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Growth, Decomposition, and Nutrient Retention of Sawgrass and Cattail in The Everglades

by

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ABSTRACT

This study estimates phosphorus (P) and nitrogen (N) gains and losses during the growth, death, and two years of decomposition of sawgrass and cattail along a gradient of surface water nutrient concentrations in Water Conservation Area 2A. Annual rates of P and N allocation to growing leaves, nutrient loss through translocation and/or leaching from dying leaves, and retention in dead leaves all increased with soluble reactive phosphorus (SRP) and nitrate (NO_3-N) enrichment in surface water. Rates of each of these processes were accelerated in cattail in comparison to sawgrass.

The main effect of P and N enrichment on leaf nutrient flux was to accelerate translocation or leaching from dying tissue, rather than to increase retention in standing dead leaves. Freshly dead leaves retained only slightly greater quantities of P and N under enriched conditions in comparison to background conditions.

After two years of decomposition, approximately half of the leaf litter mass remained intact. Increasing P and N concentrations in decomposing leaf litter more than compensated for declining litter mass and resulted in net uptake or retention of these elements during two years. Total amounts of P that were sequestered annually by vegetation after processes of leaf production, leaf mortality, two years of decomposition, and detritus accumulation ranged from <0.1 to 1.4 g/m^2 for sawgrass and <0.1 to 1.9 g/m^2 for cattail. Corresponding rates of N sequestration were 4-17 g/m^2 for sawgrass and 5-21 g/m^2 for cattail. However, vegetation capacity for nutrient retention appeared to be limited. As concentrations of P and N increased along the gradient and during high-discharge years, cattail retention of these elements increased only up to a moderate level of enrichment. At higher enrichment levels, rates of long-term nutrient sequestration leveled off.

Key Words. Everglades, sawgrass, cattail, phosphorus, nitrogen, plant growth, decomposition.

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EXECUTIVE SUMMARY

The Everglades represent a wetland ecosystem which historically received small external nutrient inputs, but which has received increased nutrient supplies for nearly 30 years as a result of water management practices. Vegetation change has accompanied the increased nutrient inputs in the Everglades. Vast, nearly monospecific stands of sawgrass cover 65-70% of the Everglades marsh. The dominance of this large sedge has been attributed to its low nutrient requirements. Since nutrient supply has increased, cattail has invaded areas where agricultural inflows enter the marsh.

The middle of the Water Conservation Areas, Water Conservation Area 2A, receives particularly large inflows of agricultural water and nutrients because of a convergence of canal systems upon the inflow gates at the north end of the area. Nutrient concentrations decline as inflow water flows southward across the marsh, creating a gradient from high concentrations of soluble P and N near the inflow structures to values approaching detection limits in the interior marsh. A nearly monospecific cattail stand covers 2400 ha below the inflows in Water Conservation Area 2A, and cattails have permeated the sawgrass marsh to the south of this stand during the past decade.

This study estimates P and N gains and losses during the growth, death, and decomposition of sawgrass and cattail along a gradient of surface water nutrient concentrations in Water Conservation Area 2A in order to evaluate the effectiveness of the species in intercepting man-induced nutrient inputs

Annual rates of P and N allocation at growing leaves, nutrient loss through translocation and/or leaching from dying leaves, and retention in dead leaves all increased with soluble reactive phosphorus (SRP) and nitrate (NO_3-N) enrichment in surface water. Rates of each of these processes were greater in cattail than in sawgrass. For sawgrass, rates of each process increased linearly relative to the proximity of vegetation sampling sites to nutrient inflow points, but did not fluctuate with yearly variations in SRP and NO_3-N concentrations. Cattail differed from sawgrass in that annual rates for each process were strongly correlated with mean annual SRP and NO_3-N concentrations during specific sampling years.

The main effect of P and N enrichment on leaf nutrient flux was to accelerate the loss of these nutrients through translocation or leaching from dying tissue instead of increasing retention in standing dead leaves. Freshly dead leaves retained only slightly greater quantities of P and N under enriched conditions in comparison to background conditions.

After two years of decomposition, approximately half of the leaf litter mass remained intact. Increasing P and N concentrations in decomposing leaf litter more than compensated for declining litter mass and resulted in net uptake or retention of these elements for at least two years. Total amounts of P that were sequestered annually by vegetation after processes of leaf production, leaf mortality, decomposition, and detritus accumulation ranged from <0.1 to 1.4 g/m^2 for sawgrass and <0.1 to 1.9 g/m^2 for cattail. Corresponding rates of N sequestration were 4-17 g/m^2 for sawgrass and 5-21 g/m^2 for cattail. However, vegetation capacity for nutrient retention appeared to be limited. As concentrations of P and N increased along the gradient and during high-discharge years, vegetation retention of these elements increased only up to a moderate level of enrichment. At higher enrichment levels, rates of long-term nutrient sequestration leveled off.

Everglades sawgrass represents a vegetation community which became established under low nutrient inputs primarily from direct rainfall, which has limited capacity to retain higher nutrient inputs, and which is replaced by a more competitive species (cattail) when inputs increase. Plant detritus accumulation functions as a nutrient sink in the Everglades, but there appears to be an upper limit to its retention capacity above which water-borne nutrients are passed downstream.

INTRODUCTION

The use of wetlands to remove man-induced nutrients from surface water has gained popularity as a concept since Boyd (1970) and Steward (1970) noted nutrient uptake potentials of various macrophyte species. The role of plants in wetland nutrient uptake, however, has remained poorly understood until recently. Organic matter accumulation, in addition to soil adsorption, appear to be two major processes controlling long-term phosphorus immobilization in wetlands (Richardson and Marshall, 1986). Wetland nitrogen budgets are also influenced by denitrification and nitrogen fixation. The role of plants in long term nutrient retention appears to be largely related to detritus production (Davis and van der Valk, 1978) and the resulting accumulation of organic matter. At an ecosystem level, wetland plants appear to affect nutrient budgets to the extent that they (1) accumulate nutrients in biomass as they grow, (2) retain a portion of these nutrients in biomass as they die, and (3) retain or accumulate nutrients as they decompose in conjunction with the accretion of organic sediment.

Macrophyte growth and mortality contribute to nutrient uptake to the extent that nutrients remain sequestered in dying and decomposing plant biomass. As plants grow, they incorporate P, N, and other essential elements from soil and surface water into newly forming tissues (Boyd, 1970; Steward, 1970). Senescing plant tissues release nutrients which they accumulated during growth (Davis et al., 1983; Hopkinson and Schubauer, 1984). While incorporation of nutrients into growing tissue contributes to uptake by a vegetation stand, loss of nutrients from dying tissue contributes to translocation within the plants, recycling within the stand, or loss from the stand. Plants translocate nutrients from senescing tissue to growing plant parts or storage organs (Prentki et al., 1978; Davis and van der Valk, 1983; Hopkinson and Schubauer, 1984). Elements may be recycled when they are leached from dying foliage into surrounding water (Klopatek, 1978) and then reabsorbed by roots (Tukey and Mecklenburg, 1964; Clement et. al., 1972). Nutrient loss from a plant community occurs when leached nutrients escape reabsorption and are flushed downstream. In this context, the effectiveness of macrophytes in intercepting and holding exogenous nutrient supplies should be positively related to allocation to growing tissues, but should be inversely related to loss from dying or dead tissues. As a larger proportion of plant nutrients is translocated or recycled, a smaller proportion of plant nutrients must come from external sources. Therefore, any direct contribution of macrophyte growth and death to wetland nutrient uptake should depend upon amounts of nutrients that growing biomass assimilates, and proportions of assimilated nutrients that remain in biomass after death.

Macrophyte growth and death contribute to wetland nutrient uptake through the production of detritus, which acts as a substrate for subsequent nutrient flux during decomposition. Macrophyte detritus functions as a nutrient sink to the extent that (1) it accumulates as organic sediment due to incomplete decomposition and (2) it retains or assimilates nutrients as it decomposes. Leaching of soluble organic and inorganic compounds from detritus during the first few weeks of decomposition contributes to internal recycling within vegetation stands (Webster and Benfield, 1986; Howard-Williams and Howard-Williams, 1978). Subsequent changes in P and N content, as decomposition proceeds, determine the ultimate value of macrophyte detritus as a nutrient sink (Davis and van der Valk, 1983). Detritus may continue to lose P and N for one to two years (Latter and Craig, 1967; Richardson et. al., 1976; Davis and van der Valk, 1978). To the extent that this occurs, decomposition continues to function as a nutrient recycling mechanism rather than as a sink.

In other cases, macrophyte detritus either retains its initial nutrient content or accumulates nutrients during one to two years of decomposition (Puriveth, 1980; Day, 1982; Davis and van der Valk, 1983). Nutrient retention in macrophyte litter has usually been attributed to accumulation of microbial protein (Webster and Benfield, 1986), although Rice (1982) provided evidence that N accumulated during detritus decomposition may be humic rather than microbial. Inconsistent findings concerning the role of macrophyte detritus in nutrient recycling versus retention may result from variables such as nutrient supply (Saunders, 1976; Howarth and Fisher, 1976; Almazon and Boyd, 1978; Elwood et. al., 1981), seasonality in temperature

and flooding (Brinson, 1977; Puriveth, 1980; Day, 1982) and plant species (Day, 1982). The role of macrophyte detritus as a nutrient sink is determined by the amount of P and N that is immobilized throughout organic matter decomposition and sediment accumulation.

The effectiveness of wetland macrophytes in long-term nutrient retention from surface water appears to be limited and to vary from one ecosystem to another. Dying plant biomass releases most of the P and N that it assimilated during growth. Decomposing plant detritus appears to accumulate these elements in some wetlands but release them in others. There is also little information concerning the capacity of macrophyte detritus to retain larger quantities of P and N as man-induced inputs of these elements increase.

This study presents a budget for nutrient retention through macrophyte growth, death and two-years decomposition along a gradient of surface water nutrient concentrations in the Florida Everglades. Net nutrient gains and losses are quantified in the process whereby sawgrass and cattail leaf production leads to detritus accumulation and nutrient retention. Sawgrass (Cladium jamaicense) and cattail (Typha domingensis) leaf production values (Davis 1989) are combined with tissue P and N concentrations to estimate (1) annual allocation to growing leaves, (2) annual retention in standing dead leaves, and (3) how these processes change along the nutrient gradient. The P and N content of sawgrass and cattail leaf detritus is followed from the time the leaves die through two years of decomposition in order to (1) examine effects of surface water nutrient concentrations on detritus decomposition rate, (2) determine if leaf detritus releases or accumulates P and N during decomposition, (3) estimate rates of uptake or release, and (4) examine effects of surface water nutrient concentrations on these rates. These results are utilized to evaluate the effectiveness of Everglades sawgrass and cattail in intercepting P and N as surface water concentrations increase.

Both aboveground and belowground plant production contribute to nutrient immobilization in organic detritus in wetlands (Richardson and Marshall, 1986). In the Florida Everglades, however, Toth (1987, 1988) demonstrated that individual sawgrass and cattail plants accumulated and held P and N primarily through leaf production and aboveground detrital accumulation. Long-term nutrient retention by these species through growth and decomposition of belowground organs amounted to less than a quarter of the retention associated with leaf production and decomposition. Sawgrass and cattail thus appear to sequester nutrients primarily through aboveground production and accumulation of leaf litter in the Everglades.

STUDY AREA

The Everglades (Fig. 1) represent a wetland ecosystem which historically received small external nutrient inputs, but which has received increased nutrient supplies for nearly 30 years as a result of water management practices. This subtropical, freshwater peatland historically occupied a ≥900,000 ha basin which received water and nutrients mostly from direct rainfall (Davis, 1943; Parker, 1974). As a result, nutrients probably were in short supply (Steward and Ornes, 1975). The Everglades are presently contained within 500,000 ha of Water Conservation Areas and Everglades National Park. Nutrient supply into the Water Conservation Areas has increased due to the pumping of agricultural runoff from drained lands to the north. Vegetation change has accompanied the increased nutrient inputs in the Everglades. Vast, nearly monospecific stands of sawgrass cover ~65-70% of the Everglades marsh (Loveless, 1959). The dominance of this large sedge in the Everglades has been attributed to its low nutrient requirements (Steward and Ornes, 1975). Since nutrient supply has increased, cattail has invaded areas where agricultural inflows enter the marsh (Davis, 1989).

The middle of the Water Conservation Areas, designated Water Conservation Area 2A in Figure 1, receives particularly large inflows of agricultural water and nutrients because of a convergence of canal systems upon the inflow gates at the north end of the area. A nearly monospecific cattail stand covers 2400 ha below the inflows in Water Conservation Area 2A (Davis, 1989). Scattered cattail have also been observed to permeate the sawgrass marsh to the south of this stand during the past decade.

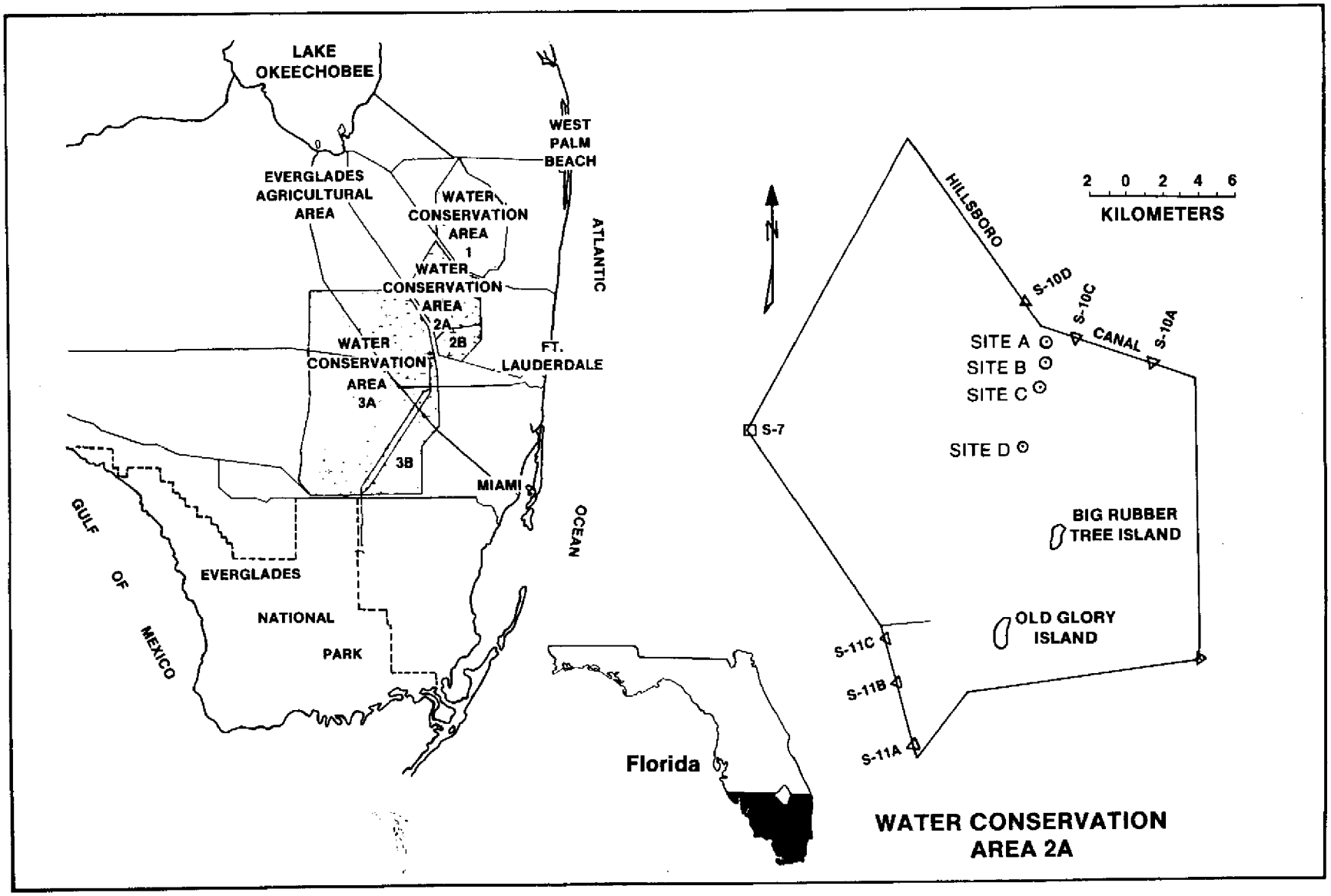


FIGURE 1. Location of Florida Everglades, Water Conservation Area 2A, and vegetation sample sites.

Nutrient concentrations drop as inflow water flows southward across the marsh, creating a gradient from high P and N concentrations near the inflow structures to values approaching detection limits in the interior marsh (Table 1). Declining soluble reactive phosphorus (SRP), and nitrate (NO_3-N) concentrations account for most of the drops in total P and total N along the gradient. It is possible that the southward decline in NO_3 along the gradient resulted partly from denitrification, rather than biological uptake; however, Gordon et al. (1986) reported low denitrification rates for peat sediments in the Everglades. Considerable temporal variation in nutrient concentrations, as evidenced by the wide ranges in Table 1, result partly from pulses of water and nutrient inflows into Water Conservation Area 2A each year. The P and N gradient is further characterized by strong year to year fluctuations in surface water nutrient concentrations, depending upon annual variations in rainfall, agricultural runoff, and discharges into the marsh. Surface water nutrient inputs appear to have raised soil P concentrations, but not N concentrations, in the vicinity of inflow structure S-10D (Davis, 1989). It is likely that soil water rather than surface water provides the major source of P and N nutrition for plants, but it can also be argued that surface water nutrients are the main source of enrichment for both soil and plants. Surface water concentrations are used as an indicator, but not a measure, of nutrient enrichment at sites along the gradient. The marsh typically remained flooded year-round due to a prescribed water regulation schedule for the area, as was the case throughout this study (Davis, 1989).

METHODS

Leaf Biomass Turnover and Nutrient Flux

Leaf production and nutrient flux in sawgrass and cattail were estimated at 4 sites along the nutrient gradient in Water Conservation Area 2A (Fig. 1). These sites were located on a line extending roughly S-SW into the marsh, at distances of 0.8, 1.6, 3.2, and 6.4 km from the N levee. Estimates were made for two sampling years. Sites B, C, and D were sampled April 1975-April 1976, while Sites A, B, and D were sampled during April 1979-April 1980. This combination of three sites per year during two sampling years yielded six estimates of leaf production and nutrient accumulation for each plant species.

Methods for estimating annual leaf production were detailed by Davis (1989). Two sampling techniques were employed. The first technique involved quadrat sampling to determine mean annual live leaf biomass. Five replicate 0.5 m^2 quadrats were collected monthly from sawgrass and cattail stands during the first sampling year. Sampling frequency was reduced to bimonthly during the second year, except at Site A where samples were collected monthly. Living leaves within quadrats were weighed after oven-drying for 72h at 90°C. The second sampling technique estimated annual leaf turnover rate. At least 5 newly emerged sawgrass and cattail plants were tagged at each site during each vegetation sampling year. Leaf lengths of each plant were measured monthly throughout the plants' life spans. Cumulative lifetime leaf growth of each tagged plant was divided by years longevity to estimate annual growth. Annual growth of each plant was divided by mean leaf biomass during its life span to calculate an annual turnover rate of leaf biomass. The mean leaf turnover rate for each stand was multiplied by mean annual leaf biomass, as determined by quadrat sampling, to estimate annual leaf production.

Nutrient accumulation and release by growing and dying leaf biomass were estimated by combining annual production estimates with tissue P and N concentrations. Living leaves collected in biomass samples were analyzed for tissue P and N concentration. Intact standing dead leaves attached to living plants were also collected from quadrats for nutrient analysis, although biomass was not measured. Annual nutrient accumulation by growing leaves was estimated by multiplying annual leaf production by mean annual tissue P and N concentrations in living leaves. Annual nutrient retention in dead leaves was estimated by multiplying annual leaf production by mean annual tissue P and N concentrations in freshly dead leaf material. Annual nutrient loss from dying leaves (amounts translocated or leached) was calculated as accumulation during growth minus retention in dead leaves.

TABLE 1. Gradients of Surface Water P and N Concentrations (mg/L) during 1976 through 1980. Values Represent Annual Means and Ranges. N = 65.

	TOTAL P	SRP	TOTAL N	NO_3-N	NH_4-N
Inflows S-100	.097(.018-.564)	.062(.002-.468)	4.35(1.40-12.78)	1.038(.004-8.059)	.034(0.01-1.02)
Site A*	.109(.016-.490)	.065(.002-.391)	4.25(1.24-7.42)	.034(.004-.408)	0.23(0.01-1.49)
Site B	.076(.014-.229)	.031(.002-.167)	3.58(1.06-9.62)	.014(.004-.028)	0.26(0.01-6.66)
Site C	.024(.008-.067)	.005(.002-.033)	3.37(1.44-7.49)	.012(.004-.154)	0.03(0.01-0.17)
Site D	.008(.002-.038)	.003(.002-.014)	2.89(1.13-5.19)	.009(.004-.158)	0.05(0.01-1.14)

*SITE A values represent only 1979 and 1980. N = 26.

Leaf Decomposition and Nutrient Flux

Litterbag experiments were initiated in July 1977, October 1977, and February 1979 at locations of previous production studies. Experiments that began in July and October 1977 compared sites B, C, and D, while 1979 experiments compared sites A, B, and D. This yielded 9 combinations of sites and sampling periods.

Intact standing dead leaves were collected from living sawgrass and cattail plants at each site the month before litterbags were placed in the marsh. Leaves were cut into 10 cm lengths and oven dried at 45°C for 96 h. Litterbags were constructed from 30x30 cm squares of fiberglass window screening (6 meshes/cm) which were loosely folded to contain the leaf material while allowing entry of macroinvertebrates into the bags. Each bag contained 5 g dry mass of dead leaf material. Litterbags were placed in the water in the sawgrass and cattail stands where the dead leaf material had been collected. The bags floated for the first few days until the litter became water logged, after which they gradually sank to the bottom and became incorporated into the litter layer. Three to four replicate bags from each setout were retrieved after one month, one year, two years, and varying periods in between.

Litter remaining in retrieved bags was dried at 90°C for 48 h plus 45°C for 24 h, weighed, and analyzed for tissue P and N concentrations. Nutrient contents of retrieved litter were calculated by multiplying dry mass by P and N tissue concentrations.

Leaf Tissue Nutrient Analysis

Leaf material from quadrat samples and retrieved litterbags was ground in a Wiley mill after weighing. Analyses for P and N were made using a Technicon Autoanalyzer II, after solubilization of P by lithium metaborate fusion (Medlin et al., 1969) and Kjeldahl digestion of N using a block digester. For quality control, National Bureau of Standards (NBS) 1571 was used as an external reference standard for each set of nutrient analyses. Analyses were accepted if values for standard were ± 10% of NBS values.

Water Sampling and Nutrient Analyses

Water samples were collected and water depths were measured at sawgrass and cattail sites monthly throughout the study. Samples for analysis of dissolved nutrient fractions were filtered through 0.45 micron Nucleopore filters. Samples for total P analysis were digested by autoclaving at 121°C (15 PSI) using the persulfate procedure. Samples for total N analysis were digested by the Kjeldahl procedure. Analyses were made using a Technicon Auto Analyzer II according to procedures SM424G for total PO_4 and SRP (APHA, 1980), SM418F for NO_3-N (APHA, 1980), SM417G for NH_4-N (APHA, 1980), and EPA351.2 for total Kjeldahl nitrogen (EPA, 1979). Total PO_4 and SRP are reported in mg/L as P. Analyses for SRP and NO_3-N were conducted throughout the study, while analyses for total P, total N, and NH_4-N began in mid-1976.

RESULTS

Leaf Biomass Turnover and Nutrient Flux

Surface water SRP and NO_3-N concentrations (Table 2) are used to examine vegetation response to the nutrient gradient because these parameters were measured throughout both vegetation sampling years. SRP represents the major phosphorus fraction that plants assimilate, while NO_3-N represents one of the two major nitrogen fractions, along with NH_4-N, assimilated by plants. Although concentrations tended to decrease southward along the nutrient gradient, year-to-year variation caused deviations from the long-term means presented in Table 1. Mean SRP and NO_3-N concentrations at nutrient-enriched Site B were elevated during the second sampling year in comparison to the first. These differences corresponded to higher water and nutrient influx through inflow structure S-10D during the second year. Inflows of 106,477 acre feet (131.286×10^6 m^3) during the first year contained mean concentrations of .028 mg/L SRP and .800 mg/L NO_3-N, while inflows of 169,957 acre feet (209.557×10^6 m^3) during the second year contained .062 mg/L SRP and 1.083 mg/L NO_3-N. Another deviation from long-term means occurred at transitional Site C, where unusually high NO_3-N concentrations averaged

.025 mg/L during the first sampling year. The reason for high NO_3-N values from this site is not readily apparent, but elevated concentrations were the norm there throughout the first year. Nutrient gradients in combination with yearly variations yielded mean annual SRP concentrations of .002-.036 mg/L and NO_3-N concentrations of .005-.050 mg/L for the six combinations of vegetation sites and sampling years.

TABLE 2. Soluble Reactive Phosphorus and Nitrate Concentrations in Surface Water during Years of Vegetation Biomass Sampling. Values Represent Annual Means and Ranges. N = 13.

Sites and Sampling Years	SRP	NO_3-N
A 79-80	.027(.002-.076)	.050(.004-.408)
B 75-76	.006(.002-.050)	.012(.004-.068)
B 79-80	.036(.002-.153)	.030(.004-.228)
C 75-76	.004(.002-.022)	.025(.004-.154)
C 79-80	.007(.002-.028)	.005(.004-.008)
D 75-76	.002(.002-.011)	.010(.004-.054)
D 79-80	.003(.002-.014)	.005(.004-.010)

Tissue nutrient concentrations in sawgrass and cattail leaves reflected surface water nutrient concentrations. Phosphorus concentrations in leaf tissue of both sawgrass and cattail differed significantly ($p\alpha = 0.01$) among the six site/sampling year treatments. Mean annual tissue P concentrations in living and standing dead leaves were positively correlated with mean annual SRP concentrations in surface water ($r = 0.84$ for sawgrass live leaves, 0.93 for sawgrass dead leaves, 0.95 for cattail live leaves, and 0.86 for cattail dead leaves) (Fig. 2). Unlike phosphorus, nitrogen tissue concentrations did not differ significantly among treatments. Lack of significant differences for nitrogen may have resulted in part from the larger variability of nitrogen tissue concentrations in comparison to those of phosphorus (Fig. 2). Despite the lack of significant differences, a correlation of tissue N concentration to NO_3-N was apparent for cattail live leaves ($r = 0.95$).

Tissue nutrient concentrations were significantly higher ($p\alpha = 0.05$) in live leaves in comparison to dead leaves. Concentrations in live sawgrass leaves exceeded those in dead leaves on the average by factors of 2.4 for P and 1.6 for N (Fig. 2). Concentrations in live cattail leaves exceeded those in dead leaves by factors of 4.4 for P and 2.0 for N. The decline in tissue nutrient concentrations during leaf senescence was proportionately greater for P in comparison to N and for cattail in comparison to sawgrass. Higher nutrient concentrations in live leaves, in comparison to dead leaves, indicated substantial translocation or leaching from leaves during mortality.

Cattail accumulated higher tissue nutrient concentrations than sawgrass during leaf growth, although concentrations after mortality were similar for both species. Phosphorus and nitrogen concentrations in live leaf tissue were significantly higher ($P\alpha = 0.05$) in cattail in comparison to sawgrass. Phosphorus concentrations in live cattail leaves averaged two times those in sawgrass, while cattail N concentrations averaged 1.5 times those in sawgrass (Fig. 2). In contrast, dead leaf nutrient concentrations did not differ significantly between species. Although growing cattail leaves were more effective than those of sawgrass in concentrating nutrients, dying cattail leaves held a smaller proportion of assimilated P and N. After growth and senescence, the two species were about equally effective in retaining nutrient concentrations in dead leaf tissue.

Combining leaf tissue nutrient concentrations with annual production estimates (Davis, 1989) indicated that growing sawgrass leaves assimilated 0.22 to 1.51 $g \cdot m^{-2} \cdot yr^{-1}$ phosphorus and 4.7 to 16.6 $g \cdot m^{-2} \cdot yr^{-1}$ nitrogen, as shown by the upper sets of points in Figure 3. These points represent uptake estimates for the six combinations of sites and sampling years. Dead sawgrass leaves retained 0.07 to 0.74 $g \cdot m^{-2} \cdot yr^{-1}$ phosphorus and 2.9 to 10.8 $g \cdot m^{-2} \cdot yr^{-1}$ nitrogen, as indicated by the lower sets of points.

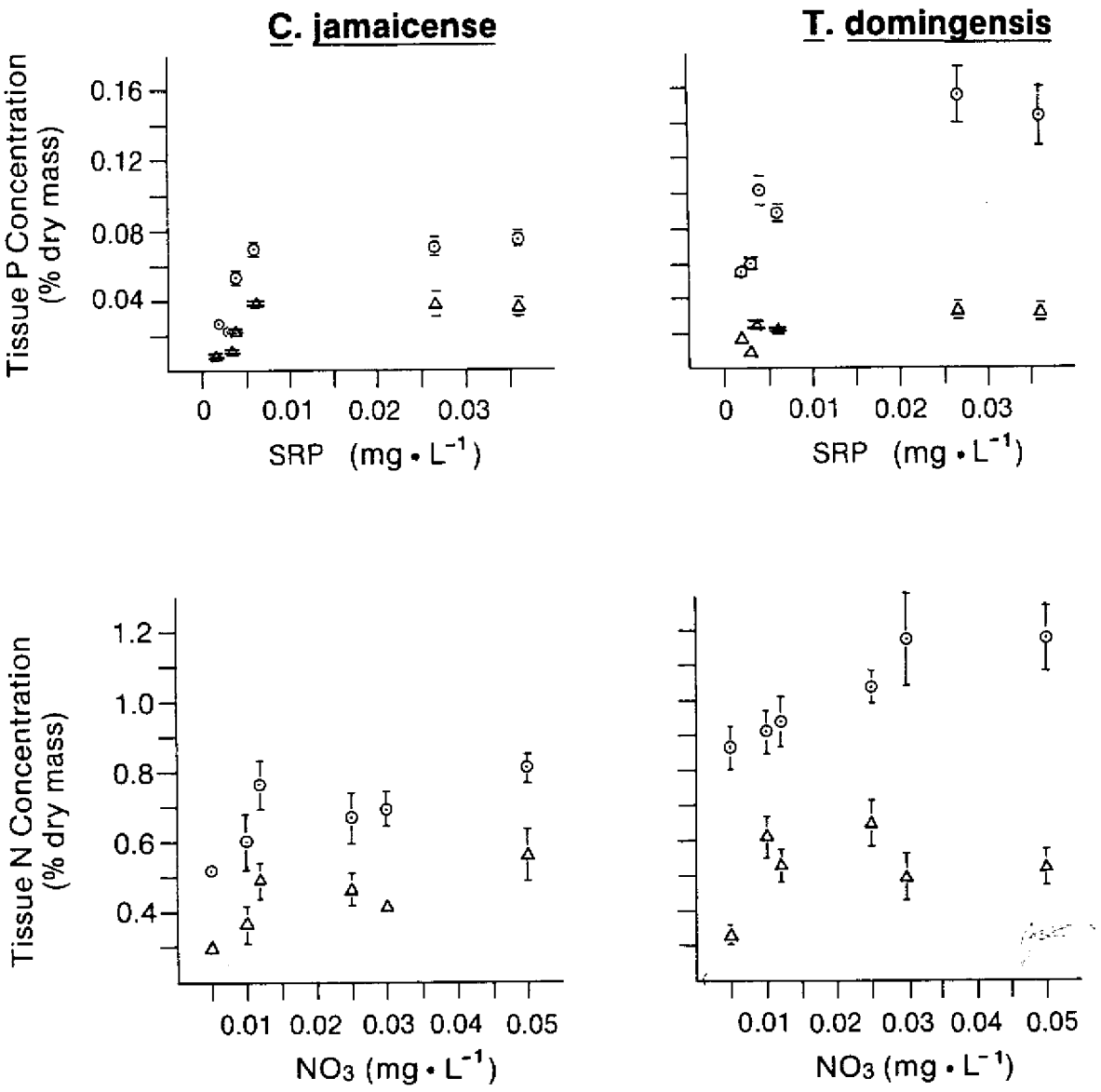


FIGURE 2. **Tissue P and N concentrations in living (O) and dead (Δ) leaves in relation to mean annual SRP and NO_3 concentrations. Values represent annual means ± standard errors.**

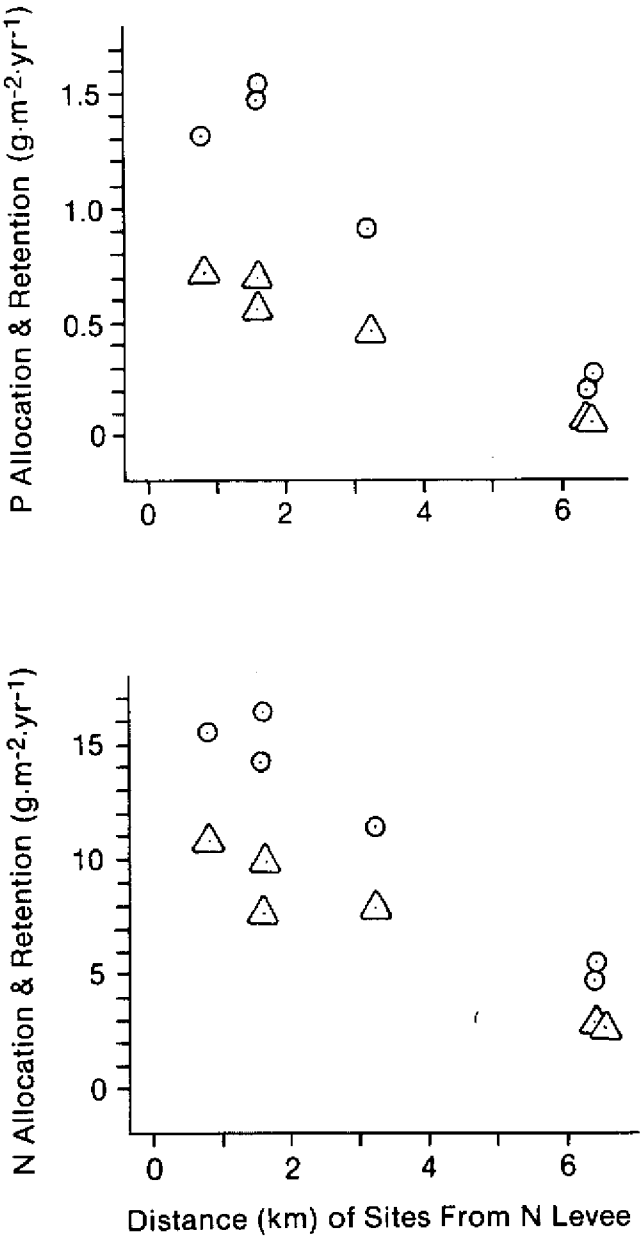


FIGURE 3. **Sawgrass nutrient allocation to growing leaves (O), and retention in dead leaves, (△), in relation to distance from the N levee in Water Conservation Area 2A.**

Differences between upper and lower points represent nutrient leaching or translocation from sawgrass leaves during mortality. Because of drops in tissue P and N concentrations during leaf death, dying sawgrass leaves lost 44-68% of the phosphorus and 31-46% of the nitrogen which they accumulated during growth.

Nutrient allocation to growing sawgrass leaves and retention in dead leaves both decreased with distance from the N levee, where inflow structures were located ($r = -0.97$ for P allocation, $r = -0.99$ for P retention, $r = -0.98$ for N allocation, $r = -0.97$ for N retention) (Fig. 3). Thus P and N uptake and retention were highest where concentrations were greatest in surface water and soil, toward the upper end of the nutrient gradient. Dying sawgrass leaves also lost larger amounts of P and N where water and soil concentrations were higher, as indicated by the widening gap between allocation and retention toward the upper end of the nutrient gradient.

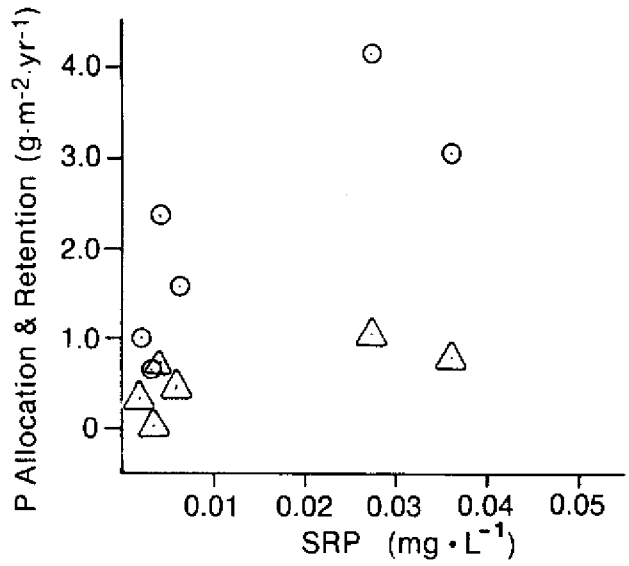
Even though nutrient accumulation by sawgrass leaves increased with surface water concentrations in terms of distance from inflows, sawgrass failed to reflect differences in NO_3-N and SRP concentrations between the two sampling years at the sites which were sampled both years. Phosphorus uptake by growing leaves and retention in dead leaves at the 1.6 km site varied little from one sampling year to the next in spite of higher SRP concentrations during the second year (Fig. 3). Sawgrass N uptake and retention at the 1.6 km site were slightly higher during the first sampling year when NO_3-N concentrations were lower. Sawgrass N flux at the 3.2 km site was not unusually high during the first sampling year although NO_3-N was unusually high there during that period. Thus nutrient flux resulting from sawgrass leaf turnover corresponded to general site characteristics of nutrient enrichment, as indicated by long term surface water nutrient gradients and soil P concentrations, but not to yearly variations in surface water concentrations.

In comparison to sawgrass, cattail assimilated larger quantities of phosphorus and nitrogen during leaf growth, translocated or leached larger quantities during leaf mortality, and retained larger quantities in dead leaves (Fig. 4). Cattail P uptake rates of 0.64 to 4.16 $g \cdot m^{-2} \cdot yr^{-1}$ averaged 2.7 times those of sawgrass, while cattail N uptake rates of 9.6 to 33.4 $g \cdot m^{-2} \cdot yr^{-1}$ averaged twice those of sawgrass. Greater nutrient uptake by cattail resulted from higher leaf turnover and production rates (Davis, 1989) as well as from higher tissue P and N concentrations (Fig. 2). Upon mortality, cattail leaves translocated or leached proportionately larger amounts of nutrients than sawgrass. Dying cattail leaves lost 71-83% of the phosphorus and 33-63% of the nitrogen which they accumulated during growth. After allocation during growth and translocation or leaching during mortality, rates of P retention in dead cattail leaves of 0.11 to 1.00 $g \cdot m^{-2} \cdot yr^{-1}$ averaged 1.6 times those of sawgrass, while cattail N retention rates of 3.6 to 15.9 $g \cdot m^{-2} \cdot yr^{-1}$ averaged 1.8 times those of sawgrass.

Cattail also differed from sawgrass in that nutrient accumulation in leaves was weakly correlated with distance of sites from inflows, but was strongly correlated with mean annual nutrient concentrations in surface water during the particular sampling years (Fig. 4). Mean annual NO_3-N concentration accounted for 98% and 85% of cattail live leaf N allocation and dead leaf retention, respectively ($r=0.99$ and 0.92), while SRP accounted for 75-76% of P allocation and retention ($r=0.87$). The gap between live leaf allocation and dead leaf retention widened as SRP and NO_3-N concentrations increased, indicating that dying cattail leaves leached or translocated larger quantities of P and N when surface water concentrations were higher. Cattail resembled sawgrass in that both species responded to higher surface nutrient concentrations by increasing rates of allocation by growing leaves, release from dying leaves, and retention in dead leaves. But only cattail responded to yearly variations in surface water concentrations.

Leaf Decomposition and Nutrient Flux

Leaf decomposition was evaluated in relation to surface water concentrations of total P, SRP, total N, NO_3-N and NH_4-N since the full range of those parameters was measured throughout litterbag setouts (Table 3). Mean concentrations during each two-year setout indicated total P, SRP, NO_3-N and NH_4-N enrichment at sites A and B in comparison to



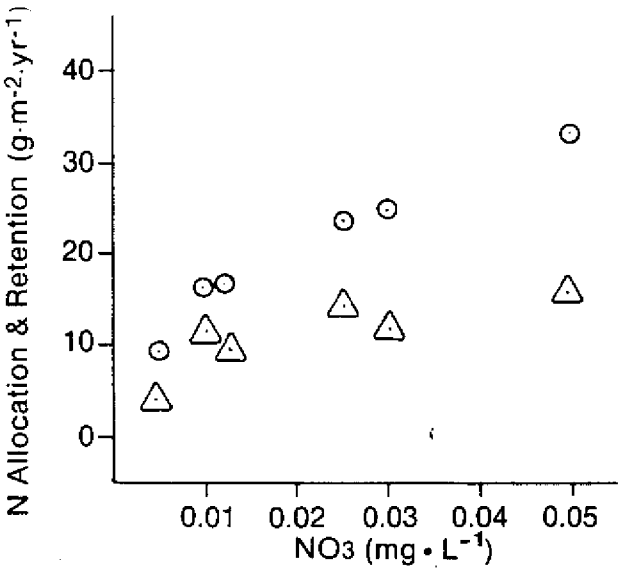


FIGURE 4. **Cattail nutrient allocation to growing leaves (O), and retention in dead leaves (△), in relation to mean annual surface water SRP and NO_3 concentration.**

TABLE 3. **Surface water P and N Concentrations (mg/L) during Litterbag Experiments. Values Represent Means and Ranges for each Two Year Decomposition Period. N = 26.**

Sites and Starting Dates	Total P	SRP	TOTAL N	NO_3-N	NH_4-N
A Feb 79	.116(.016-.490)	.066(.002-.391)	4.60(1.24-8.05)	.031(.004-.408)	0.31(0.01-2.98)
B Jul 77	.073(.014-.187)	.029(.002-.153)	3.26(1.44-9.62)	.007(.004-.020)	0.32(0.01-6.66)
B Oct 77	.071(.014-.187)	.029(.002-.153)	3.28(1.06-9.62)	.019(.004-.228)	0.32(0.01-6.66)
B Feb 79	.096(.017-.299)	.054(.002-.167)	4.72(1.06-9.62)	.019(.004-.228)	0.58(0.01-6.66)
C Jul 77	.022(.008-.052)	.003(.002-.024)	3.08(1.44-6.24)	.005(.004-.008)	0.02(0.01-0.09)
C Oct 77	.026(.008-.067)	.004(.002-.028)	3.22(1.44-6.24)	.006(.004-.008)	0.03(0.01-0.10)
D Jul 77	.006(.002-.016)	.003(.002-.014)	2.67(1.88-4.40)	.006(.004-.010)	0.02(0.01-0.07)
D Oct 77	.006(.002-.016)	.002(.002-.014)	2.57(1.13-4.40)	.006(.004-.010)	0.02(0.01-0.09)
D Feb 79	.008(.002-.020)	.003(.002-.017)	3.50(1.13-5.56)	.008(.004-.041)	0.11(0.01-1.26)

background conditions at site D. Intermediate total P concentrations at Site C indicated that this site represented a transitional situation between enriched and background conditions. Sample sites were less distinguishable based on total N concentrations that showed considerable overlap between sites. In comparison to 1977-79 litterbag setouts, 1979-81 litterbags were subjected to higher surface concentrations of most nutrient parameters at nutrient-enriched site B. Higher water and nutrient inputs through inflow structure S-10D beginning in 1979, as described previously, raised surface water concentrations during the 1979-81 litterbag experiments. Nutrient gradients in combination with yearly variations yielded mean concentrations of .006 to .116 mg/L total P, .002 to .066 mg/L SRP, 2.57 to 4.72 mg/L total N, .006 to .031 mg/L NO_3-N, and 0.02 to 0.58 mg/L NH_4-N during the nine litterbag setouts.

Patterns of litter decomposition and nutrient flux, as illustrated for July 1977 litterbag setouts, were similar for all experiments. Leaf mass loss over two years of decomposition is plotted for July 1977 litterbag setouts in Figure 5 and is summarized for all litterbag setouts in Table 4. Approximately half of the litter mass remained intact in the bags after two years for sites and species combined. Elevated surface water P concentrations resulted in accelerated decomposition rates of both sawgrass and cattail, as evidenced by the smaller litter mass remaining in bags at enriched sites relative to transitional and background sites. Cattail decomposed more rapidly than sawgrass at each site.

Phosphorus concentrations in decomposing litter increased over two years at enriched and transitional sites (Fig. 6). Increases in litter P concentration were higher at enriched sites in comparison to transitional, and in cattail in comparison to sawgrass. In contrast, litter P concentrations at the background site changed little over two years. Increasing P concentration in decomposing litter more than compensated for decreasing litter mass and resulted in a net immobilization of P over two years at enriched and transitional sites. Litter at the background site neither gained nor lost significant amounts of P during this period. Litter accumulated more P as surface water P concentration increased toward the upper end of the nutrient gradient. Cattail litter accumulated more P than sawgrass at each site.

TABLE 4. Leaf Mass Loss during Two Years of Decomposition. Values are Expressed as Loss in mg per g of Freshly Dead Leaves. Initital Mass of Freshly Dead Leaves was 5g per Litterbag. Values Represent Means with Standard Errors in Parentheses. N = 3 for 1977 Setoutsand 4 for 1979 Setouts.

Site and Starting Date	Sawgrass	Cattail
A Feb 79	571 (12)	646 (16)
B Jul 77	537 (9)	645 (14)
B Oct 77	467 (46)	683 (15)
B Feb 79	488 (24)	648 (20)
$\bar{X}$	497	659
C Jul 77	420 (15)	538 (23)
C Oct 77	407 (25)	467 (22)
$\bar{X}$	414	502
D Jul 77	338 (13)	486 (18)
D Oct 77	520 (42)	617 (57)
D Feb 79	496 (16)	324 (15)
$\bar{X}$	451	476

Litter N concentration also increased over two years decomposition and showed most of the site and species differences that were described for P (Fig. 7). Rises in litter N concentration were greater closer to nutrient inflows, and concentrations in cattail exceeded those of sawgrass. Unlike P, however, litter N concentration increased at background site D in addition to nutrient enriched and transitional

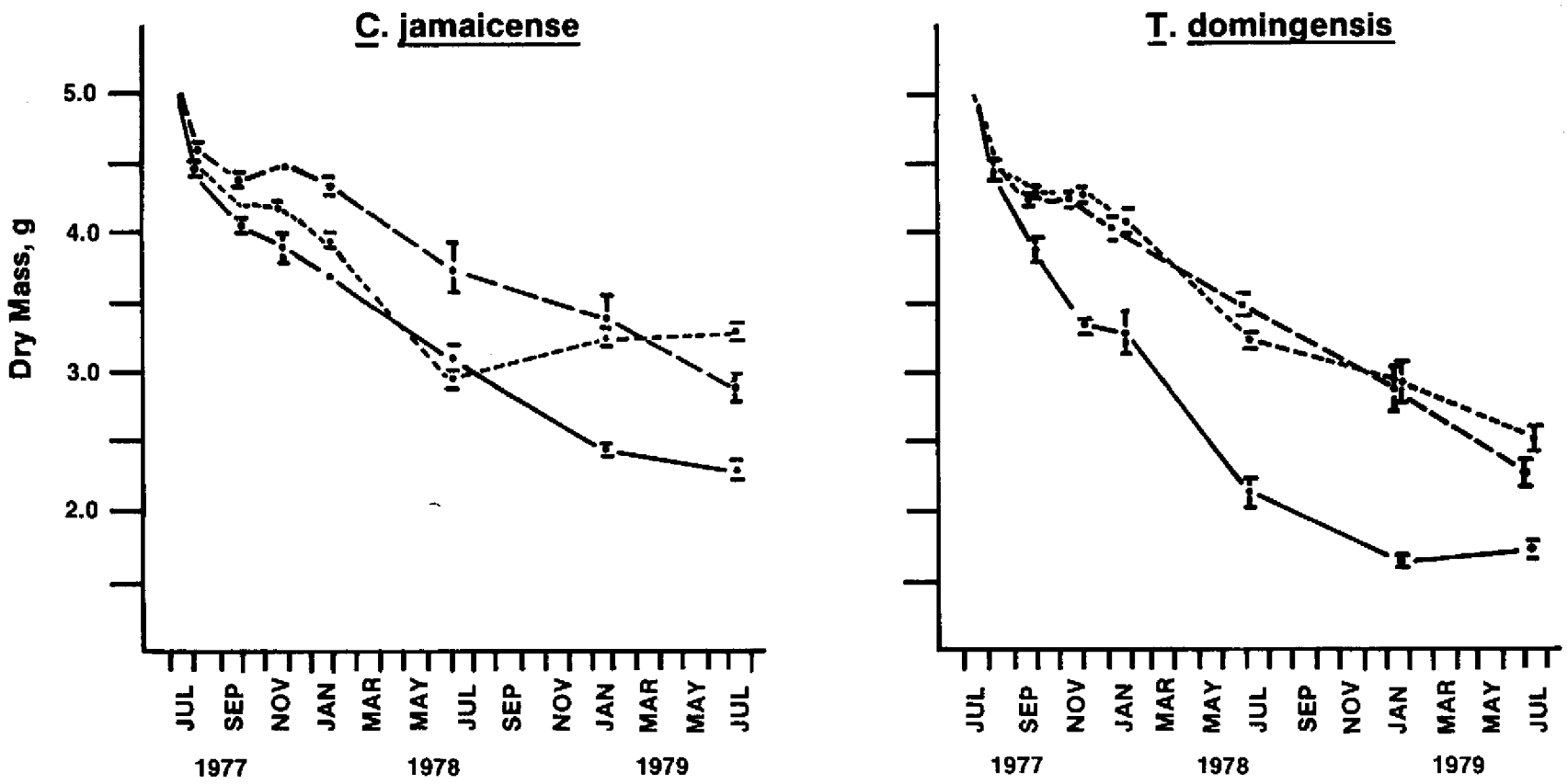


FIGURE 5. Dry mass of sawgrass and cattail leaves retrieved from litterbags during two years of decomposition. Values represent mean ± standard error N=3.

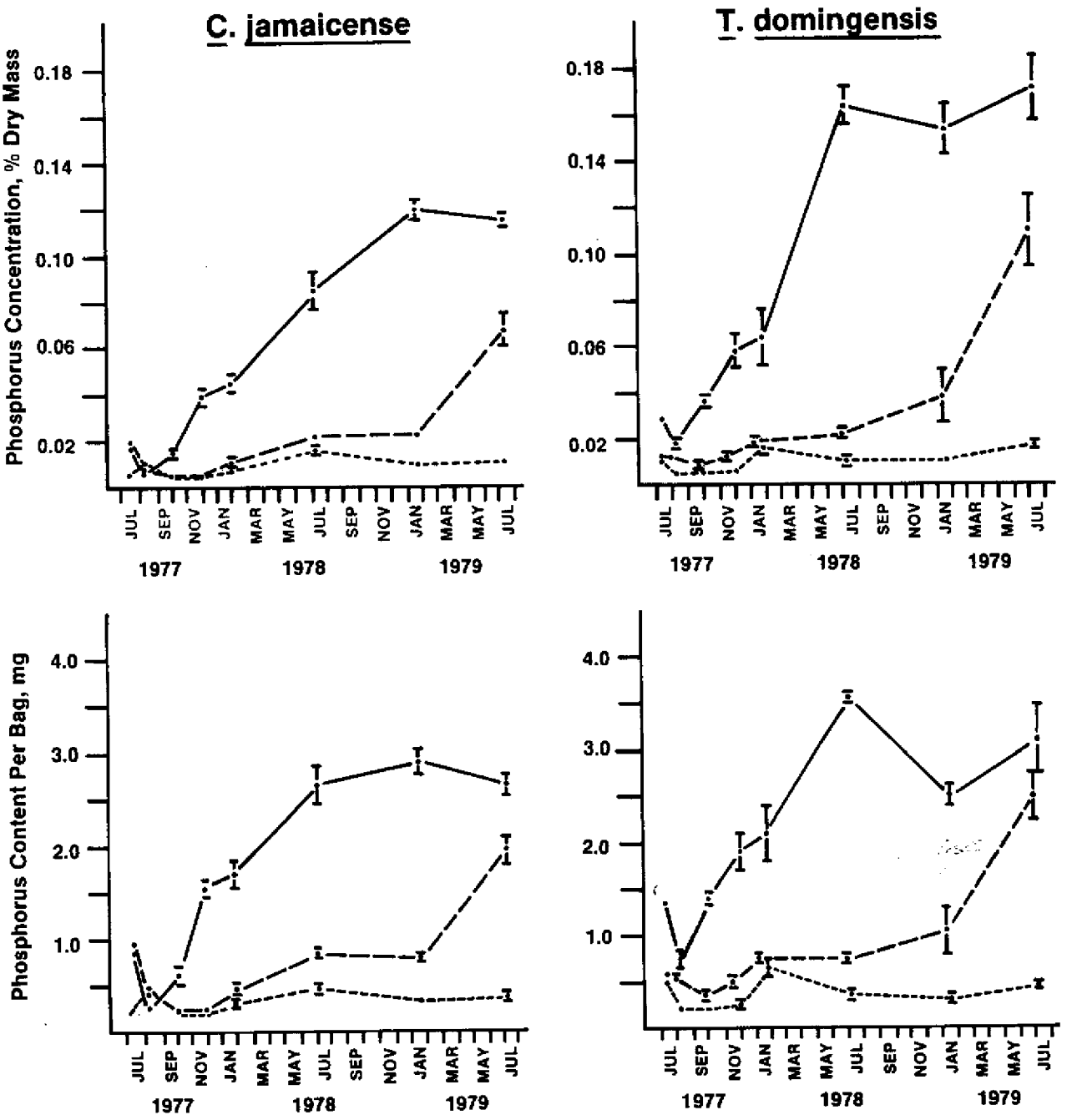


FIGURE 6. **Tissue phosphorus concentration and content in sawgrass and cattail leaves during two years of decomposition. Values represent mean ± standard error N=3.**

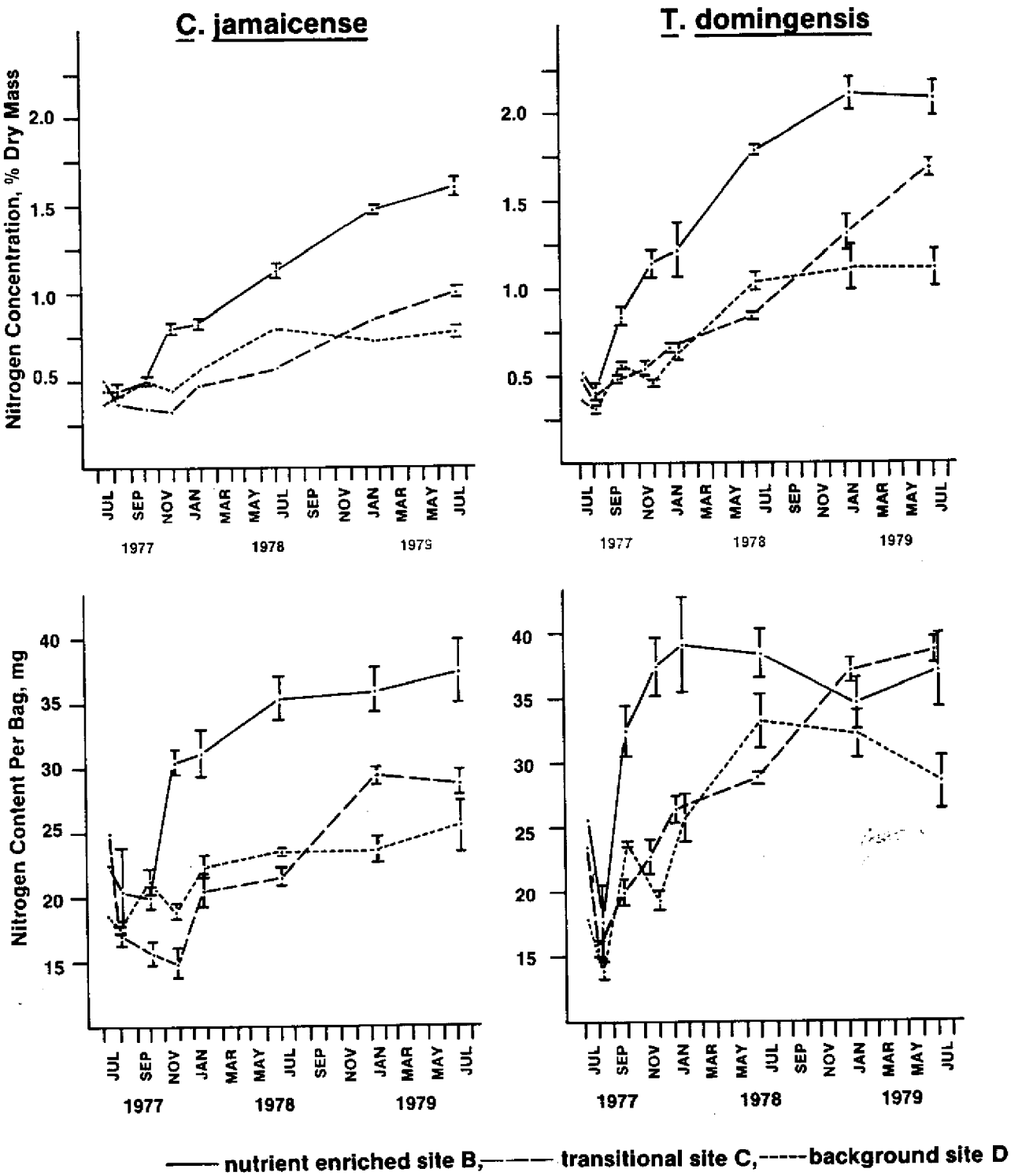


FIGURE 7. Tissue nitrogen concentration and content in sawgrass and cattail leaves during two years of decomposition. Values represent mean ± standard error N=3.

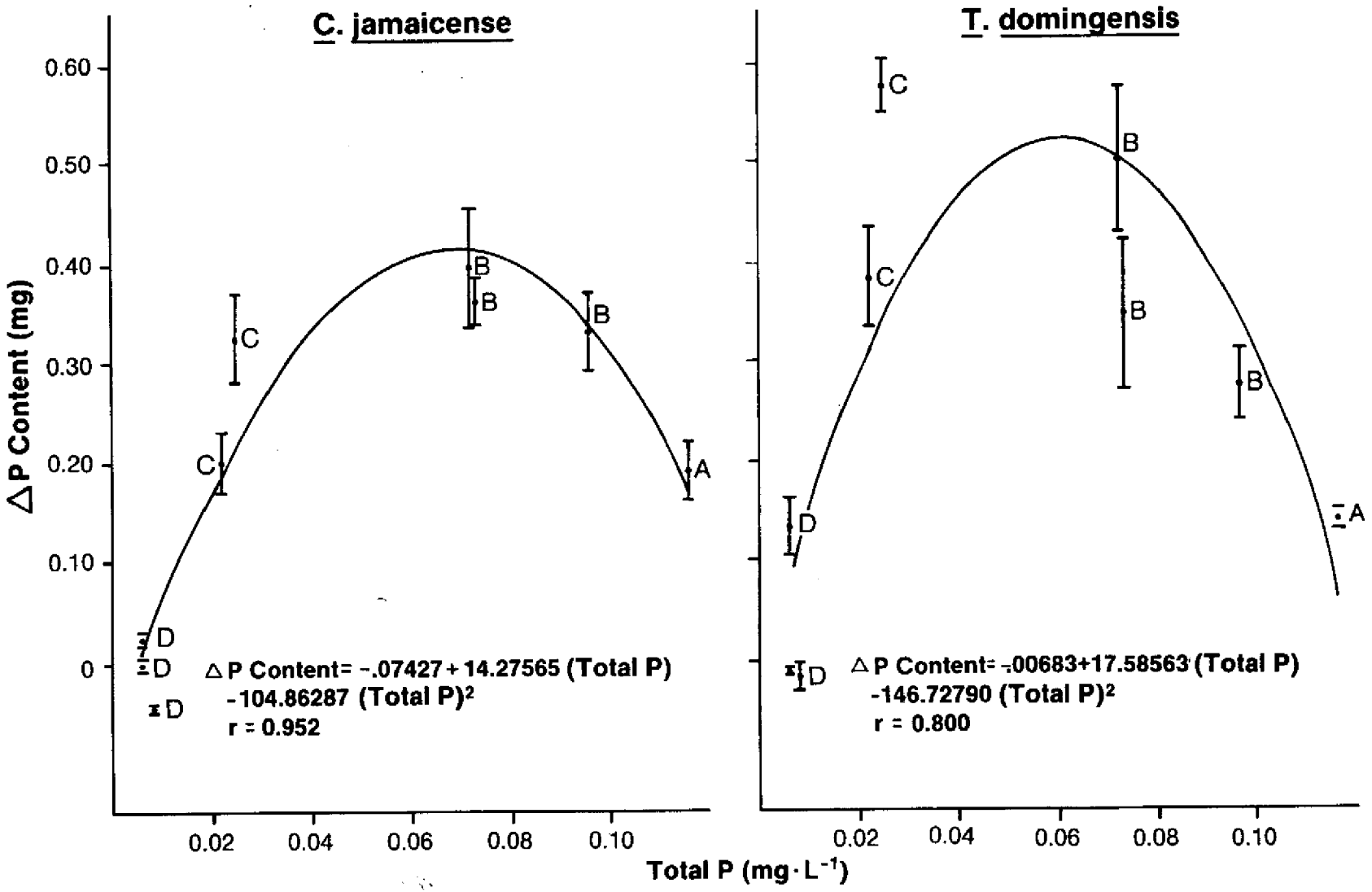


FIGURE 8. **Changes in phosphorus content of sawgrass and cattail leaves during two years decomposition in relation to mean surface water Total P concentrations. Values represent changes in mg phosphorus per g freshly dead leaf material ± standard error. N = 3 for 1977 setouts and 4 for 1979 setouts.**

TABLE 5. Net P and N Immobilization ($g \cdot m^{-2} \cdot yr^{-1}$) during Two Years of Leaf Decomposition Compared with Annual Retention in Freshly Dead Leaves.

	Site A	Site B			Site C		Site D		
	FEB 79	JUL 77	OCT 77	FEB 79	JUL 77	OCT 77	JUL 77	OCT 77	FEB 79
					PHOSPHORUS				
SAWGRASS									
Dead leaf P retention	0.74	0.59	0.59	0.68	0.45	0.45	0.07	0.07	0.10
Litter P immobilization	0.37	0.73	0.80	0.62	0.34	0.54	0.02	≤ 0.00	-0.05
Total	1.11	1.32	1.39	1.30	0.79	0.99	0.09	0.07	0.05
CATTAIL									
Dead leaf P retention	1.00	0.41	0.41	0.78	0.58	0.58	0.29	0.29	0.11
Litter P immobilization	0.42	0.61	0.89	0.66	0.86	1.34	-0.02	0.24	-0.02
Total	1.42	1.02	1.30	1.44	1.44	1.92	0.27	0.53	0.09
					NITROGEN				
SAWGRASS									
Dead leaf N retention	10.82	9.88	9.88	7.72	7.83	7.83	2.93	2.93	2.94
Litter N immobilization	6.57	6.08	5.35	6.60	.21	4.50	1.11	0.75	1.83
Total	17.39	15.96	15.23	14.32	9.04	12.33	4.04	3.68	4.77
CATTAIL									
Dead leaf N retention	15.90	9.38	9.38	12.08	14.48	14.48	10.97	10.97	3.58
Litter N immobilization	2.37	4.08	3.20	7.12	6.82	6.82	3.75	2.13	1.16
Total	18.27	13.46	12.58	19.20	21.30	21.30	14.72	13.10	4.74

sites. Increasing N concentration resulted in net accumulation of N in decomposing litter over two years at all sites. Site differences in litter N accumulation were less distinct than those for P, particularly for cattail, principally because of N uptake at the background site.

The amount of P that leaf litter accumulated during two years of decomposition was related to mean surface water TPO_4 concentration during that period (Fig. 8). Sawgrass litter accumulated increasing amounts of P as TPO_4 increased from background levels of <0.01 mg/L to intermediate levels of enrichment of $\simeq$ 0.06 mg/L. However, once TPO_4 concentrations exceeded $\simeq$ 0.06 mg/L, litter P uptake leveled off and then declined with higher levels of enrichment. An identical pattern of increasing P uptake as TPO_4 increased to $\simeq$ 0.06 mg/L, followed by declining uptake as TPO_4 further increased, was evident for cattail litter. A relationship of litter P uptake to SRP was less evident, probably because SRP concentrations during litterbag setouts approached detection limits by the time the water reached the transitional site (Table 3). Unlike P, litter N uptake was not clearly related to mean surface water N concentrations.

Leaf Turnover, Decomposition, and Nutrient Flux

Total amounts of P and N that were sequestered as a result of annual leaf growth, death and two years decomposition are estimated in Table 5 by summing annual rates of nutrient retention by dead leaves and rates of detritus nutrient immobilization. Annual crops of dead sawgrass leaves retained 0.07 to 0.74 g/m^2 P and 2.93 to 10.82 g/m^2 N, while those of cattail retained 0.11 to 1.00 g/m^2 P and 3.58 to 15.90 g/m^2 N. Subsequent nutrient accumulation by dead leaves as they decomposed over two years was calculated by multiplying annual crops of dead leaf material (Davis, 1989) by changes in P and N content per unit mass of freshly dead leaf material. Decomposing sawgrass leaves accumulated -0.05 to 0.80 g/m^2 P and 0.75 to 6.60 g/m^2 N, while those of cattail accumulated -0.02 to 1.34 g/m^2 P and 1.16 to 7.12 g/m^2 N. The sum of nutrient retention in freshly dead leaves and nutrient accumulation by decomposing leaves represents the total contribution of sawgrass and cattail leaf turnover and two years decomposition to nutrient immobilization. Total amounts of P that were sequestered annually ranged from <0.1 to 1.4 g/m^2 for sawgrass and from <0.1 to 1.9 g/m^2 for cattail. Corresponding rates of N sequestration ranged from 4 to 17 g/m^2 for sawgrass and from 5 to 21 g/m^2 for cattail. These estimates should be interpreted with caution, since surface water nutrient concentrations under which the leaves grew (during biomass sampling years) differed from concentrations under which they decomposed (during litterbag experiment years). They thus reflect only general site characteristics of nutrient enrichment rather than specific surface water nutrient concentrations during sampling years. These estimates also should be interpreted with caution since decomposition was followed only over a two-year period. Nutrient sequestration by both species tended to increase upgradient from background to transitional or enriched sites, but cattail sequestration leveled off or decline further upgradient toward the most highly enriched sites.

DISCUSSION

Leaf Biomass Turnover and Nutrient Flux

Nutrient allocation to growing leaves was greater for cattail than for sawgrass. Cattail leaves accumulated more P and N than sawgrass under equivalent conditions, and cattail was capable of allocating more nutrients to leaves during years of elevated nutrient enrichment. Cattail leaf turnover rates, being two to three times that of sawgrass (Davis, 1989), produced a faster pace of emergence of new leaves, which allowed nutrient allocation to better reflect temporal changes in surface water concentrations. Thus leaf nutrient allocation was augmented by flexibility of the vegetation to respond to temporal variation in nutrient enrichment. The ability of cattail to allocate larger quantities of P and N to growing leaves corresponded to its observed spread into sawgrass in Everglades areas receiving high-nutrient inflows. A similar intrusion of cattail (Typha latifolia) into macrophyte stands, with an eventual shift to a cattail-dominant community, was noted by Kadlec (1987) in the vicinity of effluent discharge in a Michigan wetland. Thus, with increasing nutrient enrichment, species composition shifted toward a plant that was

more effective in accumulating nutrients in leaf tissue. These findings are compatible with models of Shaver and Melillo (1984) and Richardson and Marshall (1986), which predict a vegetation shift toward macrophyte species that are more efficient in nutrient uptake as nutrient supply increases.

Contrasting responses of sawgrass and cattail to the nutrient gradient are characteristic of low-nutrient status plant species competitive in infertile habitats (sawgrass) versus high-nutrient status species competitive in fertile habitats (cattail) (Chapin, 1980; Grime, 1977). The relatively small leaf growth response of sawgrass to temporal variations in surface water nutrient inputs (Davis, 1989) is typical of low nutrient status plants. The relatively low uptake capacity of sawgrass leaves, approximately half that of cattail, under high-nutrient conditions is another trait of low nutrient status species. A lower rate of nutrient loss from senescing sawgrass leaves (via a combination of translocation and leaching) also indicates a low nutrient status species. The longer leaf longevity, lower leaf growth rate, and slower leaf turnover rate of sawgrass (Davis, 1989), plus its well developed leaf cuticle, are adaptations that reduce leaching loss in low-nutrient status plants. In comparison, cattail's larger growth response to changing nutrient availability, larger uptake capacity under high-nutrient conditions, higher rate of nutrient loss from senescing leaves, shorter leaf longevity, faster leaf growth rate, and more rapid leaf turnover are all characteristics of high nutrient status plants which tend to be competitive when nutrient supply increases. In the fertile habitat near the upper end of the nutrient gradient in Water Conservation Area 2A, relatively high rates of growth, biomass turnover and nutrient allocation may have allowed cattail to outcompete sawgrass and partially explain the observed spread of cattail into sawgrass in nutrient-enriched areas.

The effectiveness of sawgrass and cattail leaf turnover in retaining P and N remained nearly constant as surface water concentrations of these elements increased. Nutrient retention in freshly dead leaves increased with enrichment at a slower rate than did allocation by growing leaves. Elevated quantities of nutrients which were assimilated by growing leaves subjected to enrichment were mostly translocated or leached from the leaves by the time they died. As a result, dead leaves retained only slightly greater quantities of nutrients under enriched conditions in comparison to background conditions. The main effect of enrichment on leaf nutrient allocation was to accelerate translocation or leaching from dying tissue, rather than to increase retention in dead leaf material.

It could be argued that nutrients lost from dying leaves via translocation might be permanently immobilized through accumulation in belowground storage tissue. But Toth (1987, 1988) demonstrated that this was not the case for Everglades sawgrass and cattail; long-term nutrient retention through growth and mortality of belowground organs amounted to less than a quarter of the retention associated with leaf production and mortality.

Since leaf biomass turnover alone was an inefficient mechanism for trapping elevated surface water nutrient inputs, long-term nutrient retention by Everglades vegetation appeared to depend largely upon the nutrient dynamics of litter decomposition. The main role of leaf turnover in nutrient retention appeared to be the production of detritus as a substrate for subsequent physical-chemical and microbiological processes. Davis and van der Valk (1978) drew similar conclusions from temperate cattail (Typha glauca) stands.

Leaf Decomposition

The net effect of production and two years of decomposition was an accumulation of leaf detritus. The finding that approximately half of the leaf litter remained intact after two years indicates that decomposition proceeded less rapidly than production, as would be expected in a peatland. Everglades decomposition rates are comparable to the two-year litter half-life reported by Kadlec (1989) in a Michigan peatland. Nutrient enrichment appeared to influence both the annual rate of detritus accumulation and the physical structure of deposited sediments. Detritus accumulation can be estimated by combining decomposition rates from this study with production estimates of Davis (1989). The interior sawgrass marsh at site D produced $\simeq$ 894 g/m^2 of dead leaf material annually of which $\simeq$ 45% was lost during two

years decomposition and ≃ 55% remained as relatively compact, fibrous organic sediment (personal observation) on the marsh floor. In contrast, nutrient enriched areas that had converted to cattail (Sites A and B) produced ≃ 2417 g/m^2 of dead leaf material annually of which ≃ 52% was lost during two years decomposition and ≃ 48% remained as relatively fine, mush-like sediment (personal observation). As a net result of production and two years decomposition, background sawgrass deposited ≃ 492 g·m^{-2}·yr^{-1} of relatively intact and compact leaf detritus, while nutrient-enriched cattail deposited ≃ 1160 g·m^{-2}·yr^{-1} of finer more flocculent sediment.

Nutrient Retention Through Detritus Deposition

The results of this study indicate that Everglades sawgrass and cattail deposited phosphorus and nitrogen in the detritus that resulted from leaf growth, death, and two years decomposition. Sawgrass and cattail stands accumulated detritus after two years of decomposition, contributed to the accretion of organic sediment, and deposited nutrients within these sediments. Rates of nutrient storage in organic matter found in this study represent Everglades values under conditions of continuous flooding; these values may change under more dynamic hydrologic conditions. Rates of nutrient storage reported here do not include contributions by belowground biomass, which may increase rates by approximately 12 to 16 percent for sawgrass and cattail respectively (Toth, 1987 and 1988). The relevance of nutrient retention after leaf production, and two years decomposition to longer term nutrient sequestration in accreting organic sediments cannot be fully evaluated in this study. However, comparison of Everglades two-year nutrient decomposition estimates with nutrient accretion measurements in other wetlands suggests that the two parameters may be comparable.

Nutrient deposition estimates for the non-enriched Everglades site are approximately equivalent to accretion estimates for oligotrophic peatlands and backwater marshes. Mean retention rates of 0.18 g·m^{-2}·yr^{-1} phosphorus and 7.5 g·m^{-2}·yr^{-1} nitrogen at the Everglades background site (Site D, species combined) are comparable with calculated values of < 0.1-0.2 g·m^{-2}·yr^{-1} phosphorus retention and 0.1-4.7 g·m^{-2}·yr^{-1} nitrogen retention through peat accretion in northern oligotrophic wetlands (Nichols, 1983). Nutrient retention estimates at the Everglades background site are also similar to measurements of 0.5 g·m^{-2}·yr^{-1} phosphorus and 9 g·m^{-2}·yr^{-1} nitrogen retention in accreting sediments in a Louisiana backwater marsh (Hatton et al., 1982), although Louisiana sediments contained mineral matter in addition to organics. Litter breakdown has been reported to be largely complete after two years in some wetlands (Latter and Cragg, 1967; Chamie, 1976; Day, 1982). Detritus nutrient release slowed before two years in the Everglades, as evidenced by little change in litter nutrient content during the last 6 to 12 months of the two-year decomposition period. Subsequent oxidation and mineralization of detritus may have been impeded by continuous flooding and reducing conditions in the detrital layer (Reeder and Davis, 1983). Slowing of nutrient release rates in Everglades detritus before two years of decomposition may explain the similarity of nutrient retention estimates at the background site to nutrient sequestration estimates in other non-enriched wetlands. Rates of long term nutrient sequestration in accreting organic sediment in the Everglades and other oligotrophic peatlands appear to be comparable. Similar litter half-lives in the Everglades and in a Michigan peatland (Kadlec, 1989) support this interpretation.

Where surface water nutrient concentrations were higher in the Everglades, nutrient retention rates in two-year old detritus were higher, but apparently only up to a finite capacity. Rates of 1.4 g·m^{-2}·yr^{-1} phosphorus and 18 g·m^{-2}·yr^{-1} nitrogen retention by cattail at Site A may represent upper limits of nutrient retention resulting from leaf production and two years decomposition in nutrient-enriched Everglades habitat; these rates were equalled or exceeded downstream along the surface water nutrient gradient at transitional sites between Sites A and D. Higher rates of nutrient retention at enriched sites are consistent with results from other studies. The finding of higher rates of detrital nutrient retention at enriched Everglades sites, in combination with the decline in surface water P and N concentrations along the nutrient gradient below inflow structures,

agree with the conclusion of Kadlec (1989) that the litter zone in a Michigan peatland receiving secondary effluent contained a large fraction of the nutrients added over a 10-year period. Greater detrital nutrient retention at enriched Everglades sites also agrees with the review of Richardson and Nichols (1985) of loading-retention relationships in northern wetlands receiving wastewater, where P removal increased up to 4.5 $g \cdot m^{-2} \cdot yr^{-1}$ as loading increased. But a corresponding decrease in nutrient uptake efficiency (% of inputs) as loading increased (Richardson and Nichols, 1985) also suggests that wetland nutrient retention capacity may be limited, as appears to be the case for Everglades macrophytes stands. Thus rates of long-term nutrient sequestration may increase with loading, to a limited extent, in a wide variety of wetland systems. The Everglades results suggest that the capacity of this system for long-term nutrient sequestration in accumulating detritus can increase, but only up to a finite level, as anthropogenic nutrient inputs increase.

Application of Phosphorus Retention Estimates to Wetland Treatment Systems

A proposed plan to reduce surface water P inputs into the Water Conservation Areas includes the creation of flow-through wetlands utilizing cattail and other macrophyte species to retain P in accumulated detritus. The results of the present study provide preliminary estimates of P and N retention capacities of Everglades cattail marshes which may be applied and tested in the planning and operation of the wetland treatment systems. The north end of WCA2A represents an Everglades cattail stand that has received P inputs through the S-10 structures since 1962. The results of this study indicate that after two decades the area continued to work as a P sink, as evidenced by the decline in surface water P concentrations to background levels as water flowed southward across the marsh. Cattail stands subjected to highly P-enriched water at Sites A and B in WCA2A had a P retention capacity of approximately 1.4 $g.m^{-2}.yr^{-1}$ due to leaf growth, two years decomposition, and organic sediment buildup. The estimate of 1.4 $g.m^{-2}.yr^{-1}$ represented 86-88% of the total retention by cattail, the remainder being sequestered through the growth and decomposition of belowground plant parts (Toth, 1988). Combining aboveground and belowground contributions yields approximately 1.6 $g.m^{-2}.yr^{-1}$ as an estimate of the total P retention capacity of Everglades cattail under highly enriched conditions. Implicit in this estimate is the assumption that continuous flooding minimizes P loss from detritus after two years of decomposition. Given these conditions, 1.6 $g.m^{-2}.yr^{-1}$ has been recommended as a preliminary projection of treatment system P retention.

CONCLUSIONS

Sawgrass and cattail communities do function as P and N sinks in the Everglades through the process of production, mortality, two years of decomposition, and detritus accumulation. However, vegetation capacity for long-term nutrient retention as a result of these processes appears to be limited. As surface water concentrations of P and N increase along the gradient and during high-discharge years, retention of these elements by cattail increases only up to a level of moderate enrichment, as is the case between Sites B and C in this study. Upgradient, rates of long-term nutrient sequestration level off, uptake capacity is exceeded, and vegetation community change occurs. Contrasting competitive strategies of nutrient allocation by sawgrass and cattail partially explain the observed spread of cattail into sawgrass stands subjected to nutrient enrichment. Although nutrient retention capacity of cattail exceeds that of sawgrass, even cattail retention levels off upgradient. While soil absorptive processes remain unquantified, they likewise appear inadequate to sequester elevated nutrient inputs, as evidenced by deeper penetration of surface water phosphorus and nitrogen downgradient during years of higher inputs.

The concept that emerges is an Everglades sawgrass community which became established under low nutrient inputs primarily from direct rainfall, which has limited capacity to retain higher nutrient inputs, and which is replaced by more competitive species (cattail, in this case) when inputs increase. The observed progressive spread of cattail into sawgrass in nutrient-enriched areas of the Everglades apparently occurs when vegetation uptake capacity is exceeded, nutrients pass further downstream,

and cattail competitive strategies allow it to dominate sawgrass in the affected area. Wetland vegetation which developed under conditions of low nutrient supply may offer limited potential for accelerated vegetation nutrient retention, but great potential for community change when exogenous nutrient supply increases as a result of human activities.

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