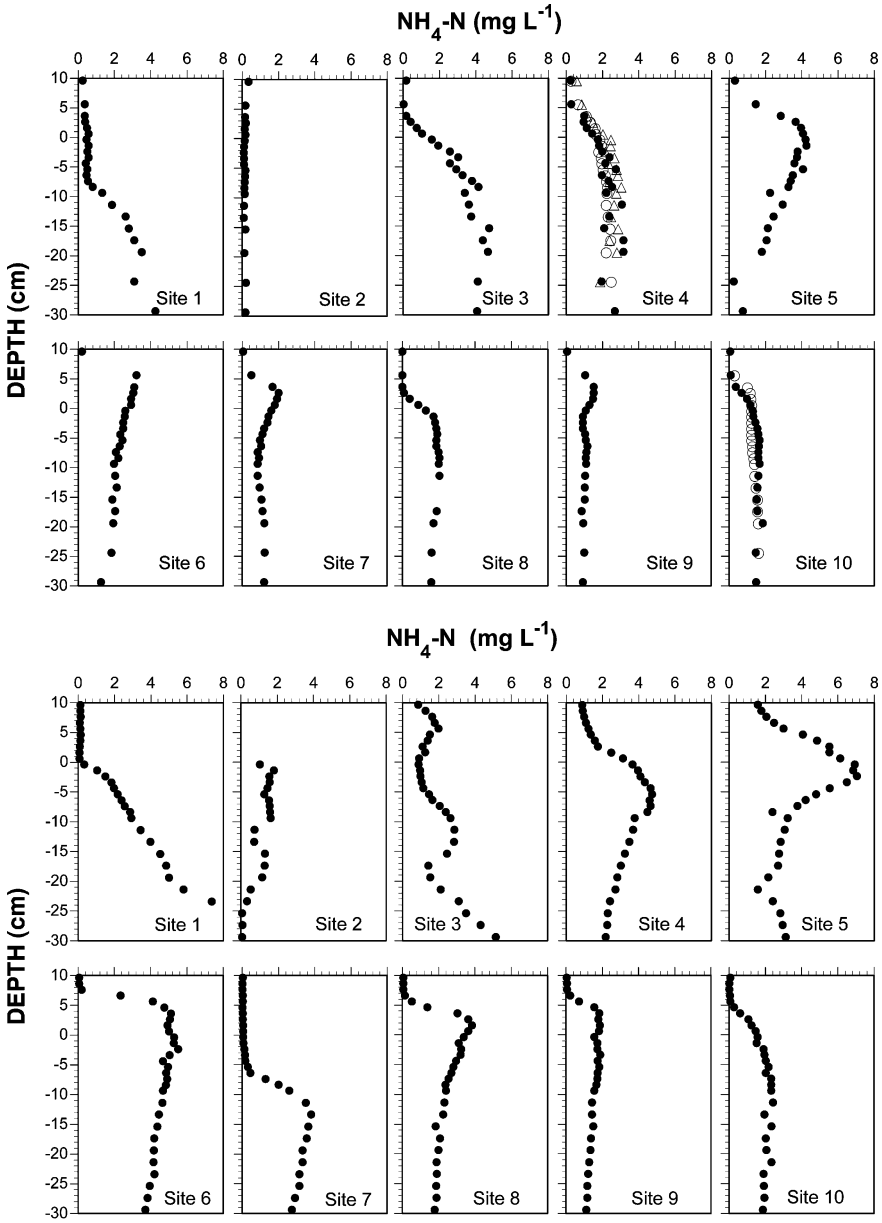

Figure 3. Concentration of ammonium-N along the vertical soil-litter-surface water profile at each decomposition study site, at the beginning (top graphs) and end (bottom graphs) of the decomposition study. Sites 4 and 10 were sampled in triplicate for the initial sampling event; replicate measurements are denoted by different symbol types.

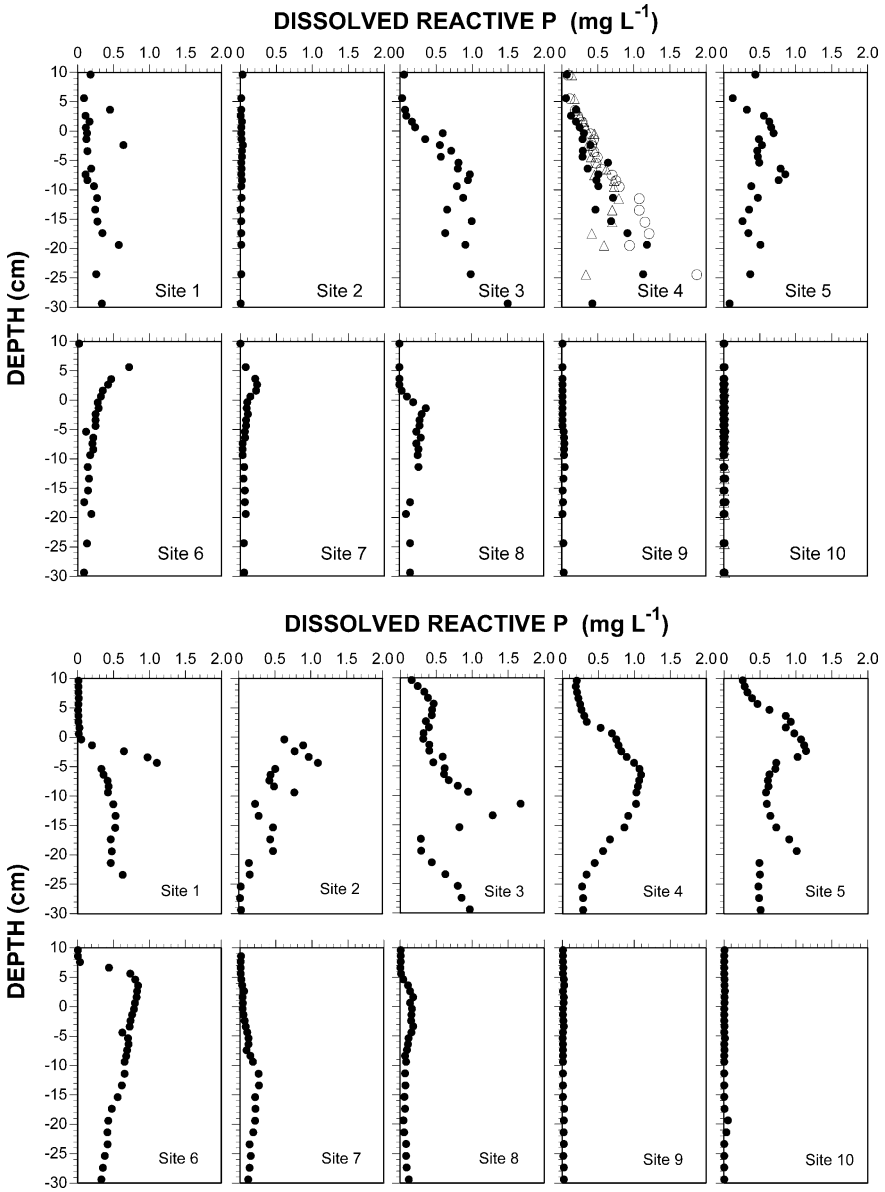

Figure 4. Concentration of soluble reactive P (SRP) along the vertical soil-litter-surface water profile at each decomposition study site, at the beginning (top graphs) and end (bottom graphs) of the decomposition study. Sites 4 and 10 were sampled in triplicate for the initial sampling event; replicate measurements are denoted by different symbol types.

at sites closer to the S-10C inflow. Overall, ammonium concentrations were slightly lower at the interior sites (e.g., sites 8–10) than at the ecologically altered sites near the inflow. High temporal variability of ammonium was

indicated at several sites by differences in concentration profiles between the initial and final samples. Some differences may have been related to local-scale spatial variability, since the physical characteristics of the litter layer and surficial peats are not uniform, but instead may be patchy (litter) and pitted or fractured (peat). For example, at site 2 the upper layer of peat, containing the porewater sampler, separated from lower peat during first sampling event, resulting in uncharacteristically low nutrient concentrations in the profile, apparently due to increased diffusion of solutes from the soil porewater. However, triplicate samples were in good agreement at sites 4 and 10, suggestive of relatively low spatial variability. The median standard error of triplicate ammonium measurements at each depth interval was 182 μg N l^{-1} at site 4 and 73 μg N l^{-1} at site 10.

Concentration of SRP in the surface water, 10 cm above the peat surface, ranged from < 10 μg P l^{-1} at sites ≥ 4 km from the S-10C inflow (sites 7–10) to approximately 10–250 μg P l^{-1} at the sites < 3 km from the inflow (sites 1–6). Typically, SRP concentration was higher in the soil profile, and generally peaked within the surficial peat (0–10 cm depth) and litter layer at sites 1–6 (ecologically altered sites). Porewater SRP concentration at these sites exceeded 1000 μg P l^{-1} in several instances. In general, substantial SRP enrichment of the soil profile was confined to sites 1–6. Enrichment of soil porewater with SRP was negligible by comparison at sites 9 and 10 in the interior sawgrass marsh, where concentrations did not exceed 60 μg P l^{-1}. Within-site spatial variability, as indicated by replicate sampling (March), was low for site 10. At site 4, triplicate samples were in good agreement for soil depths less than 10 cm, but diverged at greater depths. Median standard error of triplicate SRP measurements at each depth interval was 57 μg P l^{-1} at site 4 and 3 μg P l^{-1} at site 10.

Table 1. Soil total N and P concentrations at sites 1–10 along the WCA-2A transect originating at the S-10C water inflow structure.

Site no.	Distance from inflow (km)	Total N (g kg^{-1})			Total P (mg kg^{-1})		
		LIT	0–10 cm	10–30 cm	LIT	0–10 cm	10–30 cm
1	0.1	26.6	28.2	25.4	1582	1497	1195
2	0.3	26.7	28.6	30.3	1291	1337	1172
3	0.6	25.7	30.7	24.4	1461	1622	880
4	1.2	25.0	24.8	31.5	1833	1416	982
5	2.0	27.8	28.3	32.2	1743	1353	611
6	2.9	20.1	29.1	35.8	1084	1060	284
7	3.9	17.5	27.0	31.3	928	1146	466
8	4.8	19.6	26.1	26.3	1038	905	279
9	6.6	12.2	28.8	29.0	345	696	269
10	9.8	16.4	28.9	24.7	275	475	236

Soil samples were collected June, 1995. Discrete analyses were performed for the litter layer (LIT) and peat (0–10 and 10–30 cm depth increments).

Bulk soil analysis for total N and P indicated a pattern of nutrient enrichment associated with the S-10C inflow (Table 1), particularly within the litter layer overlying the peat. In fact, N enrichment near the inflow was confined to the litter layer, in which total N concentration ranged from about 26 g kg^{-1} near the inflow to about 15 g kg^{-1} in the interior sawgrass marsh. No significant trend in total N content was found within the 0–10 and 10–30 cm peat layers. Mean total N concentrations in the peat were 28 and 29 g kg^{-1} for the 0–10 and 10–30 cm depth intervals, compared to a mean concentration of 22 g kg^{-1} in the litter layer.

Enrichment of P in the soil near the S-10C inflow was more pronounced than soil N enrichment, and was reflected in the peat as well as the litter layer. Total P concentration of the litter layer decreased sharply between the inflow and the interior marsh, roughly forming 3 groups of sites along the transect. Total P concentrations in the 1300–1800 mg kg^{-1} range were observed at sites 1–5, while concentrations averaged approximately 1000 mg kg^{-1} at sites 6–8 and about 300 mg kg^{-1} at sites 9 and 10. Total P concentrations in the 0–10 cm layer of peat were similar to those in the litter layer, generally in the 1400–1600 mg kg^{-1} range near the inflow (sites 1–5) and decreasing in a linear fashion to 475 mg kg^{-1} at site 10. Within the 10–30 cm layer of peat, total P concentration was significantly lower overall. Total P concentration exhibited a roughly linear trend between sites 1 and 6, decreasing from 1195 to 284 mg kg^{-1}, and ranged from 466 to 236 mg kg^{-1} between sites 7 and 10. A steep gradient of soil P enrichment in the northern region of WCA-2A was previously documented by DeBusk et al. (1994).

Table 2. Initial chemical analysis of standing dead leaf material used for field decomposition study in Everglades WCA-2A. Each sample was composed of subsamples from five plants.

Site no.	Distance from inflow (km)	Plant type	Total C (g kg^{-1})	Total N (g kg^{-1})	Total P (mg kg^{-1})	Ash (%)
1	0.1	Cattail	466	8.0	339	2.3
2	0.3	Cattail	460	7.3	343	2.8
3	0.6	Cattail	463	5.7	375	2.0
4	1.2	Cattail	457	5.3	277	2.5
5	2.0	Cattail	457	6.4	373	2.3
6	2.9	Cattail	463	6.0	310	2.2
		Sawgrass	466	4.3	487	3.1
7	3.9	Cattail	468	4.7	315	2.4
		Sawgrass	457	5.3	478	4.2
8	4.8	Cattail	468	4.0	205	2.8
		Sawgrass	456	5.7	241	4.5
9	6.6	Sawgrass	454	4.0	140	4.8
10	9.8	Sawgrass	447	4.6	61	4.2

Plant tissue decomposition

Concentration of N and P in fresh plant litter, measured at the outset of the decomposition study, varied significantly among sampling sites (Table 2). Linear regression analysis indicated that initial tissue N and P concentration decreased significantly ($\alpha = 0.05$) with increasing distance from the S-10C inflow structure. This trend apparently was due to the nutrient gradient downstream from the inflow, rather than inherent differences between cattail and sawgrass, since there was no significant difference in tissue N and P between cattail and sawgrass litter, i.e., standing dead leaves, sampled at the transitional sites (mixed cattail–sawgrass stands). Ash content of the plant litter increased significantly with distance from the inflow; however, this was primarily a function of the vegetation shift along the transect, reflecting differences between cattail and sawgrass leaf composition.

Short-term (6.5 months) decomposition of cattail and sawgrass litter resulted in only partial, but highly variable, loss of sample mass. An overall mean of 37.8% ash-free dry mass loss occurred during the study, with cattail mass loss (mean = 43.4%; range = 19.1–87.1%) typically exceeding sawgrass mass loss (mean = 30.2%; range = 13.1–47.7%). Decomposition kinetics were accurately described by a simple first-order decay model, utilizing a single rate constant k. For plant material containing a significant proportion of labile organic C compounds (i.e., 'fresh' material), an initial rapid phase of mass loss may be observed during decomposition studies. In such cases decomposition may be more appropriately described by a two-stage (or multi-stage) first-order model utilizing multiple rate constants (Moran et al. 1989). The plant tissue collected for our study presumably had already undergone leaching of soluble constituents and, to some extent, decomposition of labile C compounds while still attached to the plant.

Overall, the mean decomposition rate, expressed as the first-order rate constant k, across all sites and plant types was 2.3×10^{-3} day^{-1} (S.D. = 0.9×10^{-3}). Decomposition rate for cattail litter ranged from 1.0 to 9.2×10^{-3} day^{-1} (mean = 2.8×10^{-3} day^{-1}), and from 6.7×10^{-4} to 3.0×10^{-3} day^{-1} (mean = 1.7×10^{-3} day^{-1}) for sawgrass. At all sites with the exception of site 8, k decreased significantly with depth (linear regression analysis, $\alpha = 0.05$), that is, from top to bottom of the water–soil profile (Figure 5). In addition, depth-averaged (by site) decay rate decreased significantly with increasing distance from the inflow ($\alpha = 0.05$). Comparison of depth-averaged values of k among individual sites indicated that the mean decay rate was significantly higher at sites 1, 2, 4 and 5 than the remaining sites, and was significantly lower at sites 9 and 10. When decay rates of cattail (sites 1–8) and sawgrass (sites 6–10) were evaluated separately, the same trend of decreasing rate with increasing distance from the inflow was observed. At sites 6–8, where both cattail and sawgrass samples were located, the depth-averaged decay rate of cattail was significantly higher than sawgrass at all three sites.

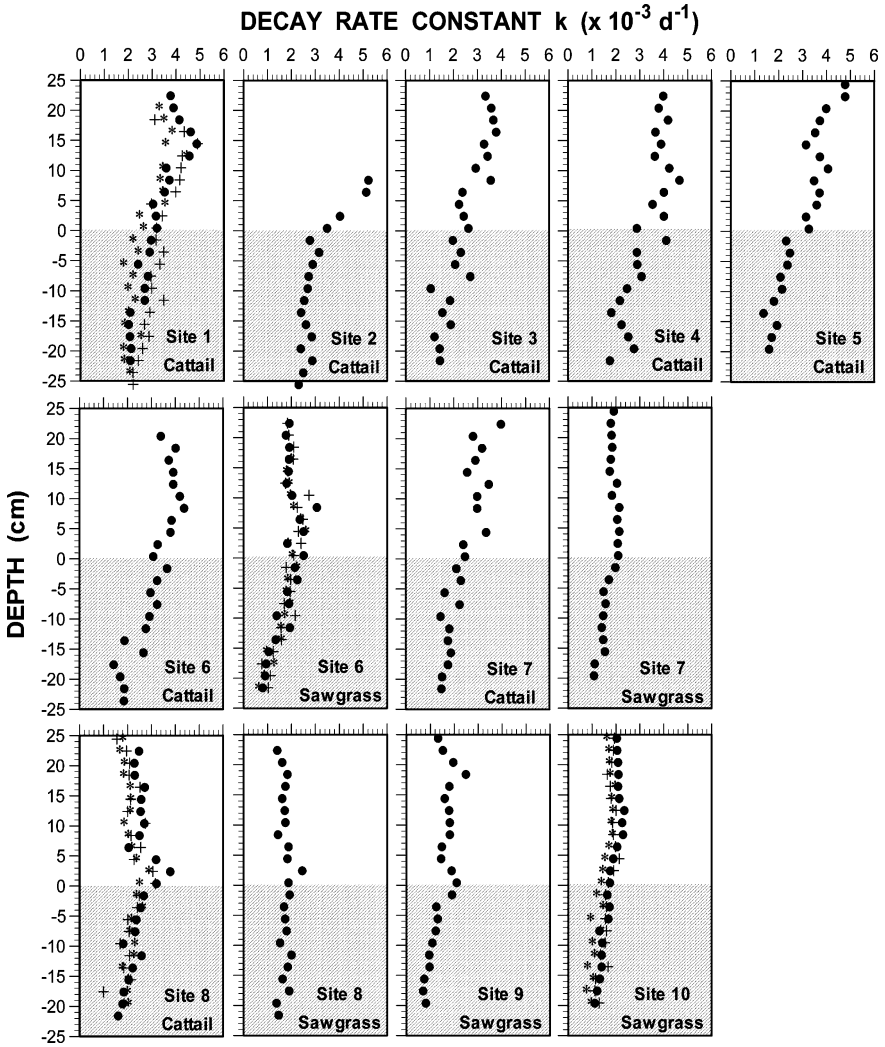

Figure 5. First-order decay rate constant (k), calculated from ash-free dry mass loss (see Eq. (1)), for cattail and sawgrass litter incubated *in situ* for 6 months at 10 sites along the WCA-2A experimental transect. Decomposition chambers were deployed in triplicate at sites 1, 6 (sawgrass only), 8 (cattail only) and 10; replicate measurements are denoted by different symbol types.

N and P immobilization

Comparison of initial and final nutrient concentrations in the decomposing substrate at sites 1, 4, 6, 9 and 10 showed that N and P enrichment had occurred in the substrate during the incubation period (Figures 6 and 7). Presumably, the primary mechanism of enrichment was assimilation by microbial decomposers (immobilization). Generally, immobilization of N was

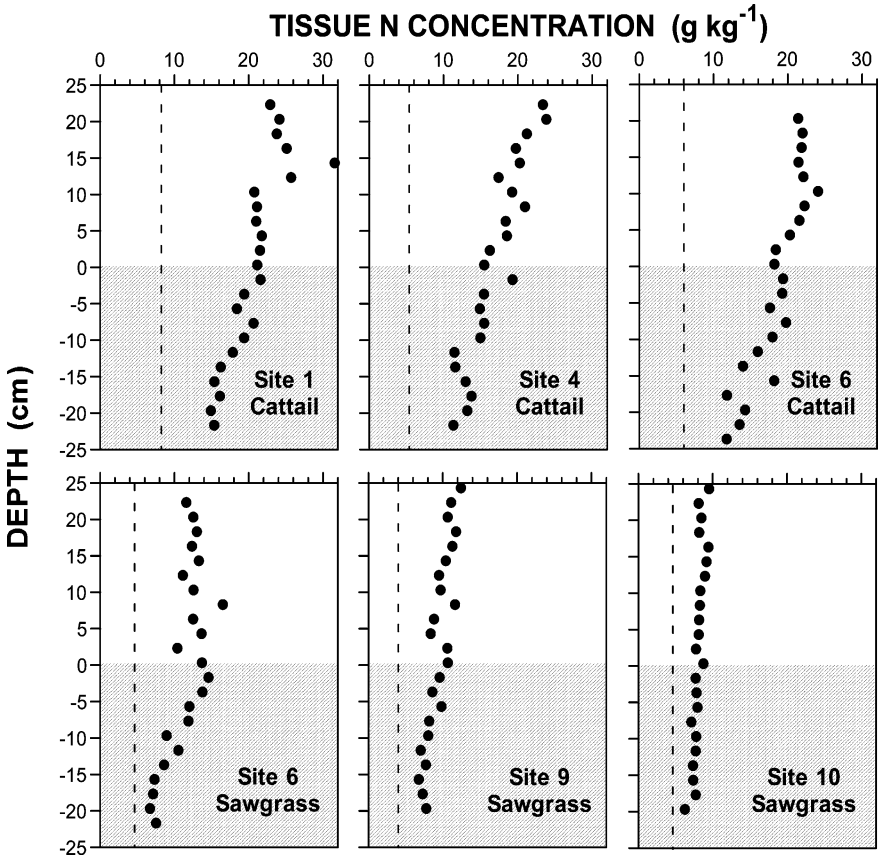

Figure 6. Total N concentration in leaf litter (total dry mass basis) from selected sites at the conclusion of the field decomposition study. Vertical dashed lines represent initial N concentration of the substrate (plant litter) for individual sites.

more pronounced at sites closer to the S-10C inflow (Figure 6). The degree of N immobilization also decreased slightly from top to bottom of the water–soil profile, following the trend for decay rate at these sites. In addition, mean N immobilization was greater in cattail than sawgrass litter at transitional site 6.

Similar spatial patterns were observed for final substrate P concentration and P immobilization (Figure 7). The relative extent of P immobilization was generally higher in proximity of the S-10C inflow structure, while minimal P enrichment of substrate occurred at the interior sites (sites 9 and 10). Mean P immobilization was higher in cattail leaves than in sawgrass at site 6, presumably due to higher substrate (organic C) availability for microbial growth in the cattail leaves. Maximum P enrichment was typically found near the soil–water interface, possibly a manifestation of rapid turnover of organic P in the

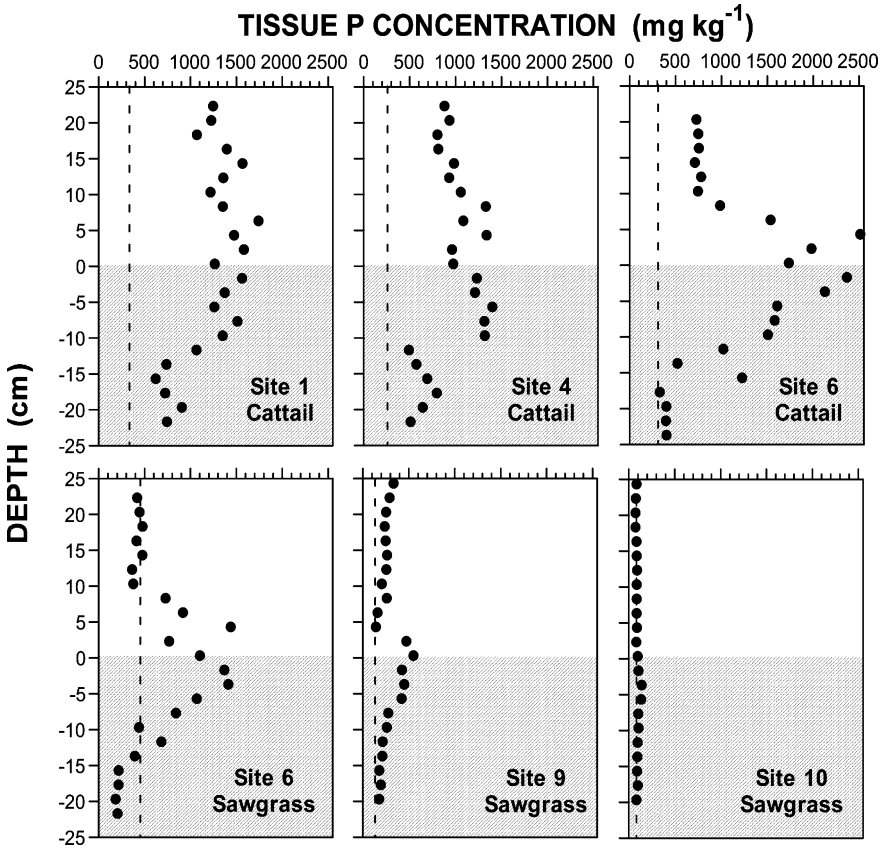

Figure 7. Total P concentration in leaf litter (total dry mass basis) from selected sites at the conclusion of the field decomposition study. Vertical dashed lines represent initial N concentration of the substrate (standing dead leaf tissue) for individual sites.

detrital layer (internal loading) enhancing P availability for the resident microbial consortium in the decomposition chambers. The occurrence of relatively high P immobilization in both cattail and sawgrass litter near the soil–water interface at site 6 (Figure 7) is not readily explained by the P content of bulk soil and soil porewater at this site, but was presumably related to increased P bioavailability. It is possible that highly localized nutrient enrichment may occur in association with wildlife or human disturbance.

Based on the mass increase of N during the decomposition study, the range of net N immobilization in litter at sites 1, 4, 6, 9 and 10 was 0.4–5.1 mg g^{-1} initial substrate mass. Net P immobilization ranged from −0.30 to 0.77 mg g^{-1} initial substrate mass, where negative immobilization is equivalent to net

mineralization of P. However, given that net nutrient immobilization is a function of both initial and final concentration in the substrate, rates of immobilization are not strictly comparable among sites, since initial substrate composition is not uniform among sites.

Factors controlling decomposition

Our study results suggest that the rate of decomposition of both sawgrass and cattail litter was governed largely by exogenous factors such as nutrient availability and vertical position within the water–soil profile, although in the short-term initial substrate composition may also play a significant role. Based on initial analysis of substrate composition, ash content and N concentration were significantly correlated with decomposition rate (k). Linear regression analysis indicated that initial ash content explained 69% ($r^2 = 0.69$) of the variability in k, while initial N concentration accounted for 48% of the variability. It is worth noting, however, that ash content was primarily a function of plant species, being significantly higher in sawgrass leaves than in cattail leaves. Unlike substrate N concentration, initial P concentration in the substrate was not related to k ($r^2 = 0.06$).

Despite similarities in patterns of soil nutrient enrichment and decomposition rates, only a very weak correlation was found between decomposition rate and dissolved nutrients (ammonium and SRP) at corresponding depths in the soil and overlying water. This held true for both March and October water/porewater chemistry data, as well as averaged data from the two sampling dates. Correlations were also examined separately for surface water and soil layers, to account for differences in oxygen availability and, consequently, metabolic rates of microbial decomposers; however, these correlations were also insignificant. The weak correlation between decomposition rate and water/porewater nutrients is likely related to the temporal variability of porewater chemistry (Figures 3 and 4). Within-site variability of porewater ammonium and SRP between sampling dates may have been influenced primarily by hydrologic factors. Surface water discharge into WCA-2A, and consequently nutrient loading, varies seasonally, and thus concentrations of N and P in surface waters tend to be variable over time, especially near the inflows (SFWMD 1992).

Comparison of decomposition rate (k) with soil total N and P concentration, averaged over the top 30 cm of the soil profile, at each site indicated that soil N concentration was poorly correlated with k, while total P was more highly correlated. Regressions of k on soil N and P concentrations showed that soil P can account for 54% of the variability in k, compared with only 7% for soil N. In contrast, decomposition rate was significantly correlated with final substrate concentrations of P and, in particular, N. Based on linear regression analysis, final substrate N concentration accounted for 85% of the variability in k, while 46% of the variability in k was explained by final P concentration. The

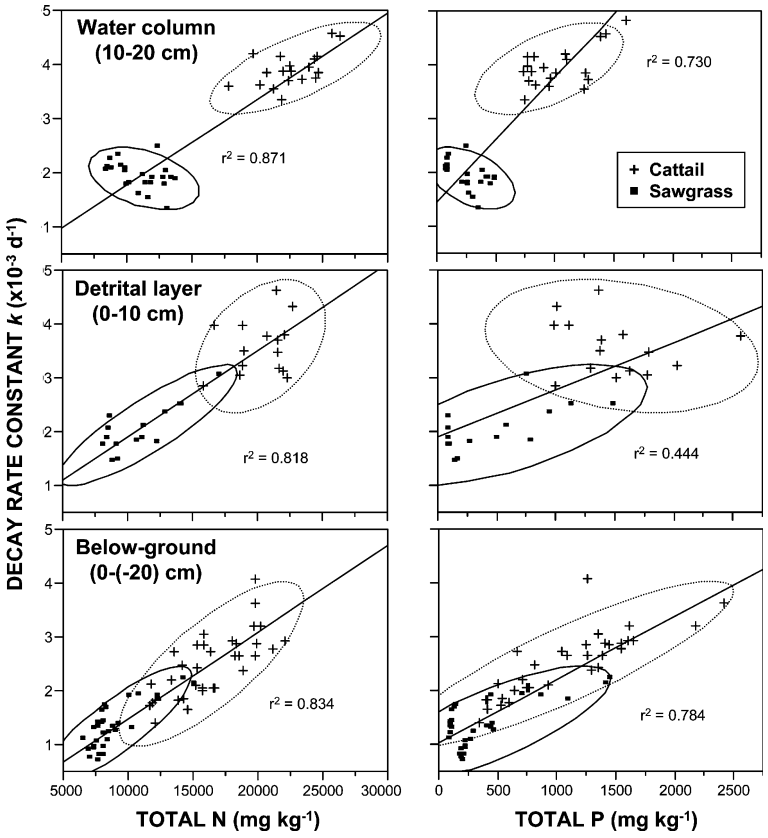

Figure 8. Relationship of decomposition rate (decay constant k) to final substrate (litter) N and P concentrations, within 3 'discrete' strata of the soil-water profile: water column (10–20 cm above soil surface), detrital layer (0–10 cm above soil surface) and below ground (0–20 cm depth of soil profile). Data for cattail (+) and sawgrass (■) are plotted separately, with density ellipses (95% probability) indicated for each plant type.

apparent discrepancy arising from the poor relationship between k and soil N and the close relationship observed between k and final substrate N is probably best explained by the tendency of a high 'quality' C substrate such as plant litter to act as a nutrient sink, coupled with the tendency of comparatively recalcitrant peat to lose N via metabolic pathways (as opposed to P) in wetland soils.

On closer examination, the relationships between decomposition rate and final substrate N and P concentration were found to vary significantly by plant species and by depth within the water–soil profile (Figure 8). For example, within the below-ground portion of the profile, the decay rate constant k was strongly related to both substrate N and P ($r^2 = 0.83$ and 0.78, respectively). However, the relationship between substrate P content and k was somewhat

weaker within the lower 10 cm of the water column (generally coinciding with the detrital layer), particularly with respect to cattail litter. In general, the influence of plant type on decomposition rate and substrate composition was more pronounced in the detrital layer than in the soil profile (below ground). The effect of plant type was even more evident within the water column above the detrital layer (10–20 cm above the soil surface). Note that although k was, in general, strongly related to substrate N and P concentration for samples in the water column, the relationship was not particularly well-defined for either cattail or sawgrass litter taken individually. In fact, most of the variability in k and substrate N and P composition was related to plant species, since cattail and sawgrass samples were rather tightly grouped and well separated along the overall regression lines for k vs. N and k vs. P.

Overall, the data presented in Figure 8 are suggestive of increased N availability and decreased P availability in the water column relative to the soil. Due to the tendency for P to accumulate in sediments, internal loading (recycling) is more strongly expressed for P than for N. The data also reflect the higher 'substrate quality', presumably related to C availability, of cattail vs. sawgrass litter, although clear indication of this (separation of cattail and sawgrass in the k vs. N and k vs. P plots) appears only in the water column. It is likely that the response of microbial activity to differences in substrate quality between cattail and sawgrass may be disproportionately enhanced under aerobic (water column) vs. anaerobic (soil) conditions, resulting in a greater absolute increase in k for cattail than for sawgrass.

Discussion

Effects of flooding on decomposition of litter and peat in wetlands have been widely documented (Tate 1979; Moore and Dalva 1993; DeBusk and Reddy 1998). Nutrient availability can also play a significant role in regulating decomposition rate in wetlands. Growth-limiting nutrients in the surrounding water and soil, primarily in inorganic form, may be used by microbial decomposers to supplement the nutrient pool within the organic substrate, primarily in organic form (Heal et al. 1981; Melillo et al. 1984). Decomposition of organic matter is also regulated by chemical composition of the substrate itself, sometimes referred to as 'substrate quality' (DeBusk and Reddy 1998; Bridgham et al. 2001). Substrate quality may refer to nutrient content as well as the susceptibility of organic C to microbial breakdown. Lignin and cellulose fractions have been cited as defining components of 'C quality' of an organic substrate (Swift et al. 1979; DeBusk and Reddy 1998). Initial lignin and N content of the organic substrate (e.g. plant tissue) have been correlated with decomposition rate (Godshalk and Wetzel 1978; Melillo et al. 1982; Aber et al. 1990).

Terrestrial decomposition studies have indicated that substrate quality and external nutrient supply are both important regulators of decomposition

during the early stages of decomposition of plant residues (Swift et al. 1979; Heal et al. 1981; Melillo et al. 1989). However, there is evidence that, during later stages of decomposition, the chemical quality of substrates of different initial compositions is reduced to a 'least common denominator', so that variability in decay rate is a function of environmental factors alone (Melillo et al. 1989).

Our short-term decomposition study focused on the early stages of the 'decay continuum' from plant litter to peat. Experimental results indicated that both substrate-related (endogenous) and environmental (exogenous) characteristics played a role in governing decomposition rate. Findings were similar in a two-year *in situ* decomposition study previously conducted at three sites in WCA-2A, representing nutrient-enriched, transitional and non-enriched areas (Davis 1991). Cattail and sawgrass litter placed in the detrital layer at the three sites decomposed more rapidly at the nutrient-enriched site, and least rapidly at the non-enriched site. In addition, first-order decay rates calculated from Davis' data were higher for cattail (18.1, 9.2 and 9.0×10^{-4} day^{-1}) than for sawgrass (10.8, 6.6 and 6.2×10^{-4} day^{-1}), at each site.

In our study, variability in the first-order rate constant k along the vertical water–soil profile was solely due to exogenous factors, given the uniformity of substrate within each of the decomposition chambers. Among the possible environmental factors controlling decomposition rate, O_2 availability probably exerted the greatest effect. Anaerobic decomposition rate for plant litter and peat in WCA-2A is approximately one-third the rate of aerobic decomposition, based on results of short-term incubations performed under controlled conditions (DeBusk and Reddy 1998). Measurement of dissolved O_2 in WCA-2A soil–water microcosms indicated that algal photosynthesis in periphyton mats may serve as a significant source of dissolved O_2 in the detrital layer (DeBusk and Reddy 2003). However, high O_2 demand in the detrital layer and peat resulted in steep concentration gradients, such that oxidized areas of the detrital layer were highly localized and total depletion of O_2 occurred near the peat surface. Therefore, litter residing above the peat surface was probably subjected to periods of aerobic conditions, increasing in frequency and duration with proximity to the water surface. The upper 3–5 cells of the decomposition chambers (depending on the site) were exposed above the water surface for approximately 5 weeks, during a period of low water level.

Our experimental results suggest that, although decomposition rate was significantly affected by initial substrate composition, the external supply or availability of nutrients probably played a more important role in controlling decomposition rate. Nutrient availability, however, was not necessarily reflected by ambient nutrient concentration, particularly water and soil porewater nutrient concentration, which may exhibit considerable temporal variability. In this case, final substrate N and P concentration would be considered a more appropriate indicator of N and P availability. Final substrate N and P concentrations were both linear functions of soil total P ($r^2 = 0.68$ and 0.62), but not of soil total N ($r^2 < 0.01$). This anomaly may be explained by

the potential discrepancy between N loading and N accumulation in flooded soils. Significant loss of N may occur in wetlands through the mineralization (ammonification) → nitrification → denitrification pathway, and to a certain extent, via ammonia volatilization (Reddy and D'Angelo 1994). Therefore, N loading to Everglades WCA-2A is mitigated to a certain extent by these loss mechanisms, while, in the absence of comparable metabolic sinks, P accumulation in the soil is proportional to P loading.

Standing dead cattail and sawgrass leaves are characterized by low N and P content, due primarily to leaching, and high C quality (high cellulose:lignin), as compared to peat. Therefore, this partially decomposed plant litter tends to act as a strong nutrient sink when added to the wetland soil surface. Results of this study suggest that microbial decomposers utilizing the readily available C source actively accumulated N and P (i.e., nutrient immobilization) in proportion to N and P loading to WCA-2A, but not necessarily in proportion to ambient nutrient concentration (especially for N). The same concept is demonstrated by the response of macrophytes to nutrient loading in WCA-2A; a significant gradient in plant tissue N concentration exists in the absence of a gradient of soil N (DeBusk and Reddy 1998).

Although our experimental results are not conclusive evidence, the N:P ratios in post-incubation litter suggest that N availability may limit decomposition in the highly P-enriched region near the S-10 inflow of WCA-2A. Substrate molar N:P ratios (depth-averaged) at sites 1, 4 and 6 (within 3 km of the inflow) ranged from 38 to 48, compared to 203 at the relatively unimpacted site 10. Soil (peat) microbial respiration studies in the Everglades have indicated that P is the primary microbial growth-limiting nutrient in pristine areas, but that N may be limiting in high-P areas (Amador and Jones 1993, 1995; White and Reddy 2000).

Conclusions

Short-term decomposition of cattail and sawgrass leaf tissue in the Everglades WCA-2A marsh increased concurrently with increasing soil and water P enrichment near the S-10C surface water inflow. Decomposition rate along the vertical surface water–soil profile reflected a general decrease from water column to detrital layer to peat, reflecting the combined influence of environmental factors, including nutrient and O_2 availability. As reflected by the short time span (6.5 months), this study represented the early stages of the 'decay continuum' from plant tissue to peat. Accordingly, decomposition of the cattail and sawgrass litter was influenced both by initial chemical composition of the substrate and environmental factors.

Substantial immobilization of N and P occurred in the decomposing plant material, especially within the detrital layer and near the inflow. The high immobilization potential, or sink strength, of the litter was due to a combination of extremely low nutrient content and relatively high C quality. Thus,

recently deposited litter in nutrient-enriched areas would be expected to serve as a strong sink for nutrients, with rapid turnover associated with high microbial activity. In this study, enhanced immobilization of P in the detrital layer at nutrient-enriched sites underscores the difference between nutrient storage, or ambient concentration, and nutrient availability. It also demonstrates the link between nutrient loading and availability, both of which are rates. Our study results may also have significant implications regarding the importance of plant litter and the soil detrital layer in short-term nutrient cycling in wetlands, as well as the functioning of wetlands in the context of water quality. A greater understanding of the impact of nutrient loading on decomposition and, conversely, on organic matter accretion, will increase our ability to evaluate ecosystem stability in natural wetlands and long-term nutrient removal performance in wastewater-treatment wetlands.

Acknowledgements

This research was supported by the Florida Agricultural Experiment Station and a grant from the U.S. Department of Agriculture, and approved for publication as Journal Series No. R-08620. The authors wish to acknowledge the South Florida Water Management District for field and technical support. We also gratefully acknowledge Ms. Yu Wang of the Wetlands Biogeochemistry Laboratory for her invaluable analytical assistance.

References

Aber J.D., Melillo J.M. and McClaugherty C.A. 1990. Predicting longterm patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Can. J. Bot. 68: 2201–2208.

Amador J.A. and Jones R.D. 1993. Nutrient limitations on microbial respiration in peat soils with different total phosphorus content. Soil Biol. Biochem. 25: 793–801.

Amador J.A. and Jones R.D. 1995. Carbon mineralization in the pristine and phosphorusenriched peat soils of the Florida Everglades. Soil Sci. 159: 129–141.

Anderson J.M. 1976. An ignition method for determination of total phosphorus in lake sediments. Water Res. 10: 329–331.

Bremner J.M. and Mulvaney C.S. 1982. Nitrogentotal. In: Page A.L. (ed.), Methods of Soil Analysis, Part 2. American Society of Agronomy – Soil Science Society of America, Madison, WI pp. 595–624.

Bridgham S.D., Updegraff K. and Pastor J. 2001. A comparison of nutrient availability indices along an ombrotrophic–minerotrophic gradient in Minnesota wetlands. Soil Sci. Soc. Am. J. 65: 259–269.

Clymo R.S. 1983. Peat. In: Gore A.J.P. (ed.), Mires: Swamp, Bog, Fen and Moor. Elsevier, Amsterdam pp. 159–224.

Cooper S.R., Huvane J., Vaithiyanathan P. and Richardson C.J. 1999. Calibration of diatoms along a nutrient gradient in Florida Everglades Water Conservation Area 2A, USA. J. Paleolimnol. 22: 413–437.

D'Angelo E.M. and Reddy K.R. 1999. Regulators of heterotrophic microbial potentials in wetland soils. Soil Biol. Biochem. 31: 815–830.

Davis S.M. 1991. Growth, decomposition, and nutrient retention of *Cladium jamaicense* Crantz and *Typha domingensis* Pers. in the Florida Everglades. Aquat. Bot. 40: 203–224.

DeBusk W.F. and Reddy K.R. 2003. Nutrient and hydrology effects on soil respiration in a northern Everglades marsh. J. Environ. Qual. 32: 702–710.

DeBusk W.F., Newman S. and Reddy K.R. 2001. Spatio-temporal patterns of soil phosphorus enrichment in Everglades WCA-2A. J. Environ. Qual. 30: 1438–1446.

DeBusk W.F. and Reddy K.R. 1998. Turnover of detrital organic carbon in a nutrient-impacted Everglades marsh. Soil Sci. Soc. Am. J. 62: 1460–1468.

DeBusk W.F., Reddy K.R., Koch M.S. and Wang Y. 1994. Spatial distribution of soil nutrients in a northern Everglades marsh: Water Conservation Area 2A. Soil Sci. Soc. Am. J. 58: 543–552.

Drake H.L., Aumen N.G., Kuhner C., Wagner C., Grießhammer A. and Schmittroth M. 1996. Anaerobic microflora of Everglades sediments: effects of nutrients on population profiles and activities. Appl. Environ. Microbiol. 62: 486–493.

Gleason P.J., Cohen A.D., Brooks H.K., Stone P., Goodrick R., Smith W.G. and Spackman W.Jr. 1974. The environmental significance of Holocene sediments from the Everglades and saline tidal plain. In: Gleason P.J. (ed.), Environments of South Florida: Present and Past. Miami Geological Society, Miami, Florida pp. 287–341.

Godshalk G.L. and Wetzel R.G. 1978. Decomposition of aquatic angiosperms. II. Particulate components. Aquat. Bot. 5: 301–327.

Heal O.W., Flanagan P.W., French D.D. and MacLean S.F.Jr. 1981. Decomposition and accumulation of organic matter. In: Bliss L.C., Heal O.W. and Moore J.J. (eds), Tundra Ecosystems: A Comparative Analysis. Cambridge University Press, Cambridge pp. 587–633.

Jenkinson D.S. and Rayner J.H. 1977. The turnover of soil organic matter in some of the Rothamsted classical experiments. Soil Sci. 123: 298–305.

Jensen J.R., Rutchey K., Koch M.S. and Narumalani S. 1995. Inland wetland change detection in the Everglades Water Conservation Area 2A using a time series of normalized remotely sensed data. Photogram. Eng. Remote Sens. 61: 199–209.

Koch M.S. and Reddy K.R. 1992. Distribution of soil and plant nutrients along a trophic gradient in the Florida Everglades. Soil Sci. Soc. Am. J. 56: 1492–1499.

McCormick P.V., Shuford R.B.E., Backus J.G. and Kennedy W.C. 1998. Spatial and seasonal patterns of periphyton biomass and productivity in the northern Everglades, Florida, USA. Hydrobiologia 362: 185–208.

McCormick P.V. and Stevenson R.J. 1998. Periphyton as a tool for ecological assessment and management in the Florida Everglades. J. Phycol. 34: 726–733.

Melillo J.M., Aber J.D., Linkins A.E., Ricca A., Fry B. and Nadelhoffer K.J. 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. Plant Soil 115: 189–198.

Melillo J.M., Aber J.D. and Muratore J.F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63: 621–626.

Melillo J.M., Naiman R.J., Aber J.D. and Linkins A.E. 1984. Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams. Bull. Mar. Sci. 35: 341–356.

Miao S.L. and DeBusk W.F. 1999. Effects of phosphorous enrichment on structure and function of plant communities in Florida wetlands. In: Reddy K.R., O'Connor G.A. and Schelske C.L. (eds), Phosphorus Biogeochemistry in Subtropical Ecosystems. Lewis Publishers, Boca Raton, Florida pp. 275–299.

Miao S.L. and Sklar F.H. 1998. Biomass and nutrient allocation of sawgrass and cattail along a nutrient gradient in the Florida Everglades. Wetlands Ecol. Manage. 5: 245–263.

Moore T.R. and Dalva M. 1993. The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. J. Soil Sci. 44: 651–654.

Moran M.A., Benner R. and Hodson R.E. 1989. Kinetics of microbial degradation of vascular plant material in two wetland ecosystems. Oecologia 79: 158–167.

Newman S., Schuette J., Grace J.B., Rutchey K., Fontaine T., Reddy K.R. and Pietrucha M. 1998. Factors influencing cattail abundance in the northern Everglades. Aquat. Bot. 60: 265–280.

Paul E.A. 1984. Dynamics of organic matter in soils. Plant Soil 76: 275–285.

Reddy K.R. and D'Angelo E.M. 1994. Soil processes regulating water quality in wetlands. In: Mitsch W.J. (ed.), Global Wetlands: Old World and New. Elsevier Science, Amsterdam pp. 309–324.

Richardson C.J., Ferrell G.M. and Vaithiyanathan P. 1999. Nutrient effects on stand structure, resorption efficiency, and secondary compounds in Everglades sawgrass. Ecology 80: 2182–2192.

Schipper L.A. and Reddy K.R. 1995. *In situ* determination of detrital breakdown in wetland soilfloodwater profile. Soil Sci. Soc. Am. J. 59: 565–568.

South Florida Water Management District (SFWMD) 1996. Hydrometeorological Database (DBHYDRO). South Florida Water Management District, West Palm Beach.

Swift M.J., Heal O.W. and Anderson J.M. 1979. Decomposition in Terrestrial Ecosystems. University of California Press, Berkeley.

Swift D.R. and Nicholas R.B. 1987. Periphyton and water quality relationships in the Everglades Water Conservation Areas. Technical Publication 87-2. South Florida Water Management District, West Palm Beach.

Tate R.L.III 1979. Effect of flooding on microbial activities in organic soils: carbon metabolism. Soil Sci. 128: 267–273.

U. S. Environmental Protection Agency (USEPA) 1983. Methods for Chemical Analysis of Water and Wastes. Environment Monitoring and Support Laboratory, Cincinnati, Ohio.

Vaithiyanathan P. and Richardson C.J. 1999. Macrophyte species changes in the Everglades: examination along a eutrophication gradient. J. Environ. Qual. 28: 1347–1358.

Webster J.R. and Benfield E.F. 1986. Vascular plant breakdown in freshwater ecosystems. Ann. Rev. Ecol. Syst. 17: 567–594.

White J.R. and Reddy K.R. 2000. The effects of phosphorus loading on organic nitrogen mineralization of soils and detritus along a nutrient gradient in the northern Everglades, Florida. Soil Sci. Soc. Am. J. 64: 1525–1534.

Wright A.L. and Reddy K.R. 2001. Heterotrophic microbial activity in northern Everglades wetland soils. Soil Sci. Soc. Am J. 65: 1856–1864.