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Hydroperiod Influence on Breakdown of Leaf Litter in Cypress-gum Wetlands

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ABSTRACT.—Many cypress-gum wetlands in the southeast United States are isolated from rivers and streams and are seasonally inundated by rainfall. Organic matter processing in these wetlands is caused primarily by biotic components (*i.e.,* microbes and invertebrates), which are influenced by timing and duration of seasonal inundation, and low dissolved oxygen levels. Using litter bags, we examined breakdown of cypress (*Taxodium* spp.) and gum (*Nyssa sylvatica* var. *biflora*) leaves in three wetlands with different hydroperiods: (1) flooded exposed (FE; 5 mo flooded/6 mo litter exposed), (2) multiple flooded exposed (MFE; 6 mo flooded/exposed/flooded/exposed) and (3) permanently flooded (PF; 11 mo flooded). Breakdown was fastest in the MFE wetland suggesting cycles of wetting and drying accelerated decomposition by promoting microbial activity through aeration. Even though ergosterol content, an indicator of fungal biomass on the litter, was similar among wetlands, we hypothesized that within the MFE wetland microbial activity was promoted by exposed conditions, but during subsequent flooding microbial biomass was kept at a low level by invertebrate consumers. Macroinvertebrate density and biomass were comparable between litter types, but were highest in the PF wetland, followed by MFE, then FE wetlands. Chironomids, oligochaetes, *Caecidotea* and *Crangonyx* were the dominant taxa indicating litter inputs are vital in maintaining the aquatic foodweb in this system. Cypress litter ($k = -1.61\ y^{-1}$) had faster breakdown rates than gum litter ($k = -1.02\ y^{-1}$), most likely because of plant morphology and greater surface area available to microbial decomposers. Ergosterol (mg g^{-1} AFDM leaf material) levels were higher on cypress (34.5) than gum (22.5) litter. In both litter types initial C:N and N:P ratios were >20, and C:P ratios were >500, indicating a possible P or N/P co-limitation in cypress-gum wetlands. Elemental gains or losses in litter were influenced predominantly by litter type and to a lesser extent by hydrologic regime. Gum leaves accumulated P, N, Ca and K and lost Mg, whereas cypress leaves had initial declines of these elements, followed by some accumulations in P and K. Temporal patterns of P showed that the drier sites (FE and MFE) immobilized more P than the wetter site (PF), suggesting that exposed conditions promoted microbial activity. In addition, N and P accumulations on gum leaves were highest in the summer at the time when wetlands would normally dry, indicating a seasonal period when moisture and temperature conditions are optimal for microbial growth. Net flux rates to the 1+ y-old component of litter indicated that the FE wetland is accumulating more organic matter (172 g $m^{-2}\ y^{-1}$) than the other wetlands (65 and 72 g $m^{-2}\ y^{-1}$), which we attributed to higher cypress litter production. We concluded that hydrologic regime influences breakdown rates and element accumulations, but that net productivity is more important in determining litter accumulation rates.

INTRODUCTION

On the Gulf Coastal Plain cypress-gum wetlands are characterized by a dense canopy of pond cypress (*Taxodium ascendens* Brongr.) and swamp black gum (*Nyssa sylvatica* var. *biflora* (Walter) Sarg.). Some of these forested wetlands are very productive with annual aboveground net production rates >400 g m^{-2} (Moore, 1970; Gomez and Day, 1982; Watt and Golladay, 1999), despite the fact that many appear to be nutrient limited (Watt and

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Golladay, 1999). Few studies have examined organic matter processing in these habitats, even though it is an important mechanism for internal nutrient cycling. Many of these seasonally inundated wetlands occupy isolated depressions (*i.e.,* not connected to rivers) that receive water through annual rainfall (Sutter and Kral, 1994) hence, breakdown of organic matter occurs not through abiotic processes (*i.e.,* current or wave action), but nearly exclusively by the biotic components (*i.e.,* microbes and invertebrates). Cypress-gum wetlands are considered a stressful habitat for many organisms because of the seasonal hydrologic regime and harsh summer conditions. In the summer dissolved oxygen (DO) levels are often <2 mg/liter at the benthic surface and temperatures can be as high as 27 C (Moore, 1970; Ziser, 1978; Battle and Golladay, 2001). These environmental factors can hinder plant breakdown by inhibiting microbial decomposer activity (Reddy and Patrick, 1975; Bärlocher *et al.*, 1978; Godshalk and Wetzel, 1978; Day, 1982; Connor and Day, 1991) and by altering the composition and density of aquatic invertebrates (Cuffney and Wallace, 1987; Golladay *et al.*, 1999; Battle and Golladay, 2001).

In the southeastern United States, depressional wetlands tend to be flooded <6 mo during the year. Many studies have reported faster litter decay rates in temporarily inundated systems due to an increase in microbes, which enhanced palatability to invertebrate consumers during subsequent flooding (Reddy and Patrick, 1975; Bärlocher *et al.*, 1978; Ryder and Horwitz, 1995). Others have found that faster breakdown occurred in permanent waters and suggested that it was due to an increase in leaching and more favorable conditions for microbes and detritivores (Herbst and Reice, 1982; Hietz, 1984). In a laboratory experiment using microcosms, Day (1983) found that litter subjected to different lengths of inundation had similar decay rates. However, using field microcosms in a south Georgia floodplain forest, Lockaby *et al.* (1996) found that a single, relatively brief, aerobic flooding period produced faster decay of litter than cycles of wetting-drying or sustained flooding.

An understanding of organic processes is fundamental to expanding basic knowledge of depressional wetland function. Our goal was to study breakdown of litter in relatively undisturbed cypress-gum depressional wetlands in the southeast U.S. Many depressional wetlands on the Coastal Plain have been damaged or altered by regional development (Tansey and Cost, 1990). Undisturbed wetlands can serve as benchmark sites, which are essential if these wetlands are to be monitored for impacts or restoration within the region (Brinson and Rheinhardt, 1996; Kirkman *et al.*, 1999). Our specific objectives were to: (1) determine breakdown rates of cypress and black gum leaves in cypress-gum depressional wetlands with different hydroperiods; (2) verify the biotic processes involved in litter breakdown; (3) examine temporal patterns of elements (K, Mg, Ca, N and P) in decomposing leaves; and (4) estimate net flux rates (organic carbon, N and P) to the pool of 1+ y-old litter.

STUDY AREA

Depressional wetlands are a common feature on the Gulf Coastal Plain. In areas like the Dougherty Plain of southwest Georgia, wetlands are formed by the dissolution of underlying limestone bedrock, followed by the collapse of the overlying sands and clay (Hendricks and Goodwin, 1952). The Dougherty Plain is an 11,400 km^2 area bounded by the Chattahoochee River and Fall-line Hills to the west and north and the Pelham Escarpment to the south and east (Beck and Arden, 1983). This is a low topographic region with elevation that ranges from 15–91 m above sea level (Hayes *et al.*, 1983).

On the Dougherty Plain there are several types of depressional wetlands ranging from grassy marshes to forested swamps (Kirkman *et al.*, 2000). Typically, wetlands tend to fill from late winter storms and dry in early summer, although ultimately inundation length is dependent on climatic conditions, as well as wetland morphology. Wetlands vary in size

TABLE 1.—Water chemistry characteristics of three cypress-gum wetlands in 1998. Means and ranges are based on the average of the 10 removal dates

Water chemistry	Mean	Range
Total carbon (mg L^{-1})	21.6	(11.2–34.7)
Inorganic carbon (mg L^{-1})	3.2	(2.3–5.0)
Organic carbon (mg L^{-1})	18.4	(29.7–8.6)
pH	5.3	(4.8–5.8)
Alkalinity (mg $CaCO_3$ L^{-1})	4.4	(1.7–6.5)
NH_4-N (μg L^{-1})	1.2	(0.1–3.9)
NO_3-N (μg L^{-1})	31.1	(14.2–86.2)
PO_4-P (μg L^{-1})	3.1	(0–10.1)

from a few to >50 km^2 and tend to be shallow with depths <1 m. We conducted our study in three relatively undisturbed cypress-gum wetlands (Collins, King, and Predest) located on the Ichauway Ecological Reserve, Baker County, Georgia. Ichauway Reserve is a 119 km^2 remnant longleaf pine (*Pinus palustris* Mill.) forest. It is a fire maintained landscape with prescribed burns occurring on a 1–3 y rotation in late winter/spring (February to April). Since the land was acquired in the 1930s, management of the uplands has consisted of limited salvage logging and some row-crop agriculture, which has resulted in minimal human impacts on the wetlands.

In the wetlands we studied, the dominant tree species were swamp black gum (*Nyssa sylvatica* var. *biflora*) and pond cypress (*Taxodium ascendens*), with a variable subcanopy of red maple (*Acer rubrum* L.), sweetgum (*Liquidambar styraciflua* L.) and smaller individuals of the dominants (Watt and Golladay, 1999). Canopy tree diameters averaged 30 cm and basal areas ranged from 43 to 55 m^2 ha^{-1} (Watt and Golladay, 1999). Cypress-gum wetlands are characterized by a distinct surface organic layer and dark-stained waters that have low DO levels (Battle and Golladay, 2001). Compared to other depressional wetland types in the region (*i.e.,* grass-sedge marshes and cypress savannas) the waters have relatively higher levels of dissolved organic carbon, NH_4-N, NO_3-N, and PO_4-P (Battle and Golladay, 2001). Water chemistry of overlying waters that characterized our study wetlands during 1998 was determined according to standard procedures (*see* Battle and Golladay, 2001) and summarized in Table 1. The study wetlands vary in size: 11.4 ha (Collins), 6.8 ha (King), and 6.5 ha (Predest).

In southwest Georgia during the late fall and winter of 1998, El Nino conditions resulted in above average rainfall and all the wetlands were inundated when the study began in January (Fig. 1a). Normally they would have dried in the early summer, however multiple rainstorms in September resulted in the following hydrology among the three wetlands (Fig. 1b). Below we listed the hydroperiod classification, followed by the wetland name, and a description of the flooding regime:

Flooded exposed (FE), Collins—5 mo flooded, followed by 6 mo litter exposed (*i.e.,* no standing water, moist soil): considered a typical annual flood regime

Multiple flooded exposed (MFE), King—6 mo flooded, litter exposed (>1 mo), re-flooded (≈1 wk), exposed (≈1 mo), re-flooded (≈3 wk), exposed (≈1 mo)

Permanently flooded (PF), Predest—flooded throughout experiment except for a brief period when soil was saturated but not inundated

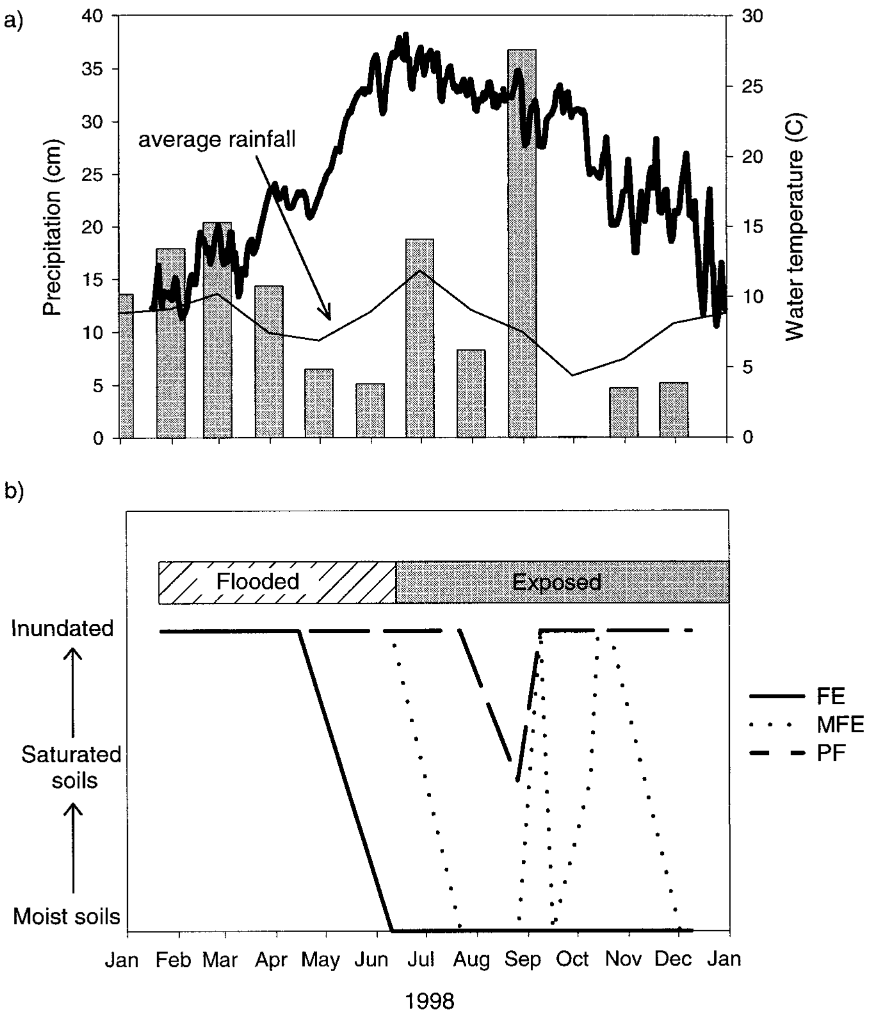

FIG. 1.—(a) Precipitation in 1998 is indicated by bars and average rainfall is based on data reported for southwest Georgia from 1895–1998 (NCDC, 1999). Average water temperature in the three wetlands shown as bold line. (b) Horizontal bar indicates normal annual hydroperiod (flooded and exposed phases). Hydrology patterns for the study wetlands during 1998 were FE (flooded exposed), MFE (multiple flooded exposed) and PF (permanently flooded)

METHODS

Litter bags.—The litter bag method was used to examine breakdown of cypress and black gum leaves (Benfield, 1996). Senescent leaves from cypress (a mixture of pond (*Taxodium ascendens*) and bald cypress (*T. distichum* (L.) Rich.)) and black gum were collected in each wetland from October through December by using a net (approximately 3-m × 7-m) stretched out under the canopy and suspended above the water. Leaves were removed before a rainfall to minimize leaching and taken to the laboratory to dry at ambient temperature for 1–2 wk. For each litter type, dried leaves were combined from all wetlands, then thoroughly mixed. Litter bags (30-cm × 16-cm) of a 5-mm mesh size were filled with approximately 5 g of dried cypress or gum leaves that were weighed to the nearest 0.01 g. Cypress leaves were misted with water before placing in litter bags to help prevent breakage. Bags were placed in the wetlands on 21 January 1998, with 20 bags of each litter type placed at three sites in each wetland for a total of 360 bags (3 wetlands × 3 sites × 2 litter types × 2 bags per removal × 10 removal dates). Litter bags were tethered to a 2-m rope so that they rested on the sediment surface and the rope was secured at both ends to 1-m tall PVC poles that were partially inserted into the soil. Water temperature was continuously measured in each wetland (Model DP212, Datalogger, Inc., Logan, Utah). One set of litter bags was immediately retrieved to determine mass loss due to handling. Bags were retrieved after the following days of incubation: 1, 14, 28, 56, 84, 140, 182, 217, 266 and 322 d. On each retrieval date, 2 bags of each type were removed from each site (2 sets of 18 bags per retrieval date). The first set of bags was used to determine mass loss and macroinvertebrate composition, and the second set of bags was used to determine ergosterol and nutrient levels. Litter bags were placed in individual plastic bags, labeled and transported on ice to the laboratory.

Laboratory procedures.—In the laboratory, leaves were removed from litter bags and macroinvertebrates were handpicked, then preserved in 70% ethanol. We then measured dry mass (48 h, 50 C) and ash mass (4 h, 550 C) of leaves and calculated ash-free-dry-mass (AFDM). Macroinvertebrates were considered those individuals visible with a 10×-power dissecting lens. Macroinvertebrates were identified usually to genus, dried (24 h, 50 C) and ashed (2 h, 550 C) to determine AFDM.

The ergosterol content of decaying litter, an indicator of fungal biomass, was measured following procedures outlined by Newell *et al.* (1988). Subsamples of fresh material (≈0.5 g) were placed in 50 ml methanol and refluxed for 2 h in large covered test tubes. The tubes were allowed to cool and then 5 ml of saponification reagent was added (4% KOH in ethanol) to each, followed by an additional 30 min of refluxing. The samples were then filtered and transferred to 120-ml separatory funnels containing 10 ml of deionized water. Each sample was extracted two times using pentane (10 ml, 10 ml). Extracts from each sample were combined and evaporated in a glass vial. The residue was redissolved in 1.0 ml of HPLC grade methanol. Three samples containing a known quantity of ergosterol standard were subjected to refluxing and extraction to estimate recovery efficiency. Ergosterol was quantified using a reverse-phase HPLC system (Shimadzu LC-10AS) configured as follows: solvent = methanol, flow rate = 2 ml min^{-1}, column = Microsorb-MV, absorbance detector = 282 nm with a range of 0.5, and quantification = Shimadzu SPD 10AV detector and Shimadzu EZ-Chrom V. 3.2.

To determine nutrient content in litter bags, dry leaves were ground with a Spex 8000D ball grinder. Carbon and nitrogen levels were determined on subsamples using a dry combustion method on a Perkin-Elmer 2400 series CHNS/O analyzer. Potassium, calcium, magnesium and phosphorus concentrations were determined on subsamples that were wet-digested in a Lachat BD-46 Block digester using sulfuric acid-hydrogen peroxide method. Potassium, calcium and magnesium concentrations were measured using a Perkin-Elmer 5100 PC Atomic Absorption Spectrophometer (methods modified from Perkin-Elmer, 1982). Phosphorus levels were determined by a Lachat QuikChem AE autoanalyzer using molybdate-blue method (Lachat Instruments, 1992).

Statistical analysis.—Breakdown rates ($k\ y^{-1}$) were determined by exponential decay model (Olson, 1963); $X_t/X_o = e^{-kt}$, where X_t/X_o = fraction remaining of original AFDM leaf material at time t, t = elapsed time in years, and k = the decay constant. To determine if differences existed among breakdown rates a general linear model with a dummy variable

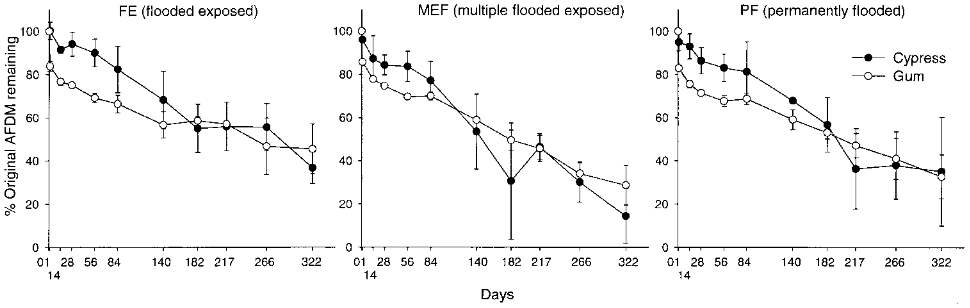

FIG. 2.—Mass loss (1 ± SD) of cypress and gum leaves in three wetlands with different hydrologic regimes. Mass loss is expressed as the percentage of original AFDM remaining and each point represents n = 3

was used to make pairwise comparisons between interactions (wetland and litter types; Zar, 1984). Density of macroinvertebrates was expressed as number of macroinvertebrates g^{-1} AFDM leaf material, densities were transformed (log + 1), means taken and then back transformed. Invertebrate mass was multiplied times the conversion factor 1.21 to adjust for weight loss due to preservation in ethanol (Leuven *et al.*, 1985). In separate analyses, macroinvertebrate biomass and ergosterol levels were normalized to g^{-1} AFDM leaf material, transformed to improve normality and compared among wetlands, litter types and dates using analysis of variance. Significant differences were determined with Scheffe post-hoc test; significance level was set at $P = 0.05$. Temporal patterns of percentage of total N, P, Ca, K, and Mg remaining were graphed and compared qualitatively.

RESULTS

Leaching within the first day accounted for >15% of the mass loss in gum litter, whereas little leaching occurred in cypress litter (<2% mass loss; Fig. 2). By the end of the study (322 d) the percentage of original mass remaining averaged 23% for cypress litter and 37% for gum litter (Fig. 2). Cypress leaves decayed faster than gum leaves ($P < 0.05$, Table 2). Mean decay rate for cypress litter was $k = -1.61\ y^{-1}$ ($r^2 = 0.52$) and gum litter was $k = -1.02\ y^{-1}$ ($r^2 = 0.82$). The MFE wetland had the fastest breakdown rates compared to the other wetlands for both litter types ($P < 0.05$). Cypress leaves had similar decay rates in both the FE and PF wetlands. Gum leaves decayed faster in the PF than the FE wetland.

TABLE 2.—Breakdown rates (k), correlation coefficients for the decompostion models and the initial and final elemental ratios for cypress (*Taxodium*) and gum (*Nyssa*) in the wetlands. Different letters following the decay rate indicates significant differences in breakdown rates for each plant species among the wetlands

		Cypress					Gum				
	Sites*	k (y^{-1})	r^2	C:N	N:P	C:P	k (y^{-1})	r^2	C:N	N:P	C:P
Initial	All wetlands			59.1	21.7	1271			57.9	28.4	1643
Final	FE	1.04a	0.84	43.4	17.1	742	0.77a	0.77	26.1	19.8	517
	MFE	2.33b	0.57	37.3	23.6	887	1.26c	0.90	20.2	25.3	514
	PF	1.47a	0.63	42.8	32.4	1410	1.04b	0.86	22.2	26.0	578

* FE, flooded exposed; MFE, multiple flooded exposed; PF, permanently flooded

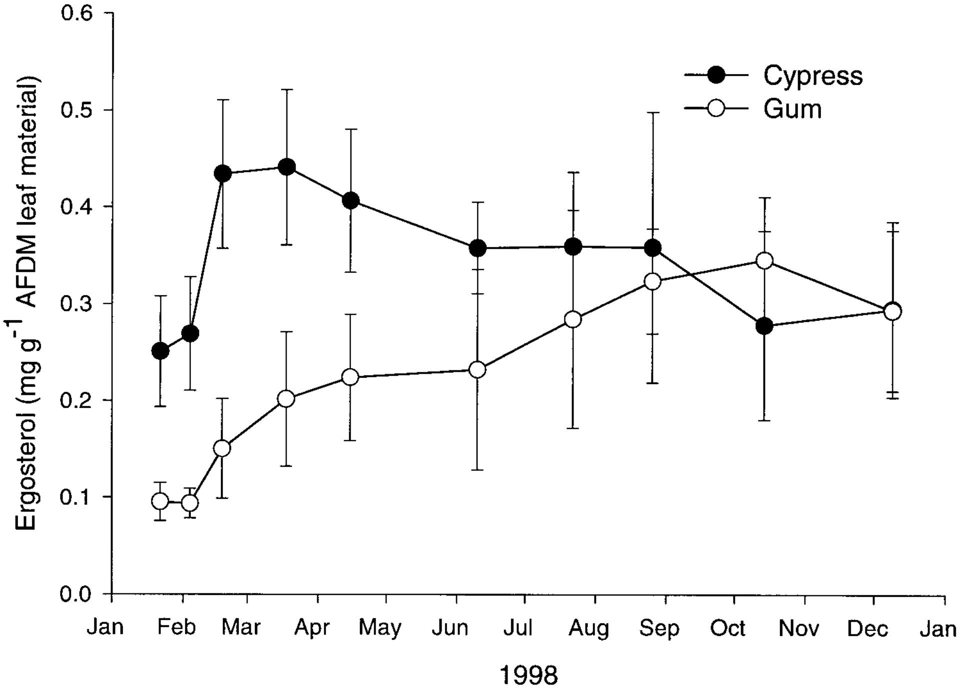

FIG. 3.—Mean ergosterol content (1 ± SD) for decomposing cypress and gum leaves. Each point is a mean of the wetlands (n = 3)

Ergosterol content did not differ significantly among wetlands, but was different between litter types and over time (Fig. 3; ANOVA: $n = 60$, $df = 12$, $F = 6.11$, $P < 0.001$). For the first 4–5 mo, ergosterol levels were much higher on cypress than gum leaves, with peak levels on cypress leaves ranging from 0.43 to 0.48 mg ergosterol g^{-1} AFDM leaf material. Gum leaves exhibited a steady increase in ergosterol concentrations over the study with levels reaching a maximum of 0.33–0.39 mg ergosterol g^{-1} AFDM leaf material after 8 mo (Fig. 3).

Macroinvertebrate numbers were similar between litter types but not among wetlands. Mean macroinvertebrate density was 0.38, 0.64 and 1.05 individuals g^{-1} AFDM leaf litter in the FE, MFE and PF wetlands, respectively (Fig. 4). The number of different taxa per wetland and date combination ranged from 3–19 taxa and averaged 7 taxa overall. Chironomini (dipteran) and oligochaetes had the highest numbers followed by *Caecidotea* (isopod) and *Crangonyx* (amphipod). Biomass of macroinvertebrates was similar between litter types ($P > 0.05$), but significantly different among wetlands ($P < 0.05$). The FE wetland had the lowest biomass, followed by MFE, then PF wetland; mean biomasses for the three wetlands were 0.14, 0.30 and 0.36 mg AFDM of macroinvertebrates g^{-1} AFDM leaf litter (Fig. 4). Based on biomass, *Caecidotea* was dominant during initial colonization followed by an abundance of oligochaetes, then Chironomini. Predators, composed mainly of aquatic beetles, were dominant in the FE and MFE wetlands when they started to dry. Taxa present in low numbers and represented by the 'other' category were zooplankton (copepods, cladocerans and ostracods), crayfish, gastropods, collembola and non-predator insects (Fig. 4).

C:N ratios were initially >55 for both litter types, then decreased to final values of 41 in

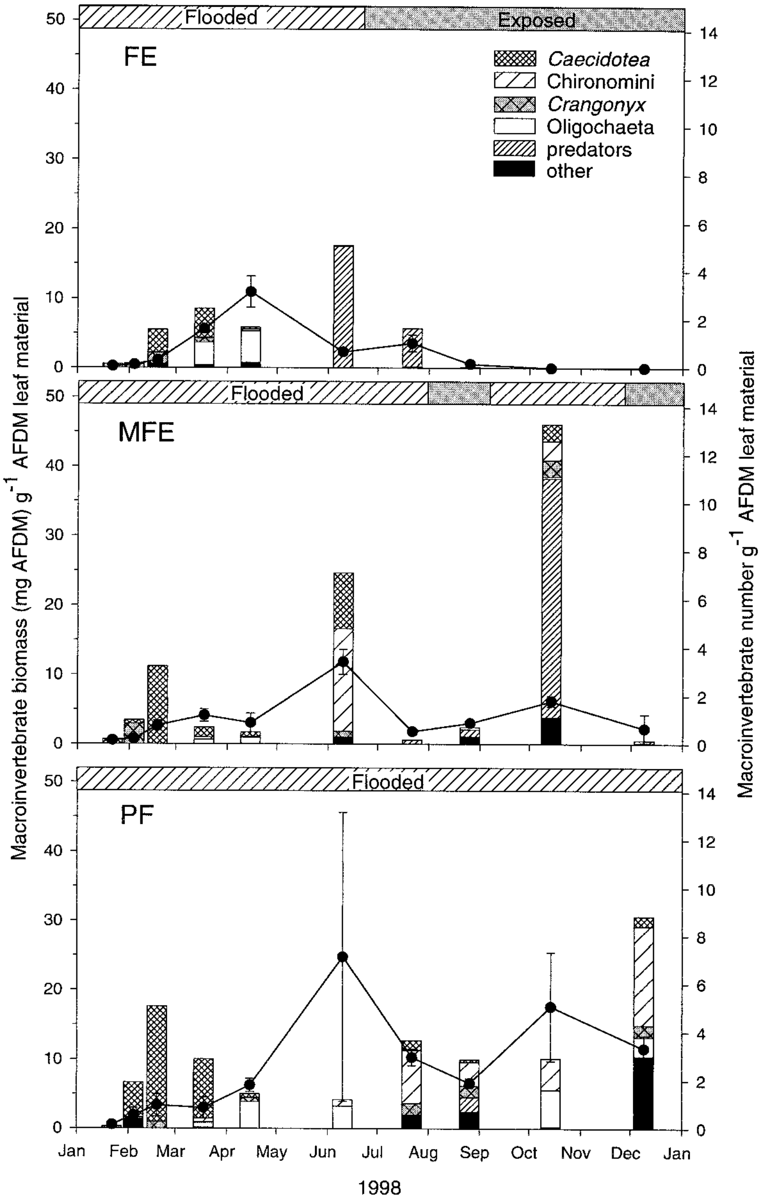

FIG. 4.—Biomass of macroinvertebrates in each wetland indicated by bars. Lines indicate mean macroinvertebrate density g^{-1} leaf material (± 1 SD) and are labeled on the y-2 axis. Whether litter bags were flooded or exposed is indicated by the shaded horizontal bar on top of each graph

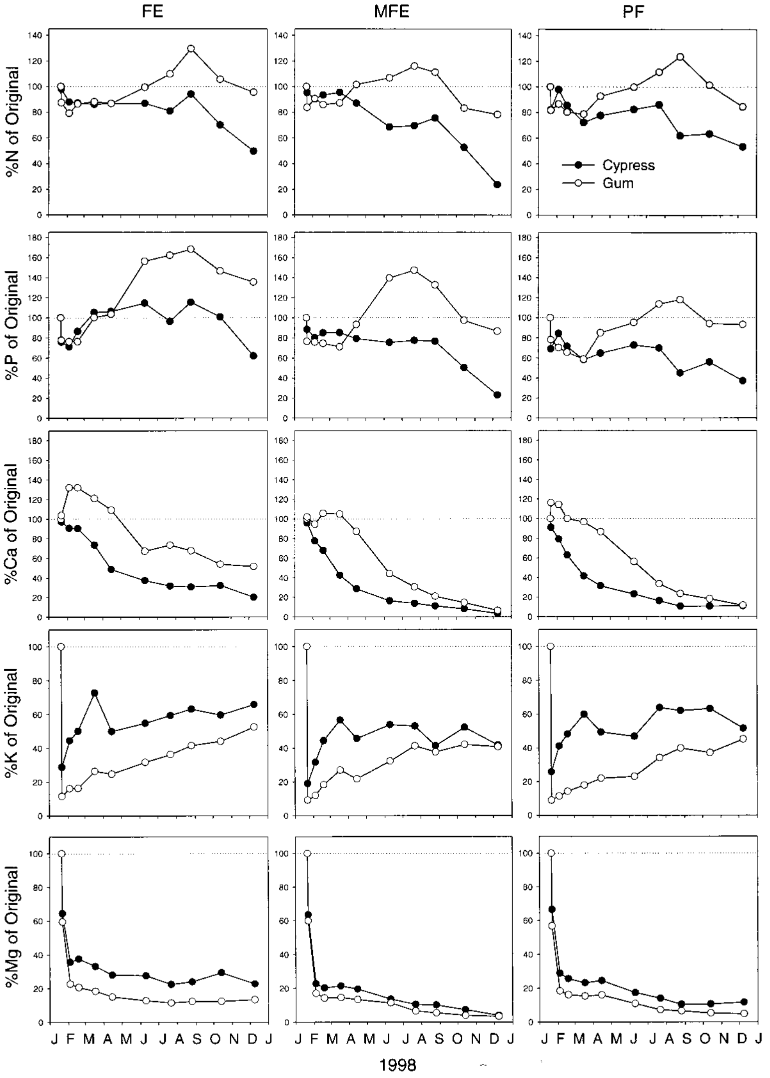

FIG. 5.—Amount of nitrogen, phosphorus, calcium, potassium and magnesium for two litter types in three wetlands. Each point (n = 3) indicates the percent of the original amount remaining in the litter bag. Wetland hydrologic regimes: FE (flooded exposed), MFE (multiple flooded exposed) and PF (permanently flooded)

cypress and 23 in gum leaves (Table 2). For both litter types, N:P ratios ranged from 17 to 32, while C:P ratios were >500. Temporal patterns of elements showed some obvious differences between cypress and gum leaves (Fig. 5). During the study, cypress litter tended to have higher levels of K and Mg and gum leaves tended to have higher levels of N, P and Ca. In gum leaves, net immobilization of N occurred for part of the study, while cypress leaves had net mineralization of N. In gum leaves highest levels of N and P occurred in August–September (Fig. 5). Patterns of P and Ca remaining in litter indicated differences between litter types and among hydroperiods. In gum leaves, accumulation of P was greatest in the FE wetland, followed by the MFE site, then the PF wetland. In cypress leaves, some P immobilization occurred in the FE wetland, but mineralization occurred in the MFE and PF wetlands. For gum leaves, Ca concentrations peaked in March, with accumulation occurring immediately in all the wetlands, but to the greatest extent in the FE wetland. For cypress leaves, Ca showed steady declines with approximately 40–60% losses after 3 mo. For both litter types, K and Mg were mobile with 60–90% losses within the first couple of days. Following leaching, K showed accretion in all wetlands for both litter types but to a greater extent for cypress. Percentage of Mg remaining was also higher in cypress than gum leaves and Mg levels in the FE wetland were slightly higher than the other wetlands (Fig. 5).

DISCUSSION

Breakdown rates.—Moisture and temperature are considered the primary external environmental factors responsible for regulating organic material processing (Webster and Benfield, 1986). Many studies have established that flooded areas have more rapid breakdown than adjacent upland areas (Brinson, 1977; Deghi *et al.*, 1980; Shure *et al.*, 1986). Wet-dry cycles have been shown to increase breakdown rates in terrestrial systems by promoting microbial decomposers (Swift *et al.*, 1979). In seasonal wetlands, predicting breakdown rates can be complex because of variable cycles of flooding and drying (Day, 1982, 1983; Yates and Day, 1983; Wylie, 1987; Lockaby *et al.*, 1996). In our study breakdown rates were fastest in the MFE wetland compared to the FE and PF wetlands, indicating different hydroperiods had an effect on the rate of organic matter processing. In cypress-gum wetlands, litter breakdown was stimulated by occasional aerobic conditions brought about by drawdown and then subsequent inundation. The alternation between flooded and moist aerobic condition is probably optimal for maximum microbial activity in this habitat. Our results were consistent with Ryder and Horwitz (1995) who noted greatest decomposition under a MFE hydrologic regime. They attributed this in part to stimulated microbial activity that peaked following reflooding. In addition, Lockaby *et al.* (1996) found using field microcosms that cycles of wet-dry accelerated breakdown in a floodplain forest in Georgia compared to nonflooded conditions. However, alternating cycles of flooding and drying did not accelerate decomposition (Lockaby *et al.*, 1996). They concluded that well-oxygenated flooding, followed by moist soil conditions during drawdown maximized decomposition (Lockaby *et al.*, 1996). Using laboratory microcosms, Day (1983) also observed that variations in hydroperiod did not alter breakdown rates, but unlike our study, his was conducted under continuously aerobic conditions.

Many wetland studies support the premise that litter breakdown occurs more readily in aerobic than anaerobic conditions (Reddy and Patrick, 1975; Cuffney and Wallace, 1987; Neckles and Neill, 1994; Ryder and Horwitz, 1995). Cuffney and Wallace (1987) established the following ranking of organic matter processing in a floodplain forest in Georgia: river > well-oxygenated, permanent floodplain ponds > shallow, low oxygen floodplain ponds. They concluded that oxygen levels complicated generalizations concerning breakdown and moisture (Cuffney and Wallace, 1987). In a prairie marsh, comparison of flooded versus nonflooded sites indicated that flooded sites had more rapid processing of macrophytes aboveground (O_2 available), but slower processing belowground (anoxic) (Neckles and Neill, 1994). Ryder and Horwitz (1995) found in a seasonal wetland in Australia that permanently flooded areas had slower processing of organic material than litter exposed to seasonal inundation and suggested reduced oxygen concentrations in the permanently inundated sites were responsible. Similarly, in our study low oxygen levels in the PF wetland caused by extended inundation resulted in reduced processing rates; whereas, aeration brought about by drawdown in the FE and MFE most likely promoted microbial activity and increased the rate of breakdown.

Water chemistry has also been shown to influence detritus processing (Webster and Benfield, 1986). Suberkropp and Chauvet (1995) demonstrated that litter breakdown is accelerated in systems with higher concentrations of nutrients, particularly N and P. Although slightly higher N concentrations in litterfall have been previously recorded in the FE wetland (Watt and Golladay, 1999), other work in these wetlands has established that they have comparable water quality, soils and vegetation (Kirkman *et al.*, 2000; Battle and Golladay, 2001). Thus, we do not believe differences in breakdown rates are related to nutrient availability.

Comparison of our study to other southern wetlands showed that our breakdown rates were similar to those obtained in floodplain forests (*i.e.,* gum leaves; Table 3). Typically, it would be expected that litter breakdown would be slower in depressional wetlands than floodplain forests for the following reasons: (1) absence of flow-related mechanical fragmentation in depressional wetlands; (2) lack of a flood pulse and associated nutrient subsidy in wetlands; and (3) decomposers in wetlands are limited to those adapted to seasonal drying and low DO levels (Golladay *et al.*, 1999). Gum leaves in our study had a breakdown rate similar to those reported for a South Carolina floodplain forest; however, that study estimated breakdown rate using aquatic and upland sites (Shure *et al.*, 1986). When they calculated the processing rate as an average of four different litter types (red ash, black gum, red maple and sweet gum), breakdown was much slower in the upland sites ($k = 0.88–1.15\ y^{-1}$) than the 'wet' sites ($k = 1.74–1.95\ y^{-1}$; Shure *et al.*, 1986). The latter breakdown rates were similar to a study in a North Carolina floodplain forest (Brinson, 1977) and much faster than the rate we reported for gum leaves, which supports the hypothesis that processing of organic material is slower in depressional wetlands than flowing habitats (Table 3).

Yet, compared to other still-water wetlands breakdown rates were faster in our cypress-gum wetlands. This may have been due to ample microbial breakdown given that ergosterol levels were similar to those reported for litter in streams (Suberkropp *et al.*, 1993). Even though low DO has been shown to reduce ergosterol concentrations (*see* Gessner and Chauvet, 1993), fungi in cypress-gum wetlands was obviously capable of colonizing litter at fairly high levels (Fig. 3).

Another reason for the relatively high breakdown rates we reported may have been due in part to using litter bags with a comparatively large mesh size (Table 3). The limitations of the litter bag method have been well-recognized (Webster and Benfield, 1986). The mesh size of the litter bag may influence breakdown by allowing loss of coarse organic material and excluding access by certain invertebrates. In addition, the litter bags themselves can influence the breakdown by altering the microhabitat (*i.e.,* providing a surface for microbes to colonize). In our study, the loss of material from the mesh bag was more likely to occur for cypress than gum litter because of leaf morphology. However, we believe that the mesh size we used (5-mm openings) better represented actual breakdown rates because it allowed access to nearly all invertebrate taxa present and decreased the probability of anoxia due to bag design, while not causing excessive loss of cypress litter (*e.g.,* based on handling loss of 6.4% of the original mass).

Microbes and invertebrates.—Studies have shown a relationship between litter breakdown and microbial biomass, with efficient aerobic litter breakdown usually associated with higher microbial production (Brock, 1966; Ryder and Horwitz, 1995). Therefore, because the MFE wetland had the fastest breakdown rates, we expected higher fungal biomass in this wetland; however, ergosteral levels did not differ among the wetlands. Unfortunately, we lack infor-

TABLE 3.—Breakdown rates (k) for cypress (*Taxodium*) and gum (*Nyssa*) leaves in southern wetlands

Litter type	Breakdown rate (k y^{-1})	Mesh size opening or material	Wetland type	Reference
Taxodiaceae				
T. distichum	0.25[1]	fiberglass screen	Cypress strand, FL	Duever *et al.*, 1984
	0.28	1-mm	Great Dismal Swamp, VA	Yates and Day, 1983
	0.33	1-mm	Great Dismal Swamp, VA	Day, 1982
T. ascendens[2]	0.25	fiberglass screen	Scrub cypress swamp, FL	Brown *et al.*, 1984
	0.36	2-mm	Cypress dome, FL	Dierberg and Ewe, 1984
	0.46	2-mm	Cypress dome, FL	Nessel, 1978
	0.55	2-mm	Sewage enriched cypress strand, FL	Nessel, 1978
	0.69	2-mm	Sewage enriched cypress dome, FL	Dierberg and Ewel, 1984
	1.21–1.40[3]	fibreglass screen	Cypress dome, FL	Deghi *et al.*, 1980
T. ascendens and *T. distichum*	**1.61**	5-mm	Cypress-gum wetland, GA	This study
Nyssaceae				
N. sylvatica var. *biflora*	0.85	2-mm	Sewage enriched cypress strand, FL	Nessel, 1978
	1.02	5-mm	Cypress-gum wetland, GA	This study
	1.08	1-mm	Floodplain forest, SC	Shure *et al.*, 1986
N. aquatica	0.65	1-mm	Great Dismal Swamp, VA	Day, 1982
	1.89	fiberglass screen	Alluvial swamp forest, NC	Brinson, 1977

[1] Used litter from forest floor, primarily *T. distichum*. Rate based on average of four sites inundated for >50% of the study period

[2] Also known as *Taxodium distichum* var. *nutans*

[3] Range based on two sewage enriched and two control cypress domes

TABLE 4.—Net flux rates of litter, N and P to pool of 1+ y-old litter in three wetlands with different hydrologic regimes (FE = flooded exposed, MFE = multiple flooded exposed, PF = permanently flooded). Leaf litter production data are from Watt and Golladay (1999)

	FE			MFE			PF		
	Cypress	Gum	Cypress and gum	Cypress	Gum	Cypress and gum	Cypress	Gum	Cypress and gum
Leaf litter production (g m^{-2} y^{-1})	243.3	187.4		79.8	203.8		60.7	163.6	
Fraction remaining after 1 y	0.352	0.460		0.097	0.283		0.229	0.352	
Net flux to pool of 1+ y-old litter (g m^{-2} y^{-1})*	85.6	86.2	171.8	7.7	57.7	65.4	13.9	57.6	71.5
%N after 322 d**	1.18	1.91		1.39	2.40		1.25	2.26	
N net flux to pool of 1+ y-old litter (g m^{-2} y^{-1})***	1.01	1.65	2.66	0.12	1.38	1.48	0.17	1.30	1.47
%P after 322 d**	0.070	0.096		0.060	0.099		0.040	0.091	
P net flux to pool of 1+ y-old litter (g m^{-2} y^{-1})***	0.060	0.083	0.143	0.005	0.057	0.062	0.006	0.052	0.058

* Net flux to pool = leaf litter production × fraction remaining

** %N and %P are measured values

*** N (or P) net flux to pool = %N after 322 d × net flux to pool mation on microbial activity and do not have a clear understanding of the role of bacteria in litter breakdown within cypress-gum wetlands. Because of this lack of knowledge, at this point we can only hypothesize that there was a positive association between microbes and invertebrates in the MFE wetland that resulted in the fastest breakdown rates. In temporary vernal pools, microbial biomass accumulated on decaying leaves up to the time of flooding, at which time aquatic consumers had access and microbes decreased (Bärlocher *et al.*, 1978). We suspect that when drawdown occurred, there was a short period where aeration and moist soils provided optimal conditions for microbial growth, but that during subsequent flooding fungal biomass was decreased by grazing invertebrate consumers. During a drought in the Great Dismal Swamp, Yates and Day (1983) found the fastest decay occurred in the site with the highest soil moisture and suggested that the high humidity levels were beneficial for soil faunal activity. Presumably, even when litter is not saturated, soil moisture remains high and supports microbial growth. Long-term exposure that dries the soils can cause changes in the microbial community (*i.e.,* transition from aero-aquatic fungi to terrestrial hyphomycetes) and affect their ability to breakdown litter (Bärlocher *et al.*, 1978). Clearly, further research on microorganisms is needed to understand their function in decomposition within cypress-gum wetlands.

Many studies have positively correlated faster breakdown rates to higher invertebrate densities (*see* Webster and Benfield, 1986), however that was not the case in our study. Even though the PF wetland had the greatest density of detritivores, it did not have the fastest breakdown of litter. In our study, invertebrates alone probably contribute less to determining breakdown rates than microbes, but act synergistically with microbes to increase breakdown rates.

During the processing of litter, we observed a pattern of succession in the invertebrate community that related to the hydrology (Golladay *et al.*, 1999; Battle and Golladay, 2001). In the beginning of the study invertebrates did not colonize litter and this delay is probably a direct result of animals' preference for microbially conditioned litter. Palatability of litter for invertebrates is greatly increased following colonization by fungi and bacteria (Bärlocher *et al.*, 1978). For the early and mid-hydroperiod, detritivores were dominant, indicating the importance of leaf litter in supporting aquatic foodwebs. Detritivores seem to be grazing the microbial layer on the leaves because the leaves themselves were not shredded (*see* Litter types below). When water levels started to decrease in two of the wetlands (FE and MFE) macroinvertebrate density on the litter decreased. The loss of invertebrates in the FE wetland during the fall may have considerably slowed processing at that stage. When wetlands begin to drawdown, aquatic animals not only lose habitat but also experience the potentially stressful conditions of increased temperature and decreased DO concentrations. Predators appear adapted to these conditions since their numbers increased at that time. The majority of predators were adult aquatic beetles that were able to colonize drying wetlands because they have aerial dispersal and are air breathers (Merritt and Cummins, 1996).

Litter types.—Different breakdown rates between litter types may be attributable in part to their distinct morphology and structural components. Physically, gum leaves were largely intact but paper thin by the last sample date. In contrast, after extended exposure, cypress leaves tended to have the main stem remaining with few needles attached. This was particularly true for bald cypress, which has splayed needles, and not as common for pond cypress, which has appressed needles. Overall, cypress leaves had a more rapid breakdown than gum leaves, which may be a result of several elements. First, higher ergosterol concentrations on cypress litter versus gum suggest greater microbial activity (Fig. 3). The highly dissected leaves of cypress allowed greater surface area : volume for decomposers. In contrast, gum leaves are thick, leathery and have a waxy-cutin that may have initially inhibited fungal colonization. Ergosterol content increased on gum leaves after extended exposure, with highest levels taking place in fall, subsequent to peaks in N and P. For gum leaves, fungi appear to reach maximum biomass at the time when wetlands would typically be dry. Secondly, cypress leaves may have had faster breakdown because the fragile morphology made them more prone to fragmentation. Lastly, the elemental make-up of the two litter types may have influenced breakdown rates. Specifically, gum leaves had higher initial C:P ratios than cypress leaves (Table 2), indicating that the breakdown of gum may have been more strongly P-limited (Wylie, 1987; Enriquez *et al.*, 1993). In a Missouri wetland study, results suggest that not only hydrologic regime, but litter type was important in determining breakdown rates and that faster breakdown occurred in plant material with higher N and P content (*i.e.,* low C:N and C:P ratios; Wylie, 1987). Others have suggested that lignin is a better determiner of processing rates than C:N ratio, with higher lignin levels resulting in slower breakdown (Cromack and Monk, 1975; Alexander, 1977). Previous studies have reported similar lignin concentrations for *Nyssa sylvatica* (25.5%; Shure *et al.*, 1986) and *Taxodium distichium* (25.8%; Day, 1982), but these values were obtained by different methods and in different systems, so further research is needed to determine the significance of lignin in this study.

Elemental dynamics.—The study wetlands are 'closed' systems that derive nutrient inputs from rainfall and possibly runoff from the surrounding catchment. A C:N ratio of 16:1 indicates an adequate supply of N for complete decay (Brinson, 1977). Our C:N ratios were initially >57 in both litter types and remained >20 throughout the study, suggesting a possible N-limitation. C:P and N:P ratios both suggested a possible P limitation in the cypress-gum wetlands. C:P ratios we measured were >500, much higher than the 200 considered to be the optimal level required for microbial use (Brinson, 1977). N:P ratios were >20, again higher than 10:1 ratio that has been suggested as the level microbial decomposition readily occurs (Alexander, 1977). Based on litterfall, Watt and Golladay (1999) also noted a P or N/P co-limitation in these wetlands.

Elemental gains or losses in litter were influenced primarily by leaf litter type and secondarily influenced by hydrologic regime (Day, 1982; Wylie, 1987). In our study, gum leaves accumulated P, N, Ca and K, and lost Mg. Brinson (1977) observed similar patterns for *Nyssa aquatica* leaves located in a floodplain forest. In cypress litter, those elements were quickly mineralized followed by some accumulation of P and K. Elemental accumulations by leaves during decomposition reflects an ability to trap nutrients (*i.e.,* recycling) that may otherwise be in a dissolved phase. An accumulation is caused primarily through immobilization due to heterotrophic demand, which occurs when initial concentrations are low or the nutrient is limiting to decomposers (Brinson, 1977; Day, 1982). N and P accumulated in gum leaves in all the wetlands, with peak amounts occurring in August–September, perhaps signifying a seasonal time when temperatures and moisture are at optimal levels for microbial growth. In addition, before drawdown, microbes may benefit by retaining nutrients before they are leached deep within the soil (Shure *et al.*, 1986). After drawdown elements may be less accessible because sources are limited to uptake from the soil and external sources, such as throughfall and precipitation (Day, 1982). Temporal changes of P in gum litter appeared to be associated with hydroperiod. The drier sites (FE and MFE) had immobilization of P, while the wetter site (PF) had an increase in mineralization of P. Larger accumulations in the drier sites may reflect greater microbial activity during exposed conditions. Peak levels of Ca in gum leaves occurred at the start of the study but then decreased rapidly. Several floodplain forest studies reported for certain litter types a similar pattern of high initial Ca levels followed by a sharp decrease (Brinson, 1977; Shure *et al.*, 1986). Initial accumulations might be due to heterotrophic demand or physical accumulation on leaves, given that wetlands are formed on Ca-rich limestone bedrock (Hendricks and Goodwin, 1952). Similar to other studies, initial losses of Mg and K were very rapid and attributed to their high solubility (Brinson, 1977; Day, 1983; Yates and Day, 1983; Shure *et al.*, 1986). Temporal accumulations of K indicate this is a limited nutrient needed by microbial decomposers.

Previous work in these three wetlands has shown them to be some of the most productive of their type on the Coastal Plain (Watt and Golladay, 1999). A practical application of estimating breakdown rates of leaves is to determine the annual amount of litter that accumulates in the soils (*i.e.,* unrecognizable leaves) to become available for plant uptake. Our study indicates that organic material is rapidly decomposing, with only 10–46% of mass remaining after 1 y. Compared to the Great Dismal Swamp, the amount of organic matter accumulating in our wetlands is much lower primarily due to faster decay rates at our sites (Day, 1982). Net flux rates to the 1+ y-old component of litter indicated that the FE wetland, also the most productive (Watt and Golladay, 1999), accumulated more organic matter annually than the other wetlands because of the high production of cypress litter (Table 4). The FE wetland decomposed greater amounts of organic material than the other wetlands because of higher production rather than faster breakdown rates. Our finding of higher production rates occurring in conjunction with greater contribution to the 1+ y-old litter pool, is similar to results in the Great Dismal Swamp (Gomez and Day, 1982) and Florida cypress domes (Dierberg and Ewel, 1981). Vogt *et al.* (1986) survey of 12 forest types found that greater litter accumulation correlated with higher N and P bulk amount of the forest floor. Therefore, the total mass of organic inputs appears to be the driving factor for determining N and P accumulation in cypress-gum wetlands.

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