Turnover of Detrital Organic Carbon in a Nutrient-Impacted Everglades Marsh

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ABSTRACT

Phosphorus loading to the Everglades from nearby agricultural areas has become a major concern, and is considered to be a significant factor in the encroachment of cattail (Typha domingensis Pers.) and other rapidly growing vegetation into endemic sawgrass (Cladium jamaicense Crantz) marsh. The objectives of this research were to evaluate the variability in turnover of organic C in plant and soil detrital pools along a P enrichment gradient in an Everglades marsh and to identify substrate characteristics and environmental factors controlling C turnover. Potential rates of C mineralization in plant litter and peat were determined by measuring aerobic and anaerobic microbial respiration under controlled conditions in laboratory incubations. Potential C mineralization decreased with depth and, consequently, substrate age, in the plant–soil profile. Within individual detrital pools, standing dead plant material, soil litter layer, surface peat (0–10 cm depth) and subsurface peat (10–30 cm depth), potential C mineralization decreased down gradient from the source of nutrient loading to WCA-2A. Overall, 91% of the variability in aerobic C mineralization in peat and plant litter was accounted for by substrate P concentration and ligno-cellulose composition. Anaerobic C mineralization rates were consistently about one-third of aerobic rates. Results indicated that organic C turnover in detrital pools in WCA-2A is significantly affected by accelerated P loading, but is also controlled by O2 availability and substrate C quality.

A PRIMARY CHARACTERISTIC of wetlands that distinguishes them from upland ecosystems is the tendency to accumulate organic C in the soil profile. Organic C accumulation in wetlands is the net result of primary production (C fixation) and decomposition (C mineralization). Typically, the rate of decomposition of dead plant material is diminished significantly in wetlands, often resulting in the formation of extensive peat deposits. Decreased availability of O2 is the principal factor controlling microbial respiration and, consequently, organic C turnover in wetland soils (Ponnampерuma, 1972). However, decomposition of organic matter is also governed by other external, or environmental, factors as well as the chemical composition of the substrate (Swift et al., 1979; Heal et al., 1981).

Availability of nutrients and electron acceptors plays an important role in wetland C cycling (Reddy and D’Angelo, 1994). Although nutrient loading is typically greater in wetlands than in uplands due to location within the landscape, nutrient bioavailability may be low relative to the supply of available organic C in wetlands (Reddy and D’Angelo, 1994). Nitrogen and P both have been reported to be microbial growth-limiting nutrients in wetlands (Westermann, 1993). Nitrogen, unlike P, may be lost from wetlands through microbial metabolism via denitrification, as well as through NH3 volatilization (Reddy and D’Angelo, 1994). In contrast to terrestrial ecosystems, decomposition in wetlands is frequently electron-acceptor-limited. In addition to O2, alternate electron acceptors for anaerobic microbial respiration, such as NO3-, Mn4+, Fe3+, and SO42-, are often in short supply relative to the demand created by organic C, leaving methanogenesis as the principal microbial respiration pathway (Westermann, 1993).

Decomposition rate is significantly affected by chemical and physical composition of the organic substrate (Swift et al., 1979; Heal et al., 1981). The term “substrate quality” is often used in reference to the availability of C compounds and associated nutrients for microbial utilization (Heal et al., 1981; Heal and Ineson, 1984). Lignin and cellulose fractions have been proposed as defining components of the “C quality” of an organic substrate (Colberg, 1988; Moran et al., 1989). Lignin is more resistant to breakdown than cellulose, therefore substrate cellulose content decreases more rapidly during decomposition (Colberg, 1988; Melillo et al., 1989). Degradation of lignin and cellulose is slower under anaerobic conditions, although their decay rates relative to one another are approximately the same as for aerobic conditions (Benner et al., 1984). Initial substrate composition has been used as a predictor of decomposition rate (Swift et al., 1979). In several cases, the initial lignin content and lignin/N ratio of plant tissue were shown to be highly correlated with decomposition rate (Godshalk and Wetzel, 1978; Berg and Staaf, 1981; Melillo et al., 1982).

Our study examines the influence of nutrient loading on turnover of organic C pools in a nutrient-impacted area of the northern Everglades. Export of agricultural drainage water from the EAA during the past three decades has resulted in nutrient enrichment of historically oligotrophic wetlands in parts of the WCAs (South Florida Water Management District, 1992; DeBusk et al., 1994). Accelerated P loading has been a major concern in the Everglades, and is considered a significant contributor to the encroachment of cattail and other rapidly growing vegetation into the native sawgrass.


Abbreviations: Cmic/Ctot, ratio of microbial C to total organic C; EAA, Everglades Agricultural Area; GC, gas chromatograph; LCI, ligno-cellulose index; PVC, polyvinyl chloride; WCA, Everglades Water Conservation Area.
marsh (Davis, 1943; Davis, 1991; Steward and Ornes, 1983; Toth, 1987, 1988; Craft and Richardson, 1997).

The primary objectives of this research were (i) to evaluate spatial trends in the rate of organic C turnover in marsh plant and soil detrital pools along a P enrichment gradient, and (ii) to identify substrate characteristics and environmental factors controlling C turnover. It was hypothesized that P enrichment would accelerate turnover of organic C within detrital pools, and that differences in C turnover among detrital pools would be a function of substrate C composition.

MATERIALS AND METHODS

Site Description

Field study sites were located in WCA-2A, a 447-km² parcel in the northern Everglades (Fig. 1). As with all of the WCAs, hydrology in WCA-2A is managed through a system of canals, levees, and water control structures. The most significant sources of hydraulic loading to WCA-2A are the S-10C and S-10D structures along the northeastern boundary of WCA-2A. Surface water in WCA-2A flows in a general north-south direction. Water depth is usually <1 m, but may vary considerably, both seasonally and year-to-year, due to rainfall and water management (South Florida Water Management District, 1992). Surface outflow is directed primarily into WCA-3 through three control structures at the south end of WCA-2A.

Soils in WCA-2A are not mapped, but generally fall under the classifications of Everglades and Loxahatchee peats (Gleason et al., 1974). Everglades peat, the most commonly occurring soil in the Everglades, is associated with the sawgrass marsh community, and is dark brown, finely fibrous to granular, with circumneutral pH, relatively high N content, and low SiO₂, Fe, and Al content. Peat depth in WCA-2A ranges from about 1 to 2 m, and age of basal peats is estimated to be 2000 to 4800 yr. Beneath the peat lies a bedrock of Pleistocene limestone, with intermediate layers of calcitic mud, sandy clay, and sand in several areas (Gleason et al., 1974).

A steep gradient of P enrichment in water, plants, and soil has been documented in WCA-2A, between the high-nutrient region adjacent to the S-10C and S-10D inflows and the low-nutrient interior marsh of WCA-2A (Koch and Reddy, 1992; South Florida Water Management District, 1992; DeBusk et al., 1994). A transition from cattail and mixed emergent marsh (near the inflows) to sawgrass marsh and aquatic sloughs occurs along the P gradient.

Experiment Design

Ten field-sampling sites were established along the previously documented soil P gradient on a 10-km transect extending from the S-10C inflow into the interior marsh. The study area was viewed as a continuum, rather than distinct zones, of P enrichment; accordingly, the sampling sites were distributed along the transect as opposed to being grouped in “impacted” and “nonimpacted” areas. The sites, numbered consecutively from 1 through 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 downstream from the inflow (Fig. 1). Spacing between sampling sites was increased down gradient from the inflow, based on previous soil spatial characterization study (DeBusk et al., 1994) that indicated that P concentration decreased more or less exponentially with increasing distance from the S-10C inflow.

In accordance with our conceptual approach, which favored gradient analysis over site-to-site comparisons, sampling of peat and plant detritus at each of the 10 sites was performed without replication. However, sample compositing (described below) was employed as a means of increasing the size of the unit sampling area and providing a more representative sample of each site.

Plant and Soil Sampling

Standing dead (still attached to the plant) leaves were collected from either cattails, sawgrass, or both species, based on their occurrence at each sampling site, during March 1995. Standing dead cattail leaves were collected at Sites 1 through 8 and dead sawgrass leaves at Sites 6 through 10. Thus, both cattail and sawgrass plants were sampled at “transitional” Sites 6 through 8. For each site, five dead leaves were removed from each of three plants per species. Plants sampled at a given site were located within a radius of =5 m. Plant tissue samples were dried in a forced-draft drying room at 60°C then cut into pieces =2 cm long and mixed thoroughly to yield a single composite sample for each species from a given site. A subsample from each composite sample was analyzed for total N and P content. Lignin and cellulose content of standing dead leaf tissue was determined for cattails from Sites 1, 4, and 6 and for sawgrass from Sites 6, 9, and 10.

Soil cores were obtained from the ten sampling sites during June 1995. The plant litter layer overlying the peat was sampled by inserting a short section of 15-cm diam. polyvinyl chloride (PVC) pipe and manually collecting the loosely packed litter contained within the 177-cm² sample area. Next, a simple coring apparatus consisting of 7.6 cm-diam. 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. The upper 10 cm and the 10- to 30-cm layers of the peat profile were collected separately. The 0- to 10- and 10- to 30-cm layers of the peat profile were designated as "surface peat" and "subsurface peat".

Soil coring was performed in quadruplicate at each sampling site, within a radius of ~5 m. Samples contained in the sealed plastic bags were immediately placed on ice and transported to the lab within 24 h. After the removal of live roots from the samples, wet weights were recorded for each, and then replicate samples were thoroughly mixed to create a single composite sample. The composited samples were stored in leak-proof polypropylene jars in a refrigerator at 4°C. Subsamples of litter and peat were dried to constant weight in a forced-draft oven at 60°C, for determination of moisture content. Samples from all sites were analyzed for total N and P and microbial biomass C. Analysis of lignin and cellulose content was performed on subsamples from Sites 1, 4, 6, 9, and 10.

### Plant and Soil Analysis

Total N analysis was performed on dried, finely ground (<0.2 mm) samples of plant litter and peat with a Carlo-Erba NA-1500 CNS Analyzer (Carlo Erba, Milan, Italy). Total P analysis was performed on separate subsamples following 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 by an automated ascorbic acid method (Method 365.4, USEPA, 1983). Cellulose and lignin in plant litter and peat were determined by a standard procedure using acid-detergent and H2SO4 extractions (American Association of Analytical Chemists, 1990). The "lignin" fraction identified by this procedure includes actual lignin and other acid-insoluble compounds, and thus yields an apparent lignin content.

Litter and peat samples were analyzed for C in the microbial biomass using the chloroform fumigation-extraction technique (Horwath and Paul, 1994), modified for wet organic soils. Field-moist samples (>0.5-g dry mass) were fumigated in a vacuum dessicator with ethanol-free chloroform, which was initially contained in a beaker placed inside the dessicator. Immediately before fumigation, 0.5 mL of chloroform was added directly to each sample, to enhance distribution of chloroform within the wet samples (Ocio and Brookes, 1990). The remainder of the fumigation and extraction process was performed according to Horwath and Paul (1994). Triplicate fumigated and nonfumigated samples were extracted with 25 mL of 0.5 M K2SO4, centrifuged, and the supernatant filtered though glass fiber filters (Gelman A/E, Gelman Sciences, Ann Arbor, MI) using a vacuum filtration system. The ratio of extractant to dry soil was increased over the recommended 5:1 (w/v) because of the high organic C content of the soil and litter. The filtered extracts were analyzed for total organic C (soluble organic C) on a Dohrmann DC-190 TOC analyzer (Rosemount Analytical Inc., Santa Clara, CA). Microbial biomass C was calculated from the difference in K2SO4 extractable C between fumigated and nonfumigated samples. A correction factor (kEC), which accounts for the efficiency of the fumigation process, is generally used to obtain a direct estimate of microbial C from the flush of extractable C following fumigation (Horwath and Paul, 1994). Based on previous calibration for organic soils (Sparling et al., 1990), a value of kEC = 0.37 was used in this case.

### Microbial Respiration

Microbial respiration in standing dead material, plant litter, and peat was measured to determine C mineralization rates for those detrital pools. Aerobic respiration was measured for standing dead leaves using bottle incubations and measurement of accumulated headspace CO2. Triplicate 1-g (dry weight) subsamples of standing dead cattail and sawgrass leaves from all sites were placed in separate 160-mL serum bottles. Deionized water (5-7 mL) was added to the dried plant material to provide adequate moisture for microbial activity. Each bottle was stoppered with a sleeve-type rubber septum and incubated in the dark at 25°C. After a 24-h preincubation period, headspace gas was sampled in the bottles. Sampling was repeated after 12 and 24 h, and subsequently every 24 h, for a total of 4 d of sampling. Headspace gas was sampled (1 mL) using zero dead volume 1-mL insulin syringes (Becton Dickinson, Lincoln Park, NJ). Syringe needles were inserted into a rubber stopper for short-term storage of samples prior to analysis on a gas chromatograph (GC) for CO2. Increase in CO2 in the bottle headspace was linear during the 4 d. Rate of CO2 evolution was calculated from the slope of the best-fit linear regression line (CO2 accumulation vs. time).

Soil (litter and peat) respiration was measured using an air flow-through system (respirometer) that traps evolved CO2 on a continuous basis (Zibilske, 1994). Use of a continuous flow apparatus for respiration measurement is recommended for calcareous soils, such as Everglades peat, to avoid problems associated with soil retention of microbially evolved CO2, in the form of bicarbonate (Martens, 1987). These components were connected by plastic (PVC) tubing and a gas manifold to create a continuous flow of CO2-free air through each incubation vessel and into the individual CO2 traps. Air flow rate through each incubation vessel was maintained at 25 mL min⁻¹.

The NaOH traps provided continuous collection of the CO2 evolved during microbial respiration. The NaOH in the traps was changed periodically, as determined by the rate of CO2 accumulation. Free (remaining) NaOH in the traps was titrated with standardized HCl, following addition of BaCl2 to precipitate the Na2CO3 in solution as insoluble BaCO3 to determine the amount of NaOH that had reacted with CO2. Molar quantity of CO2 evolved during the incubation period was stoichiometrically determined (Zibilske, 1994).

Field-moist subsamples (10-g wet weight) of litter, surface peat (0-10 cm depth) and subsurface peat (10-30 cm depth) were placed in 50-mm diameter plastic petri dishes. A thick glass fiber filter was placed beneath each sample to increase aeration of the sample by maintaining drained, yet moist, conditions in the sample. The petri dishes containing the samples were placed inside the incubation vessels and incubated in the dark at 25°C. A 48-h preincubation period was employed in order to achieve stabilization of microbial respiration. Samples were incubated for one week following preincubation, then removed from the incubation chambers, dried at 60°C in a forced-draft oven and weighed to determine sample dry mass. The incubation was performed in triplicate using successive incubation of the entire set of samples.

Anaerobic respiration was measured in the same fashion, with the following modifications. The source air was replaced by N2 gas (purified grade) and sample size was increased to 50-g wet weight. The incubation period was shortened to 3 d, following a 48-h preincubation. A preliminary study suggested that a longer incubation period would result in deple-
tion of electron acceptors (particularly SO\textsubscript{4}\textsuperscript{2-}), and would therefore not reflect conditions in the field at the time of sampling. At the end of the 3-d incubation, the inlet and outlet ports of each incubation vessel were closed, and the NaOH traps were removed and titrated as described above. Immediately following termination of gas flow, headspace gas in each vessel was sampled through a rubber septum in the lid, using 1-mL insulin syringes. Syringe needles were inserted into a rubber stopper for short-term storage of samples, prior to analysis on a GC for methane (CH\textsubscript{4}). Sampling was repeated after 6 h, and gas samples were analyzed for CH\textsubscript{4}. Preliminary studies showed that accumulation of methane in the incubation vessels was linear over time.

Gas Analysis

Sample gases were analyzed on a Hewlett-Packard 5840A GC (Hewlett Packard, Avondale, PA), using thermal conductivity and flame ionization detectors for CO\textsubscript{2} and CH\textsubscript{4} analysis, respectively. For CO\textsubscript{2} analysis, a Porapak N (Supelco, Bellefonte, PA) column was used, with He as a carrier gas. Oven, injector, and detector temperatures were set to 60, 140, and 200°C. For CH\textsubscript{4} analysis, a Carboxen 1000 (Supelco) column was used, with a N\textsubscript{2} carrier gas. Oven, injector, and detector temperatures were 120, 120, and 200°C.

Data Analysis

Analysis of trends in soil characteristics and organic C turnover along the P gradient was performed by linear regression. Trends were considered significant where the slope of the best-fit regression line was significantly different \((P \leq 0.05)\) from a slope of zero. Comparisons among mean values for discrete detrital pools were made using one-way analysis of variance (ANOVA) and the Tukey-Kramer HSD (honestly significant difference) means comparison test. Statistical analyses were performed using the JMP software package (SAS Institute, Cary, NC).

RESULTS

Substrate Characterization

Nutrient (N or P) enrichment was found in plant and soil detrital pools near the S-10C inflow along the northern boundary of WCA-2A (Fig. 2 and 3). Total N concentration of cattail standing dead leaves decreased significantly \((P \leq 0.05)\) down gradient from the inflow (Fig. 2), but there was no comparable trend for N concentration in sawgrass standing dead leaves. Cattail standing dead tissue P did not change significantly with increasing distance from the inflow, while sawgrass standing dead tissue P decreased significantly \((P \leq 0.05)\) down gradient from the inflow. Within-site composting of samples did not allow for statistical comparison between cattail and sawgrass N or P concentration at the same site. However, there was no significant difference in either mean N or P concentration between cattail and sawgrass samples in the “transitional” area, which included (collectively) Sites 6, 7, and 8. When data for cattails and sawgrass were grouped to create a single category for standing dead leaf tissue, the trends for decreasing N and P concentration along the transect were significant \((P \leq 0.05)\).

Enrichment of P in the soil near the inflow was more pronounced than soil N enrichment. Total N concentration in the litter layer decreased significantly \((P \leq 0.05)\) away from the inflow, but did not change significantly in the peat (Fig. 2). Total P concentration, however, decreased significantly \((P \leq 0.05)\) in the litter layer as well as the surface (0–10 cm) and subsurface (10–30 cm) layers of peat (Fig. 3). Spatial trends in N and P concentration revealed a general pattern of nutrient enrichment in detrital pools associated with loading from the S-10C inflow of WCA-2A. A steep soil P gradient in the northern region of WCA-2A has been previously reported by DeBusk et al. (1994).

Comparison of means for detrital pools (all sampling sites grouped) revealed significant differences in chemical composition among the pools. Total N concentration was significantly higher \((P \leq 0.05)\) in litter and peat than in standing dead plant tissue. The overall trend for N concentration among detrital pools was: subsurface (10–30 cm) peat > surface (0–10 cm) peat > litter layer > standing dead plant tissue. In contrast, the trend for total P concentration in detrital pools was: litter layer > surface peat > subsurface peat > standing dead plant tissue. Total P concentration was significantly lower
Lignin and cellulose content of standing dead plant tissue (cattail and sawgrass) were significantly enhanced by increasing substrate P concentration (Fig. 4). Lignin content increased significantly among detrital pools with increasing LCI values. Mean aerobic CO$_2$ production in litter standing dead tissue was not significantly different ($P < 0.05$) from CO$_2$ production in sawgrass standing dead tissue or in the soil litter layer. However, mean aerobic CO$_2$ production in the soil decreased significantly with increasing soil depth, such that: litter > surface peat > subsurface peat.

Anaerobic CO$_2$ production in litter, surface and subsurface peat (standing dead material was not incubated anaerobically) also increased significantly in response to increasing P concentration (Fig. 7). As with the aerobic incubations, the magnitude of the response of anaerobic CO$_2$ production to total P concentration decreased among detrital pools with increasing LCI values. Mean anaerobic CO$_2$ production for soil detrital pools decreased significantly, in the order: litter > surface peat > subsurface peat.

Microbial Respiration

Aerobic microbial CO$_2$ production in all detrital pools was significantly enhanced by increasing substrate P concentration (Fig. 6), as determined by linear regression (slopes significant at $P < 0.05$). The magnitude of the response of CO$_2$ production (i.e., substrate C mineralization) to substrate P concentration varied considerably among the detrital pools, due, for the most part, to differences in lignin and cellulose content (discussed below). Total P concentration of the substrate explained a substantial portion of the variability in CO$_2$ production rate, ranging from 50% for the 0 – 10 cm layer of peat to 88% for standing dead leaves of cattails (Fig. 6). Mean aerobic CO$_2$ production in cattail standing dead tissue was not significantly different ($P < 0.05$) from CO$_2$ production in sawgrass standing dead tissue or in the soil litter layer. However, mean aerobic CO$_2$ production in the soil decreased significantly with increasing soil depth, such that: litter > surface peat > subsurface peat.

Fig. 6. Scatter plots of aerobic CO$_2$ production (microbial respiration) in detrital pools vs. substrate P concentration with a line of best fit, determined by linear regression, shown for each pool.
subsurface peat ($P \leq 0.05$). As with the aerobic incubations, the response of $CO_2$ production to increasing substrate P concentration was attenuated in detrital pools of increasing age, or degree of decomposition.

A significant response of $CH_4$ production (anaerobic incubation) to P enrichment was observed for litter and surface peat, but production of $CH_4$ in subsurface peat was not significantly affected by substrate P concentration (Fig. 8). Mean $CH_4$ production was significantly different among the soil components, in the order: litter > surface peat > subsurface peat ($P \leq 0.05$). Total anaerobic C ($CO_2 + CH_4$) production was significantly higher in litter than in surface and subsurface peat layers (litter > surface peat > subsurface peat). Anaerobic C production was significantly correlated with aerobic C production ($r = 0.96$). Regression of anaerobic vs. aerobic C production generated a linear relationship with a slope of 0.32, indicating that the rate of anaerobic mineralization was an average of one-third the aerobic mineralization rate for all substrates.

Differences in C mineralization rate among detrital pools could be explained by differences in lignin and cellulose content of the substrate. The proportion of lignin in the ligno-cellulose (lignin + cellulose) component, referred to as the LCI, has been correlated with relative age, or state of decomposition, of decomposing plant material (Melillo et al., 1989). The detrital pools examined in our study were characterized by increasing LCI with increasing substrate age (also depth within the plant-soil profile); mean values of LCI for standing dead plant tissue, soil litter layer, surface peat, and subsurface peat were 0.26, 0.60, 0.73, and 0.81, respectively.

Multiple linear regression was used to evaluate the combined effects of substrate total P and LCI on C mineralization rate in all detrital pools. The regression model, with total P and LCI as independent variables, explained 91% of the variability in aerobic C mineralization rate ($CO_2$ production in laboratory incubations). In contrast, simple regression analyses indicated that total P and LCI individually accounted for only 13 and 37%, respectively, of the variability. Total P and LCI explained 86% of the variability in anaerobic $CO_2 + CH_4$ production, using the multiple regression model.

The prediction equation for aerobic mineralization was:

$$Y = 0.978 + 0.0025(TP) - 1.31(LCI)$$

where $Y$ is $CO_2$ production (organic C mineralization) in mg C g$^{-1}$ d$^{-1}$ and TP is total P in mg kg$^{-1}$. Partial regression coefficients for TP, LCI, and TP × LCI have units of kg g$^{-1}$ d$^{-1}$, mg g$^{-1}$ d$^{-1}$, and kg g$^{-1}$ d$^{-1}$, respectively. Both total P ($P \leq 0.0001$) and LCI ($P = 0.001$) were highly significant effects. In addition, there was a significant interaction between total P and LCI, denoted by the TP × LCI term ($P = 0.0009$). Interaction between total P and LCI is illustrated in Fig. 6 by successively decreasing slopes of the $CO_2$ production rate vs. total P relationship for individual detrital pools with increasing LCI values.

Mean aerobic and anaerobic C mineralization rates for individual detrital pools are summarized in Fig. 9. Average C decay rate (specific C loss) for each detrital pool was calculated from gaseous C production and substrate total C content as:

$$\text{Decay rate, day}^{-1} = \frac{\text{milligrams C production}}{\text{grams substrate} \times \text{day} \times \frac{\text{milligrams substrate C}}{\text{grams substrate}}} \quad [2]$$

This quantity is equivalent to the first-order rate constant $k$ in a simple exponential decay model. Mean aerobic decay rate for detrital pools varied from about 3.5 × 10$^{-4}$ d$^{-1}$ for subsurface peat to 2.8 × 10$^{-3}$ d$^{-1}$ for litter (Fig. 9). Mean anaerobic decay rate ranged from 1.4 × 10$^{-4}$ to 9.3 × 10$^{-4}$ d$^{-1}$ for subsurface peat and litter, respectively. Estimated mean organic C turnover time (1/k) for detrital pools under strictly aerobic conditions ranged from ~1.2 yr for standing dead material and litter to 9.2 yr for subsurface peat. Mean turnover time
DISCUSSION

The broadly defined lignocellulose component has been shown to be a potentially useful indicator of substrate quality in plant residues (Colberg, 1988; Moran et al., 1989). A decay continuum for plant-derived organic matter was described by Melillo et al. (1989), for which LCI increases from 0.2 to 0.8, as plant litter is eventually transformed to soil organic matter. The decay continuum concept is based on selective loss of comparatively labile constituents and concomitant changes in chemical and biochemical characteristics of the substrate. Loss of nonlignocellulosic components of plant detritus occurs rapidly during the initial stages of decomposition; thus, lignin and cellulose become the primary C components of the substrate (Moran et al., 1989). Later stages of decomposition are characterized by enrichment of the substrate with the more recalcitrant lignin compounds as well as lignin derivatives in the form of microbial byproducts (Swift, 1982; Heal and Ineson, 1984). Increase in LCI during the decomposition process reflects the decreasing quality, or availability, of substrate C.

The relationship described by Eq. [1] indicates that P content and C quality are both significant facets of substrate composition that govern the rate of decomposition of plant litter and peat in WCA-2A. Similar findings have been reported for other peat-forming wetlands. Potential (aerobic) respiration in peat from three wetland sites in North Carolina was found to increase with nutrient availability (Bridgham and Richardson, 1992). Research on soils in Everglades National Park showed a significant positive effect of P enrichment on mineralization of added labile organic C (Amador and Jones, 1993, 1995). A study of a northern bog soil demonstrated an increased C mineralization rate in surface peat compared with subsurface (1-m depth) peat, the latter having a higher lignin and lower cellulose content (Updegraff et al., 1995).

The interactive effect of substrate C quality (LCI) and P content on substrate bioavailability is well illustrated by the plots of aerobic CO$_2$ production vs. total P concentration in Fig. 6. Each detrital pool represents a statistically homogeneous level of substrate C quality. Mean CO$_2$ production for these pools decreased with increasing LCI, resulting in a vertical shift of the regression lines. In addition, slopes of the regression lines decreased with increasing LCI, signifying attenuation of the response of CO$_2$ production to increasing substrate P content.

Of particular interest was the marked response of aerobic CO$_2$ production in cattail and sawgrass standing dead leaves to tissue P concentration (Fig. 6). This response is indicative of the high C quality of the standing dead tissue pool. Additionally, the relatively low C mineralization rate in the standing dead tissue (which was not significantly higher than in the soil litter layer) reflects a high degree of nutrient deficiency for microbial decomposers. Depletion of nutrients in this detrital material results from leaching of water-soluble constituents, including newly mineralized tissue N and P. Its high C quality and low nutrient content suggest that the standing dead material might serve as a significant nutrient sink, through microbial assimilation, following deposition of dead plant material into the litter layer. In fact, substantial immobilization of N and P by dead cattail and sawgrass leaf tissue was observed during a short-term (6 mo) site decomposition study along the WCA-2A nutrient gradient (DeBusk, 1996). Immobilization potential has been linked to initially low N and lignin content of organic substrates (Melillo et al., 1984). In northern Florida, studies of a cypress (Taxodium distichum var. nutans [Ait.] Sweet) swamp receiving municipal wastewater showed that, 3 wk after addition of $^15$N-labeled wastewater to intact soil cores, nearly all of the $^15$N remaining in the peat-floodwater profile was immobilized in the litter layer (DeBusk and Reddy, 1987).

Microbial biomass C was highly correlated with aerobic ($r = 0.98$) and anaerobic ($r = 0.94$) C mineralization rates in the soil. Furthermore, for each detrital pool, microbial biomass increased significantly in response to P enrichment. Drake et al. (1996) reported a general enhancement of culturable anaerobic microflora in the nutrient-impacted area of WCA-2A compared with a nonimpacted area in Everglades WCA-3. The ratio of microbial C to total organic C ($C_{mic}/C_{total}$) has been used as a qualitative indicator of soil organic C quality or availability (Anderson and Domsch, 1989; Sparling,
1992). The $C_{\text{mic}}/C_{\text{tot}}$ values calculated for WCA-2A soil (litter and peat) spanned the wide range of values reported for agricultural, pasture and forest soils (Anderson and Domsch, 1989). Values for surface and subsurface peat at the WCA-2A sites ranged from 0.5 to 4.0%, falling within the range of "typical" values reported for forest and pasture soils (Sparling, 1992). In comparison, $C_{\text{mic}}/C_{\text{tot}}$ values for litter in the P-enriched cattail marsh (4.6-8.3%) were similar to, or higher than, reported values for forest or agricultural soils.

Anaerobic C production (CO$_2$ and CH$_4$) was, on average, 32% of the aerobic C production rate. The anaerobic/aerobic respiration ratio did not vary significantly ($P \leq 0.05$) among litter, surface peat, and subsurface peat. In comparison, anaerobic respiration rate of peat from three North Carolina peatlands was 34 to 63% of the aerobic rate (Bridgham and Richardson, 1992). Lignocellulose extracted from (Carex walteriana) and incubated in anaerobic peat in the Okefenokee Swamp was decomposed at 37% of the aerobic decomposition rate (Benner et al., 1984).

The relative proportion of CH$_4$ produced during anaerobic incubations varied considerably, but was <25% of total gaseous C production. Partitioning between CO$_2$ and CH$_4$ production during anaerobic incubations was not significantly correlated ($P \leq 0.05$) with substrate C quality or P concentration. However, a general trend of increased CH$_4$ production (relative to CO$_2$) was observed in conjunction with decreasing substrate LCI and increasing total P concentration. Methanogenesis in soils from two northern temperate wetlands was negatively correlated with the relative abundance of recalcitrant C compounds (Updegraff et al., 1995). We found considerable variability in CO$_2$/CH$_4$ partitioning that was not explained by LCI and total P content, some of which may be attributed to variability in the supply of electron acceptors, especially SO$_4^{2-}$. Relatively high concentrations of SO$_4^{2-}$ have been measured in surface water and soil pore water in WCA-2A (Schipper and Reddy, 1994), possibly the result of seepage of brackish groundwater into the canals that convey surface water to WCA-2A. Increased productivity of SO$_4^{2-}$-reducing bacteria has been associated with availability of SO$_4^{2-}$ and P in Everglades soils (Drake et al., 1996).

Although the results of this study demonstrated that the rate of organic C turnover in detrital pools increased in response to P enrichment under both aerobic and anaerobic conditions, it may not be assumed that organic C storage has decreased in nutrient-impacted areas of WCA-2A. In fact, there is evidence, based on $^{137}$Cs dating of intact soil cores, that the rate of organic matter (peat) accumulation has increased in the nutrient-enriched areas (Craft and Richardson, 1993; Reddy et al., 1993). This can be accounted for, in part, by increased net primary productivity in these areas (South Florida Water Management District, 1992). An increase in the rate of organic matter input to the marsh detrital subsystem could potentially offset accelerated turnover of detrital pools, thereby increasing the size of the pools. It is also possible that turnover rate may be attenuated by low O$_2$ availability in some highly impacted areas.

A study of sediment O$_2$ demand in WCA-2A provided evidence that some areas, especially in the cattail marsh, that were previously dominated by aerobic conditions in the water column and litter layer have become primarily anaerobic in response to higher nutrient loading rates (Belanger et al., 1989).

**CONCLUSIONS**

Due to enhancement of overall substrate quality, nutrient enrichment of previously oligotrophic areas of WCA-2A has resulted in increased C mineralization potential in soil and plant detrital pools. Mineralization of organic C was significantly affected by C quality (as measured by LCI) and P content of the substrate. Total P concentration and LCI accounted for 91% of the variability associated with aerobic C mineralization of plant litter and peat along the WCA-2A nutrient gradient, as measured in laboratory experiments. Due to the interactive effects of these factors, total P content exerted less influence on C mineralization rate in substrates of increasing depth and age. Carbon quality in individual detrital pools did not vary significantly along the nutrient gradient; therefore, within-pool variability in potential C mineralization rate was a function of substrate P enrichment. Organic C turnover was also significantly affected by O$_2$ availability. Anaerobic C mineralization rates were approximately one-third of corresponding aerobic rates for all soil detrital pools.

Standing dead plant material and the soil litter layer are potentially the most active (rapid turnover) detrital pools because of the relatively high C quality of these pools. However, decomposition of standing dead tissue (above-water) of cattails and sawgrass is most likely nutrient- and moisture-limited. The litter layer is also potentially important in short-term nutrient cycling. With a relatively high C and nutrient availability to support a large population of microbial decomposers, the litter layer may either serve as a source or sink for nutrients. Turnover of peat, especially in the lower regions of the soil profile, is substantially reduced by poor C quality and O$_2$ depletion; therefore, this is a more stable pool of organic matter and represents a potentially long-term sink for nutrients and contaminants.

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**REFERENCES**

