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SOUTH FLORIDA WATER MANAGEMENT DISTRICT

TECHNICAL PUBLICATION 84-8

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By

STEVEN M. DAVIS

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RESOURCE PLANNING DEPARTMENT
SOUTH FLORIDA WATER MANAGEMENT DISTRICT
WEST PALM BEACH, FLORIDA

EXECUTIVE SUMMARY

A dense stand of cattail consisting primarily of Typha domingensis occupies a 2400 ha enrichment zone in WCA-2A which is subjected to high inflows of nitrogen and phosphorus enriched water, primarily from agricultural runoff, via the S-10 structures. A knowledge of the nutrient assimilation capacity of cattail and an understanding of the processes involved are important to the long term management of the water conservation areas and the protection of water quality in the remainder of the areas. The objectives of this study are to examine how cattail leaf production contributes to nutrient uptake in the enrichment zone of WCA-2A and to determine relationships among cattail production, nutrient supply, and water depth.

Cattail leaf growth patterns were determined, and annual leaf production and nutrient accumulations were estimated, at sample locations in the enrichment zone and at background locations in WCA-2A during the periods 1975-76 and 1979-80. Individual cattail plants exhibited life cycles ranging from 12-96 weeks, which were characterized by a continuum of leaf growth and mortality. Annual leaf production of cattail was estimated to be 4.8 times the mean annual standing crops of the stands.

Continual leaf turnover resulted in annual leaf productions of 1080 to 2832 g/m^2 in the cattail stands. Annual leaf production was strongly correlated with water NO_3 concentration where mean water depth exceeded 35 cm. Production appeared to be independent of water depth at these sites. Leaf production was suppressed at the most shallow site with a mean annual depth of 20 cm. The positive correlation of cattail production to NO_3 at most sites and the abnormally low production at the most shallow site suggest

that both nutrient enrichment and deeper water have augmented cattail colonization in WCA-2A.

Tissue P and N concentrations in leaves, roots, and rhizomes fluctuated seasonally with low levels during spring flowering, and high levels in fall near the end of the wet season. Mean annual tissue P concentrations were strongly correlated with OPO_4. However, tissue N concentrations were not significantly correlated with NO_3.

Annual P uptake through leaf production ranged from 0.77 to 3.65 g/m^2, while annual N uptake ranged from 11.1 to 29.3 g/m^2. Annual P uptake was strongly correlated with both NO_3 and OPO_4 concentrations in the water. Nitrate affected P uptake by influencing annual production, while OPO_4 affected P uptake by influencing P tissue concentration. Annual N uptake was correlated only with NO_3, as a result of increased production with increased NO_3.

Much of the phosphorus and nitrogen that growing cattail leaves accumulated was lost from the leaves by the time they died. Dying leaves retained only 17-28% of the annual P uptake and 37-71% of the annual N uptake. The accelerated P and N uptake by growing leaves at nutrient-enriched sites was also accompanied by a larger loss of these elements from dying leaves. The net result of leaf growth and death in nutrient enriched areas differed little from that in non-enriched areas. In conclusion, cattail leaf production in WCA-2A appears to function as a recycling mechanism more than as a sink for phosphorus and nitrogen. The annual rate of recycling is faster in nutrient-enriched areas.

Recycled nutrients possibly were leached from dying leaves back into the surface water or were translocated to belowground roots and rhizomes. The importance of roots and rhizomes as nutrient sinks would depend on the

retention of P and N in these organs after death, decomposition, and conversion to organic soil. Similarly, any value of leaf production as a nutrient sink would depend upon the retention of P and N by dead leaf material during decomposition and eventual sediment accumulation. The roles of cattail leaf detritus and belowground roots and rhizomes in Everglades nutrient cycles are subjects of future publications in this series.

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ACKNOWLEDGEMENTS

I wish to thank Linda Haunert, Michael Zaffke, Frances Worth, Dennis Cook, Suzette Green, Pamela Reeder, and Nancy Urban for major contributions during various phases of this project. I am also grateful to Morris Rosen, Ann Superchi, and other staff members of the South Florida Water Management District Chemistry Laboratory for nutrient analyses and for the perseverence which they showed in keeping up with seemingly endless sample loads.

INTRODUCTION

The water conservation area system encompasses about 350,000 ha of diked Everglades marshland in southern Florida (Figure 1). These areas are managed by the South Florida Water Management District for a variety of purposes including flood control, water storage, groundwater recharge, preservation of fish and wildlife resources, and recreational benefits. Much of the water entering the water conservation areas is runoff from agricultural lands; this water contains high phosphorus and nitrogen concentrations compared to water of the interior marshes. The 44,800 ha marsh of Water Conservation Area 2A (Figure 2) receives a particularly large supply of these nutrients through the S-10 inflow structures because of the large canal system which converges on these inflows. The absence of interior canals in Water Conservation Area 2A (WCA-2A) forces this water to flow across the marsh. Most of the P and N presently entering WCA-2A is assimilated in an enrichment zone downstream of the S-10 structures (Gleason, et al., 1974; Davis and Harris, 1978). Potential pumping of additional canal water into the water conservation areas would further increase supplies of P and N to WCA-2A; however, the ability of the marsh to store additional nutrient supplies is not known. This study is one of a series of investigations in WCA-2A to determine the effects of increased phosphorus and nitrogen supplies on sawgrass and cattail communities and their effectiveness as nutrient sinks.

A dense cattail stand consisting primarily of Typha domingensis covers approximately 2400 ha of the enrichment zone in WCA-2A. Sawgrass (Cladium jamaicense) dominates much of the remainder of WCA-2A and is broken by slough systems, occasional cattail stands, and tree islands. Although the expanse of cattail closely coincides with the area of nutrient enrichment, dominance of cattail in this area cannot be attributed entirely to increased nutrient

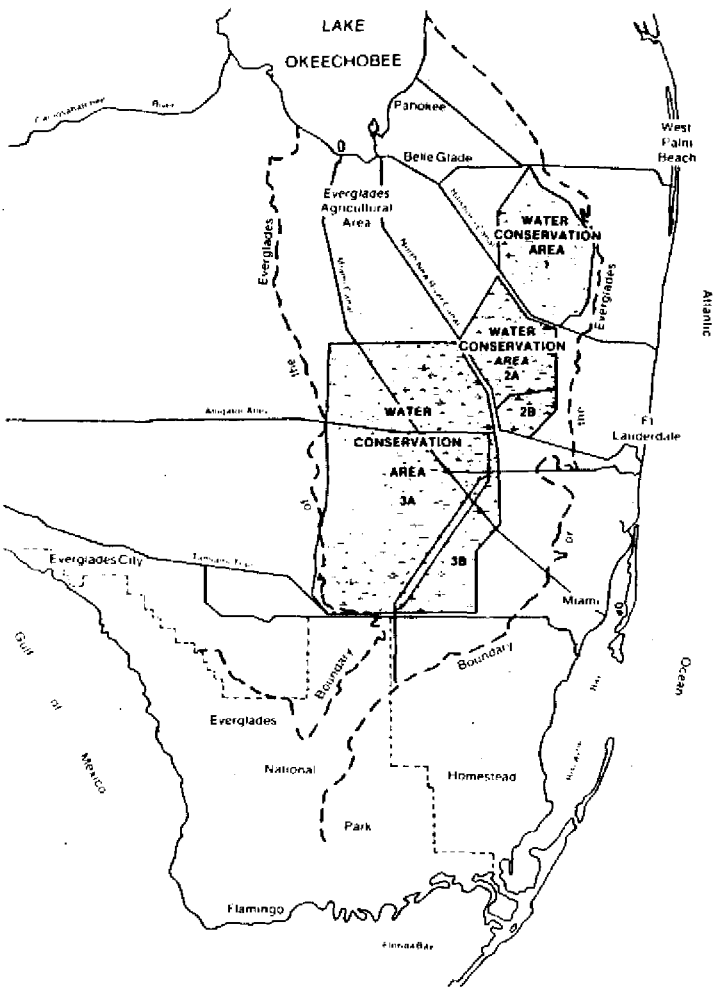


FIGURE 1 LOCATION OF EVERGLADES WATER CONSERVATION AREAS AND BOUNDARY OF ORIGINAL EVERGLADES IN SOUTH FLORIDA.

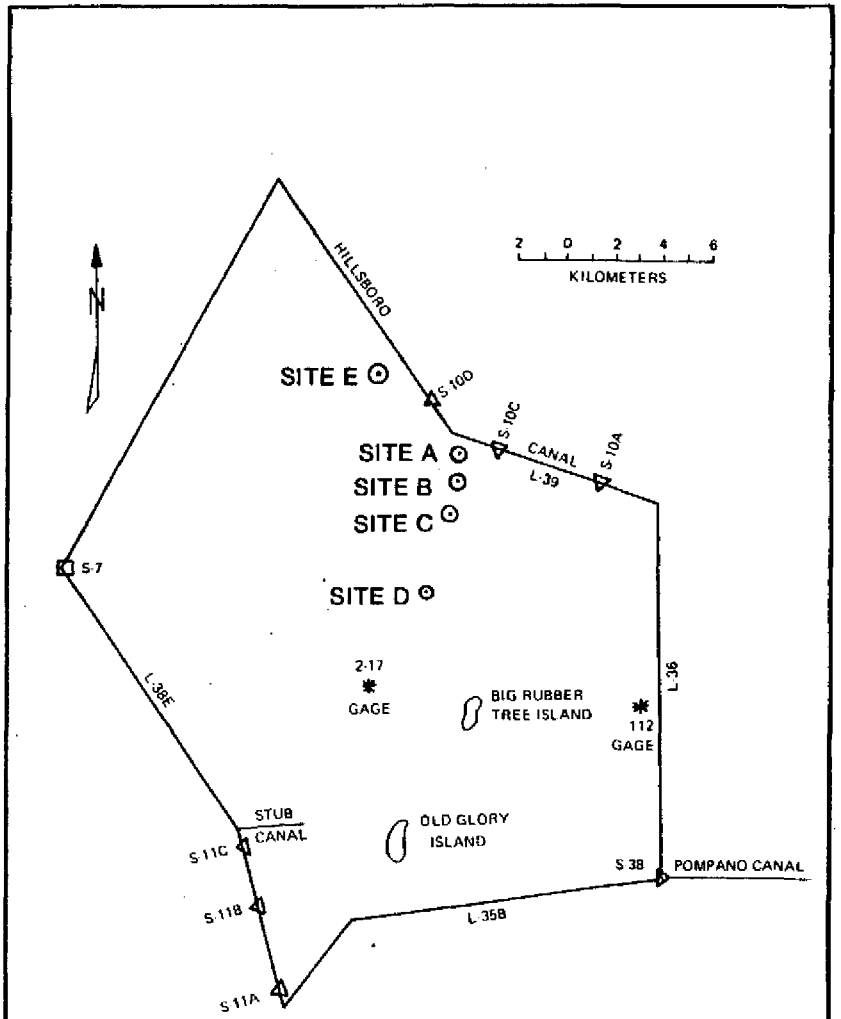


FIGURE 2 LOCATIONS OF CATTAIL SAMPLE SITES IN WATER CONSERVATION AREA 2A

supply. The drainage history of the area also must be considered. The original Hillsboro Canal along the north border of WCA-2A was dredged in 1921, well before the completion of the WCA-2A levees and S-10 structures in 1962. Shortly before completion of the water conservation areas, Loveless (1956) documented a band of willow (Salix caroliniana) along the Hillsboro Canal in the area that is now occupied by cattail. The sawgrass/wet prairie marsh to the south was dotted with tree islands. Upon completion of WCA-2A, hydroperiods were lengthened and water depths increased. Tree islands drowned, the willow band receded to a narrow margin along the north levee, and cattail invaded the former tree islands and willow band. Previous vegetation disturbance thus appears to be a common characteristic of WCA-2A cattail populations. Additional vegetation disturbance appears to be widespread, although less obvious, in areas of existing sawgrass in WCA-2A. Hofstetter (1973) observed thinning of sawgrass where water levels had been kept higher for a longer period of time. Alexander (1971) noted that cattails invaded deeper water at the expense of sawgrass and attributed this to the greater percentage of aerenchyma in cattail. The aggressive nature of cattail in invading open niches which were created by vegetation disturbance is consistent with findings of Szczepanska and Szczepanski (1973) that Typha latifolia grew more rapidly than other marsh plant species growing with it and tended to prevent immigration of other species. Relationships of cattail growth in disturbed areas to nutrient enrichment and water depth have not been clearly distinguished because elevated nutrient supplies from the S-10 structures were also accompanied by increased water depths upon completion of WCA-2A. One objective of this study is to better clarify the causes of cattail expansion in WCA-2A by determining relationships between cattail production, nutrient supply, and water depth.

Another objective is to examine how cattail leaf production contributes to nutrient uptake in the enrichment zone of WCA-2A. Although wetland vegetation can remove nutrients from polluted water (Boyd, 1970b; Steward 1970; Reddy et al., 1983), periodic plant harvesting generally has been assumed to be necessary to maintain an efficient rate of uptake. The cattail stand below the S-10 structures has never been harvested and still functions as a nutrient sink 21 years after the S-10 structures became operational. Annual phosphorus and nitrogen uptakes due to cattail leaf growth are estimated and compared with annual releases of these elements by dying leaves. Relationships between nutrient uptake, water nutrient concentrations, and water depth are examined.

Knowledge of the rate of annual plant production is prerequisite to calculating uptake and accumulation of nutrients by marsh vegetation. Marsh plant production in temperate wetlands has traditionally been estimated as the maximum standing crop during a well defined growing season (Keefe, 1972). This method is less appropriate in subtropical and tropical latitudes where growth may continue year-round. For example, Gaudet (1977) reported a continual turnover of Cyperus papyrus culms in a swamp on Lake George, Africa. A method of production estimation which appears more applicable to subtropical and tropical regions was developed by Williams and Murdock (1972). They calculated annual production of Juncus roemerianus in a North Carolina salt marsh by multiplying average standing crop by the ratio of stem growth to average stem biomass. The ratio of stem growth to average biomass was calculated as the maximum weight per stem divided by the mean weight per stem during the life span of individually tagged plants. The method used in this study to calculate annual cattail production resembles that of Williams and Murdock.

METHODS

Five sampling locations (Figure 2) were selected based on proximity to inflow structure S-10D and on previously determined nutrient concentrations in WCA-2A surface water (Gleason et al., 1974). Site locations are given as distances and compass directions from S-10D:

Site A	1.2 km	150° SSE
Site B	3.1 km	165° SSE
Site C	4.5 km	174° SSE
Site D	7.9 km	182° SSW
Site E	3.6 km	308° NNW

Sites A and B were located within the zone of nutrient enrichment adjacent to the S-10 structures. Sites D and E were outside the enrichment zone. The location of Site C was borderline between clearly nutrient-enriched and non-enriched areas. A nearly monospecific cattail stand occurred adjacent to a sawgrass stand at each site.

Water samples were collected and water depths were measured in the cattail stands at least monthly, beginning in 1975 at sites B - E, and beginning in 1979 at Site A. Water samples were analyzed by the South Florida Water Management District Water Chemistry Laboratory for phosphorus and nitrogen (dissolved inorganic, dissolved organic, and particulate). Samples for analysis of dissolved fractions were filtered through 0.45 micron Nucleopore filters. Samples for total P and total dissolved P analyses were digested by autoclaving. Samples for total N and total dissolved N analyses were digested by the Kjeldahl procedure. Concentrations of P and N were determined using a Technicon AutoAnalyzer II.

Plant biomass and tissue nutrient concentrations in each cattail stand were estimated from quadrat samples. Collections were made during two

sampling years, May 1975 - May 1976 and April 1979 - April 1980. Sites B, C, D, and E were sampled during the first year. Sites A, B, and D were sampled during the second. Collections were made at four-week intervals during the first year. Sampling was reduced to every eight weeks during the second year at Sites B and D; however, samples were collected from Site A every four weeks during that period since this site was not sampled previously. Five replicate 0.5 m^2 quadrats were collected from each cattail stand on each sampling date. Living cattail plants within the quadrats were pulled from the ground. Dead flower stalks/spikes which were still standing were also collected on each sampling date during 1975-76. Above-ground plant material from each quadrat was separated into living leaves, flower stalks and spikes. These components were weighed after oven-drying for 72 hours at 90°C prior to nutrient analyses. Roots, rhizomes, intact dead leaves, and dead flower stalks/spikes were also analyzed for nutrients, although their biomass was not estimated. Samples were ground in a Wiley Mill. Analyses for P and N were made by the South Florida Water Management District Soil Chemistry Laboratory using a Technicon AutoAnalyzer II , after solubilization of P by lithium metaborate fusion and Kjeldahl digestion of N using a block digestor. Phosphorus and nitrogen contents (g/m^2) of living leaves and flower stalks/spikes were calculated by multiplying standing crops by P and N tissue concentrations.

Newly emerged cattail plants were tagged at each site in both 1975 and 1979. The individual leaves of each plant were labelled as they emerged. Leaf lengths of each tagged plant were measured at four-week intervals. A total of 56 plants were measured. The monthly leaf measurements were continued until each tagged plant died. All tagged cattail plants died within 96 weeks.

Regressions of leaf length to dry weight were determined from individual leaves of at least 20 cattail plants at each site. Leaf length measurements were converted to leaf weights using these regressions.

Leaf growth and mortality were estimated for each tagged cattail plant. Leaf growth during each four-week interval (G interval) was calculated as the sum of weight increases of all leaves which grew during the interval. Total leaf growth during a plant's life span (G total) was calculated by adding the growths for the four-week intervals:

$$G_{total} = \Sigma\ G_{interval}$$

Annual leaf growth of a plant (G annual) over its entire life span was determined by dividing total growth by the number of four-week intervals during the life span and then multiplying by 13, since 13 four-week intervals amount to one year:

$$G_{annual} = G_{total} \div N \text{ 4-wk intervals} \times 13 \text{ intervals per yr}$$

Mean leaf weight during the life span of each tagged plant ($\bar{W}$ tagged) was calculated as the sum of total leaf weights from all measurements divided by the number of measurement dates. A growth/weight ratio which represented the entire life span of a plant was derived by dividing annual leaf growth by mean leaf weight:

$$\text{Growth/Weight Ratio} = G_{annual} / \bar{W}_{tagged}$$

Annual leaf production in a cattail stand is estimated by multiplying the mean annual standing crop of a cattail stand ($\bar{W}$ stand) by the ratio of annual leaf growth to mean leaf weight.

$$\text{Annual Stand Production} = \bar{W}_{stand} \times \frac{G_{annual}}{\bar{W}_{tagged}}$$

The growth/weight ratio is an average for the 56 individually measured plants. This is a weighted average, based on the longevity frequency distribution of the individually measured plants, because plant longevity was found to strongly affect their mean weight and annual production.

Use of the annual growth/mean weight ratio from the individually measured plants to estimate stand production requires two assumptions. The first assumption is that longevities of the individually measured plants had a frequency distribution which reflected that of the entire cattail stand. It is unlikely that leaf measurement every four weeks affected plant longevity because much care was taken not to damage leaves during measurements and because the plants appeared to receive much greater damage from high winds during storms. The second assumption is that shoot recruitment and mortality in the cattail stands were equal over the course of the year. A lack of significant standing crop differences between the beginnings and ends of two years of quadrat sampling in the cattail stands supports the assumption that recruitment and mortality were about equal. If both assumptions are valid, then the number of plants which entered the population of a cattail stand as new shoots would equal the number which died each year, and the proportions of the plants in the stand which died at ages 12, 16...96 weeks would resemble the proportions of the individually measured plants which died at these ages. Thus the individually measured plants would resemble the cattail stands in the frequency of occurrence of the various developmental stages, including shoot emergence through sensecence, of plants of varying longevity.

Annual leaf production is considered equal to annual leaf mortality in this study. Weight gains by each individual tagged plant were balanced by weight losses over the course of its life span. The similarity of leaf standing crops between the beginning and end of each sampling year provides evidence that plant density in the cattail stands remained constant. Thus

the number of new shoots which emerged appeared similar to the number of plants which died each year in the cattail stands, and growth equalled mortality in the leaf turnover by the individual cattail plants during their life spans.

Annual phosphorus and nitrogen uptakes which accompanied leaf growth are calculated by multiplying the annual growth/mean weight ratio by the mean annual P and N storages (g/m^2)in living cattail leaves at each site. Amounts of P and N which remained each year in the cattail leaves after they died are calculated as annual leaf mortality (= production, g/m^2) multiplied by the P and N tissue concentration in dead leaves. Amounts of P and N which were released annually during leaf mortality are calculated as uptake during leaf growth minus retention in the dead leaves.

Statistical analyses were conducted according to Sokal and Rohlf (1981). Analysis of variance was used to test site and date differences in the measured parameters. Least squares regressions were used to determine if site differences in water nutrient concentrations and depth were correlated with plant growth, production, nutrient content and nutrient uptake. All site differences and correlations reported in this paper were statistically significant ($p = 0.05$).

RESULTS

Hydrology and Water Quality

Water levels in WCA-2A fluctuated each year primarily from rainfall, inflows through the S-10 structures, and outflows through the S-11 structures. Rainfall patterns during the study were typical of south Florida's seasonal cycle of summer-fall rainy periods and winter-spring dry periods. Water inflows through the S-10 structures were generally higher during the wet season, although dry season discharges commonly occurred in January-April to conform with the water regulation schedule for Water Conservation Area 1. The resulting water stages at WCA-2A sample sites (Table 1) fluctuated erratically but remained above the ground surface most of the time. Water levels dropped belowground at Sites B and E during spring 1975; however, these sites were continually inundated thereafter.

Sample sites were located so that S-10D probably was their most important source of surface water nutrient supply. Mean annual nutrient concentrations at the sample sites and S-10D indicate that high concentrations in S-10D water declined to background levels typical of the interior marsh within 7.9 km from the inflow (Figures 3 and 4). The majority of phosphorus in S-10D water was ortho PO_4 (OPO_4), which also showed the largest reduction in concentration as the water flowed across the marsh. In contrast, dissolved organic PO_4 concentrations were relatively low in S-10D inflow water and showed only small decreases to the south. Nitrogen concentrations in surface water also declined from S-10D southward. Most of the N in S-10D water was dissolved organic, but this fraction showed little net change between the inflow and the most distant site. Declines in NO_x accounted for most of the decrease in N. NO_x includes both nitrate (NO_3) and nitrite (NO_2). However, NO_x actually represents nitrate in this study because

nitrite concentrations were consistently at, or below, detection limits. For this reason, NO_x is referred to as nitrate in this report. Because OPO_4 and NO_3 declined more than the other P and N fractions downstream of S-10D, these parameters are used to correlate water nutrient concentrations to cattail growth.

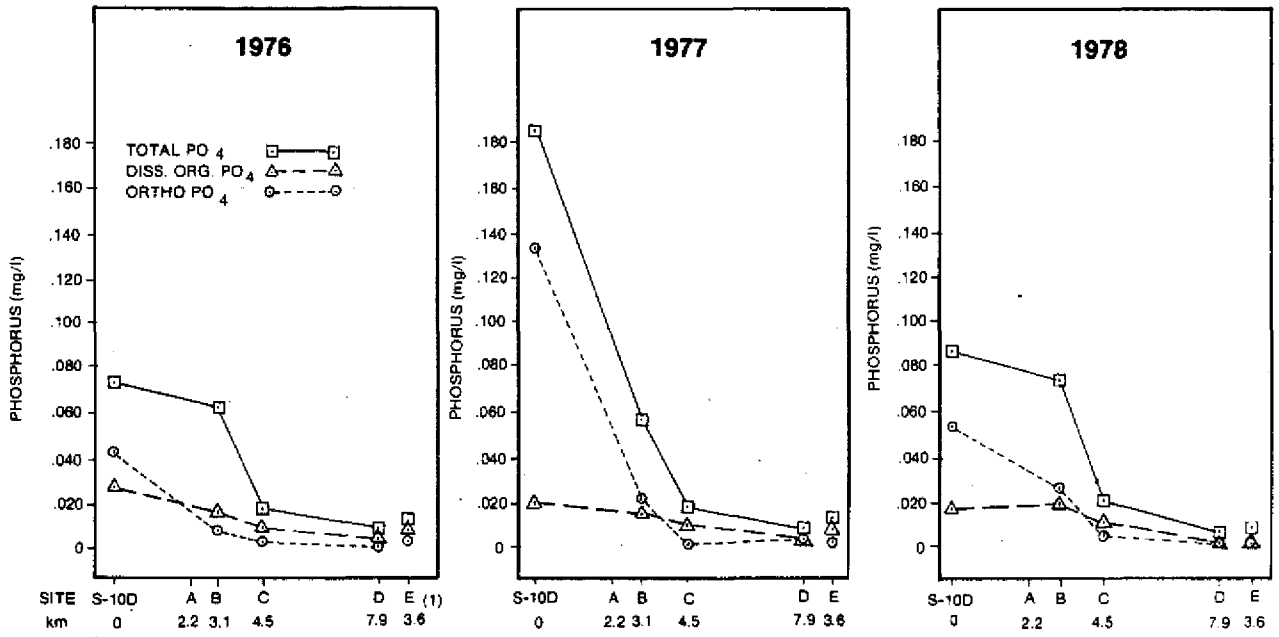
TABLE 1. MEAN ANNUAL WATER DEPTHS (CM) AND DEPTH RANGES AT WCA-2A CATTAIL SITES

	Site A	Site B	Site C	Site D	Site E
1975*	---	31 (-22-65)	53 (5-77)	71 (22-95)	18 (-23-27)
1976	---	39 (25-76)	60 (45-92)	77 (63-102)	21 (9-46)
1977	---	40 (12-61)	61 (31-81)	78 (52-100)	22 (2-47)
1978	---	51 (33-74)	72 (55-95)	88 (73-110)	31 (18-52)
1979	76 (40-118)	54 (17-100)	74 (41-100)	93 (54-124)	37 (14-59)
1980	68 (42-98)	44 (15-78)	64 (34-99)	81 (44-117)	31** (15-56)

* 1975 depth measurements began in April.

**1980 depth measurements at Site E exclude November and December.

The timing and volume of water flowing into WCA-2A through S-10D were different for the two study years (Figure 5). In 1975-76, most of the 130,000 acre-ft inflow occurred in mid-summer, while fall and winter discharges accounted for the majority of the 172,000 acre-ft inflow in 1979-80. A



(1) Due to ground elevation, Site E was outside the flow route of S-10D water and therefore was subjected to background nutrient concentrations similar to Site D.

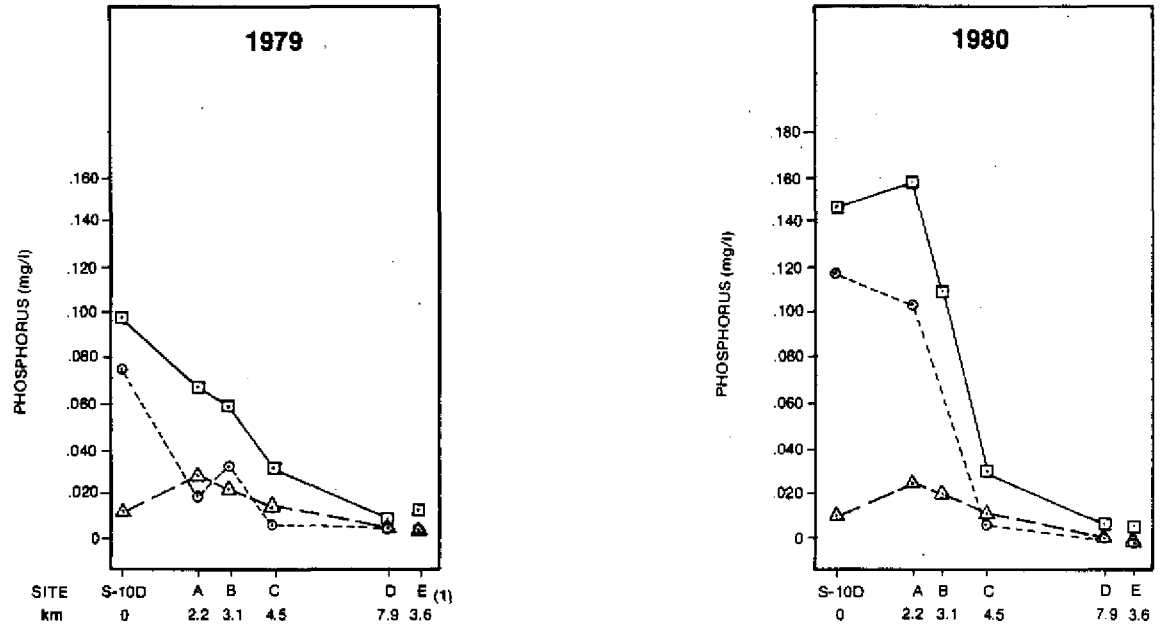
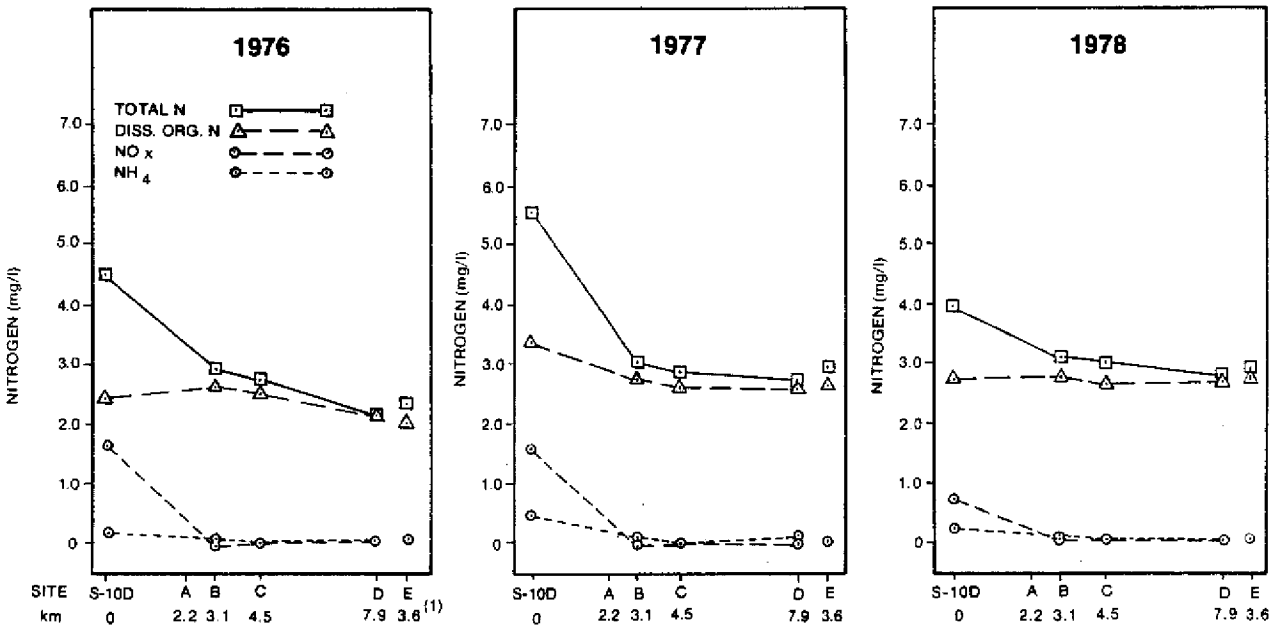


Figure 3 MEAN ANNUAL PHOSPHORUS CONCENTRATIONS (mg/l) IN SURFACE WATER IN WATER CONSERVATION AREA 2A IN RELATION TO DISTANCE (km) FROM INFLOW STRUCTURE S-10D.



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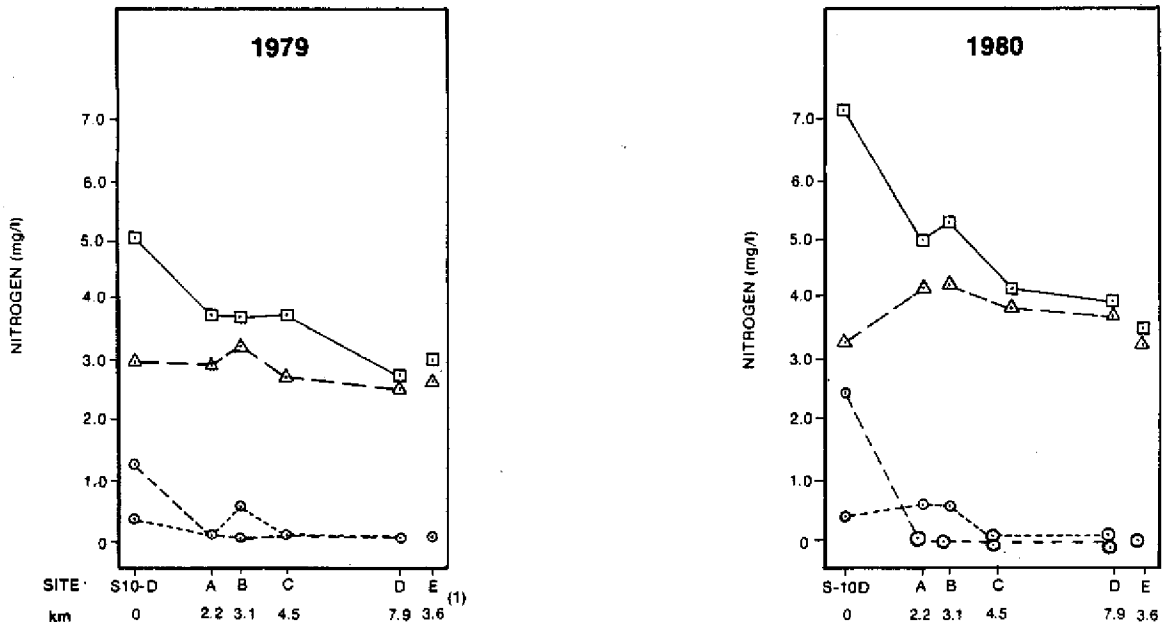


Figure 4 MEAN ANNUAL NITROGEN CONCENTRATIONS (mg/l) IN SURFACE WATER IN WATER CONSERVATION AREA 2A IN RELATION TO DISTANCE (km) FROM INFLOW STRUCTURE S-10D.

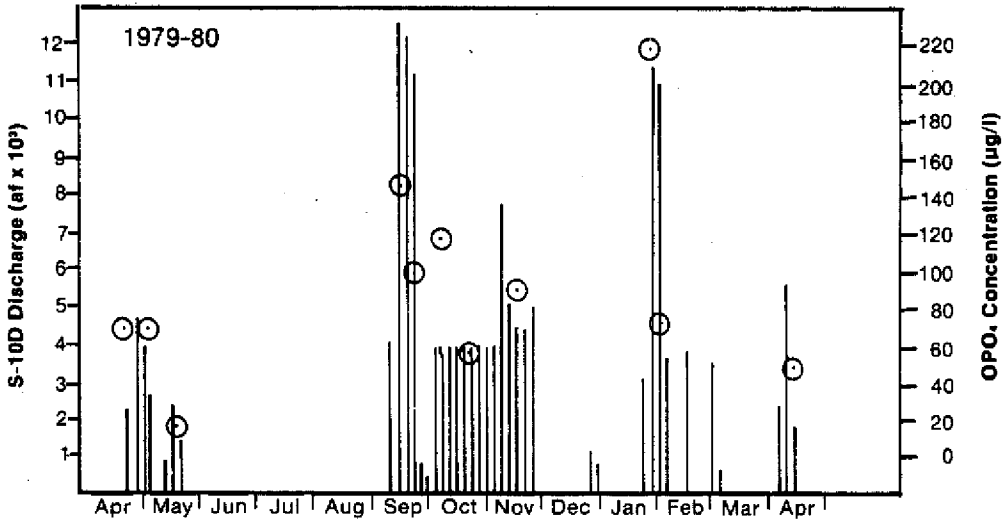
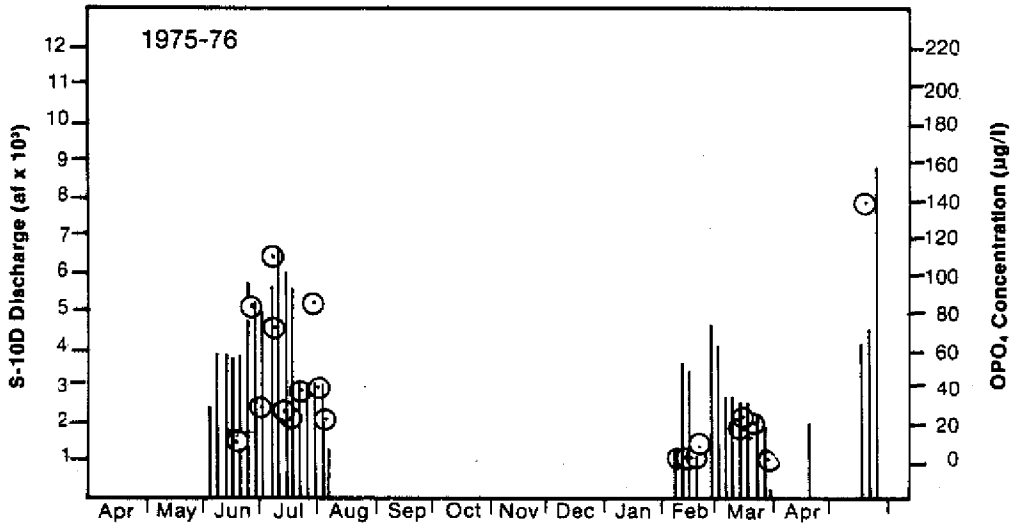


Figure 5 S-100 Discharge (bars) and OPO_4 Concentrations in S-10D Water During The Two Years of Quadrant Sampling.


1975-76
S-10D Discharge (af x 10³)
OPO₄ Concentration (µg/l)
12
11
10
9
8
7
6
5
4
3
2
1
220
200
180
160
140
120
100
80
60
40
20
0
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr

similar distinction between the two study years was apparent for water concentrations of inorganic phosphorus and nitrogen and for water depth at the sample sites (Table 2). Mean annual OPO_4 and NO_3 concentrations at the two sites closest to S-10D were considerably higher in 1979-80 than in 1975-76; however differences between the two years at non-enriched sites were not apparent. Water depths during 1979-80 averaged 20 cm higher than in 1975-76.

TABLE 2. MEAN ANNUAL WATER NUTRIENT CONCENTRATIONS (µg/l) AND WATER DEPTHS (cm) AT THE SAMPLE SITES DURING THE TWO YEARS OF QUADRAT SAMPLING.

		SAMPLE SITES				
		Nutrient Enriched			Non-enriched	
		A	B	C	D	E
OPO_4	1975-76	---	6	4	2	3
	1979-80	27	36	---	3	---
NO_3	1975-76	---	12	25	10	16
	1979-80	50	30	---	5	---
Depth	1975-76	---	36	57	75	20
	1979-80	78	56	---	95	---

Differences between the sites and study years in water nutrient concentrations resulted in three levels of nutrient enrichment (Table 2). The two sites closest to S-10D were high in both OPO_4 and NO_3 during 1979-80. The next site to the south also showed high NO_3 concentrations, although OPO_4 had already dropped close to background levels there. Background levels of both OPO_4 and NO_3 persisted at the non-enriched sites during both study years. Mean annual water nutrient concentrations and depths given in Table 2 are referred to simply as OPO_4, NO_3, and depth throughout this report.

Leaf Growth of Individual Plants

Cattail leaf weight was highly correlated with leaf length at each site (Table 3). Leaf weights of individually marked cattail plants were derived from monthly leaf length measurements using these regression equations.

TABLE 3. REGRESSION EQUATIONS FOR LENGTH-WEIGHT RELATIONSHIPS FOR CATTAIL LEAVES OVER 50 CM IN LENGTH. LENGTH MEASUREMENTS ARE IN CM AND DRY WEIGHTS ARE IN GRAMS.

Site	Number of Observations	Correlation Coefficient (r)	Regression Equation*
A	82	.97	log weight = 2.11(log length) - 4.14
B	83	.94	log weight = 2.01(log length) - 3.90
C	69	.96	log weight = 2.23(log length) - 4.57
D	84	.95	log weight = 2.02(log length) - 4.01
E	66	.98	log weight = 2.04(log length) - 3.97

*All regressions are statistically highly significant (p=0.01).

The 56 individually tagged cattail plants exhibited diverse longevities and patterns of leaf growth. The majority of these plants were first measured as recently emerged shoots during March through May, although others were added every month from June through December. No relationship was apparent between the month of shoot emergence and growth pattern or longevity of the plants. Seventeen plants died within 16 weeks after emergence. These plants grew at a relatively slow rate for eight or twelve weeks, and died abruptly during the next month. Thirty-two plants exhibited a unimodal pattern of gradual increase and decrease in total leaf weight over life spans ranging from 20 to 96 weeks (Figure 6). A clearly bimodal growth pattern, with a dip in leaf weight during the winter months which was most extreme in February, was evident in 7 other plants.

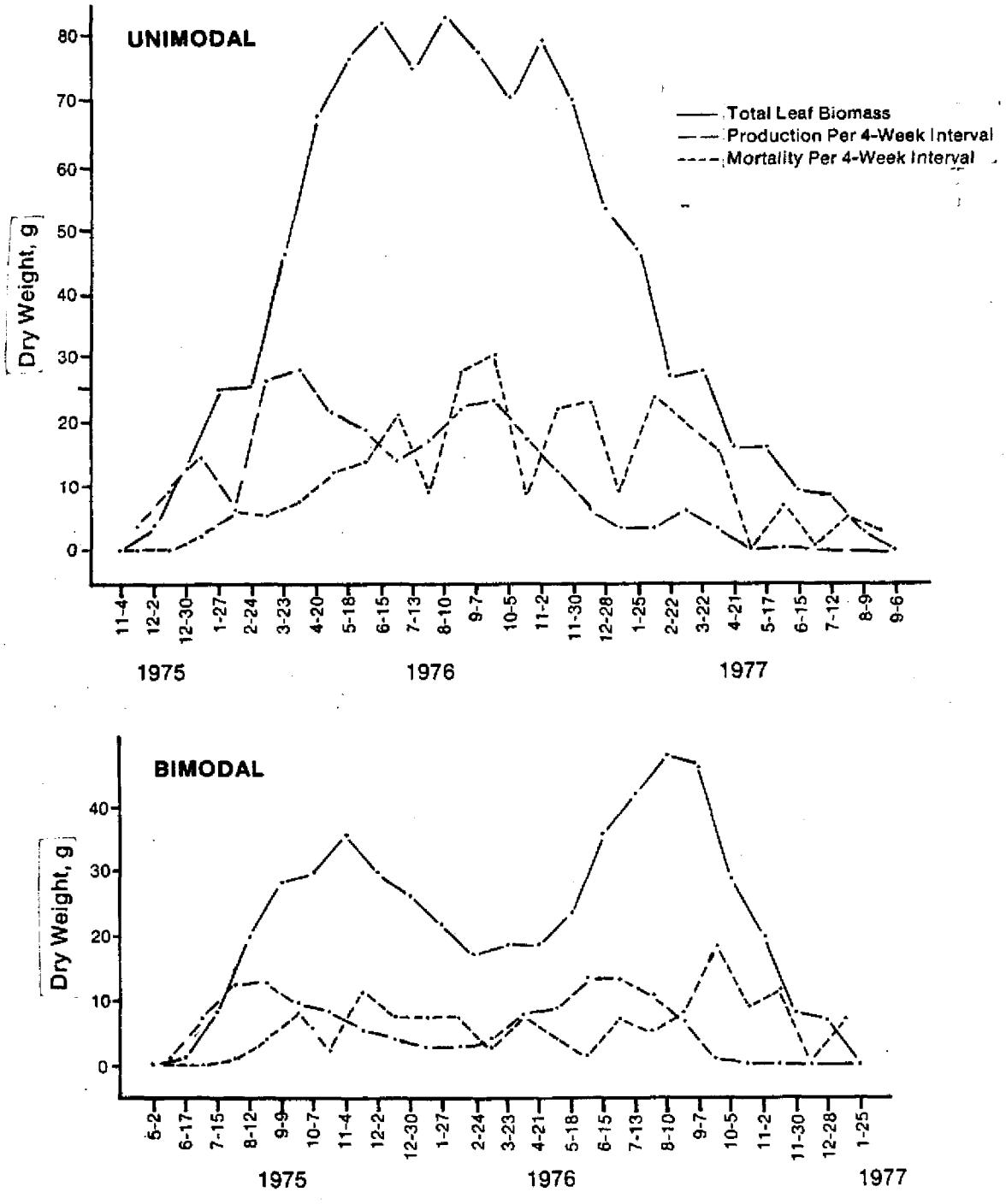


Figure 6 Leaf Growth and Mortality of Two Individual Cattail Plants Representing Unimodal and Bimodal Patterns.

Leaf growth and mortality occurred throughout most of the life span of each measured cattail plant (Figure 6). Younger leaves emerged or increased in weight, while older leaves decreased in weight or died, during nearly every month of life. The continuum of growth and mortality throughout the plants' lifespans resulted in a total leaf production which far exceeded the maximum weight reached by the plants. For example, the plant with a unimodal growth pattern in Figure 6 attained a maximum leaf biomass of 83g; however leaf production throughout its 96 week life span totalled 262g.

Growth characteristics of the individual plants were strongly related to longevity. Plant longevity alone accounted for 75% of the variation in mean weight, 61% of the variation in annual growth, and 84% of the variation in the ratio of annual growth/mean weight. Mean weight and annual growth increased with plant longevity, while the ratio of annual growth/mean weight decreased. Growth characteristics of the individual plants were not strongly correlated with mean water depths and nutrient concentrations during their life spans.

Individually measured plants were divided into 12-week longevity groups (Table 4). Although shorter lived plants were numerically predominant, they weighed less than longer lived plants. The relative abundance of each longevity group in terms of weight was calculated from the relative abundance in terms of numbers and mean weight of plants in that group.

An annual growth/mean weight ratio which could be applied to leaf standing crops of the cattail stands was estimated from growth/weight ratios of the longevity groups and the relative abundance of the groups in terms of weight. This calculation yielded a value of 4.80. Annual leaf productions of the cattail stands are thus estimated to be 4.8 times the mean annual standing crops of the stands.

TABLE 4. ABUNDANCE AND MEAN GROWTH PARAMETERS FOR INDIVIDUALLY MEASURED CATTAIL PLANTS OF VARYING LONGEVITY

Weeks Longevity	% Relative Abundance in Terms of Numbers	% Relative Abundance in Terms of Weight	Mean Weight (g) per Plant During Life Span	Annual Growth (g) per Plant During Life Span	Ratio of Annual Growth to Mean Weight
12	23.5	2.3	2.0	19.4	9.49
13-24	20.6	5.5	5.4	41.1	7.64
25-36	17.6	25.0	28.6	146.3	5.46
37-48	11.8	17.3	29.5	125.1	4.48
49-60	17.6	32.9	37.7	152.3	4.10
61-72	2.9	5.7	39.6	168.2	4.28
73	5.9	11.3	38.6	146.8	3.75

Standing Crop and Annual Production

Seasonal patterns were not evident in the monthly standing crop fluctuations of living cattail leaves; thus mean annual standing crops were compared (Table 5). Leaf standing crops differed significantly ($p = 0.05$) among the seven combinations of sites and sampling years. Leaf standing crop was strongly correlated with NO_3 at four of the five sites (Figure 7). The most shallow site NW of S-10D (Site E) stood out as having a particularly low standing crop for its NO_3 concentration. Site E is excluded from the regression in Figure 7 and will also be excluded from other relationships involving standing crop and NO_3. Standing crop was not significantly correlated with depth or OPO_4.

TABLE 5. MEAN ANNUAL DRY WEIGHT STANDING CROP (g/m^2) OF LIVING CATTAIL LEAVES.

	Site A	Site B	Site C	Site D	Site E
1975-76	---	358	590	449	225
1979-80	587	492	---	296	---

Annual leaf production, estimated by multiplying mean annual leaf standing crops by the annual growth/mean weight ratio of 4.8, ranged from 1080 to 2818 g/m^2 (Table 6). Since annual leaf production depended upon standing crop, production also was directly related to NO_3.

Seasonal production of cattail flower stalks and spikes began in February, and maximum development was reached during March, April, or May. Annual maximum standing crops of flower stalks and spikes (= annual productions) were small compared to leaf production and did not differ significantly among sites and sampling years (Table 6).

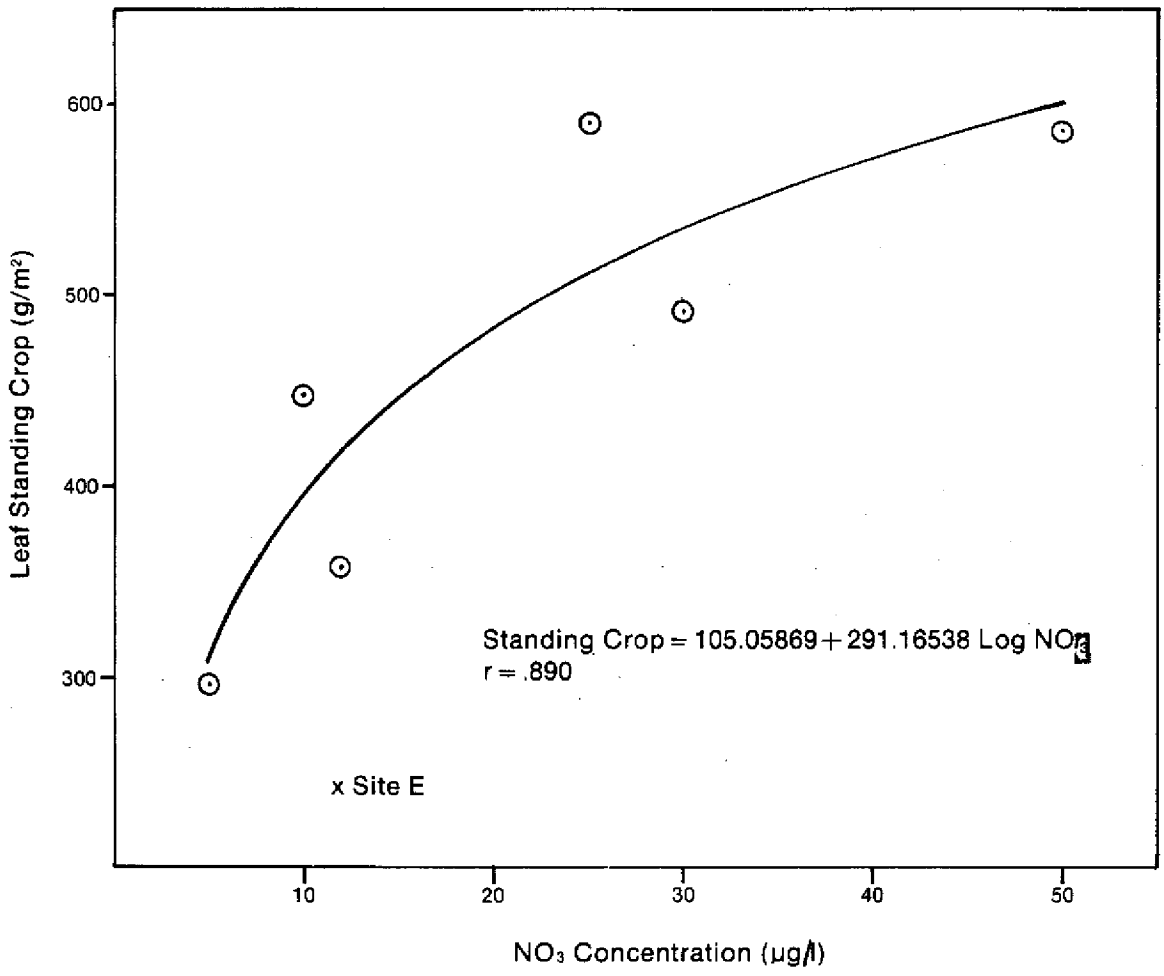


Figure 7 Mean Annual Leaf Standing Crop of Cattail Stands In Relation To Mean Annual NO_3 Concentration. Regression Excludes Site E

TABLE 6. ANNUAL ABOVEGROUND PRODUCTION ($g/m^2/yr$) OF CATTAIL STANDS

		Site A	Site B	Site C	Site D	Site E
LEAF	1975-76	--	1718	2832	2155	1080
	1979-80	2818	2362	--	1421	--
FLOWER STALK/ SPIKE	1975-76	--	35	216	198	75
	1979-80	18	0	--	9	--

Tissue Nutrient Concentrations and Storages

Phosphorus and nitrogen concentrations in living cattail leaves fluctuated seasonally at nutrient-enriched sites (Figures 8 and 9). Leaf P concentrations were highest during August-November 1975 and October-November 1979. Seasonal fluctuations in leaf N concentration were similar to that for P during 1979. Nitrogen concentrations peaked during November-December that year. These patterns appeared to be related to seasons rather than to monthly fluctuations in S-10D discharge. Nutrient concentrations reached their highest levels in leaves during the same months each year, while S-10D discharges peaked during June and July of the first sampling year and during September, October, November, and February of the second (Figure 5). Comparing the two sampling years, seasonal patterns were more distinct during the second year when S-10D discharges were greater. Seasonal fluctuations in leaf P and N concentrations were less pronounced at sites located outside the enrichment zone.

Root and rhizome concentrations of P and N increased during the same months that leaf concentrations increased (Figures 8 and 9). Roots attained maximum P concentrations during October-December both years. Rhizome P concentrations also increased during these months. Nitrogen concentrations in roots and rhizomes were also relatively high during November-December 1979.

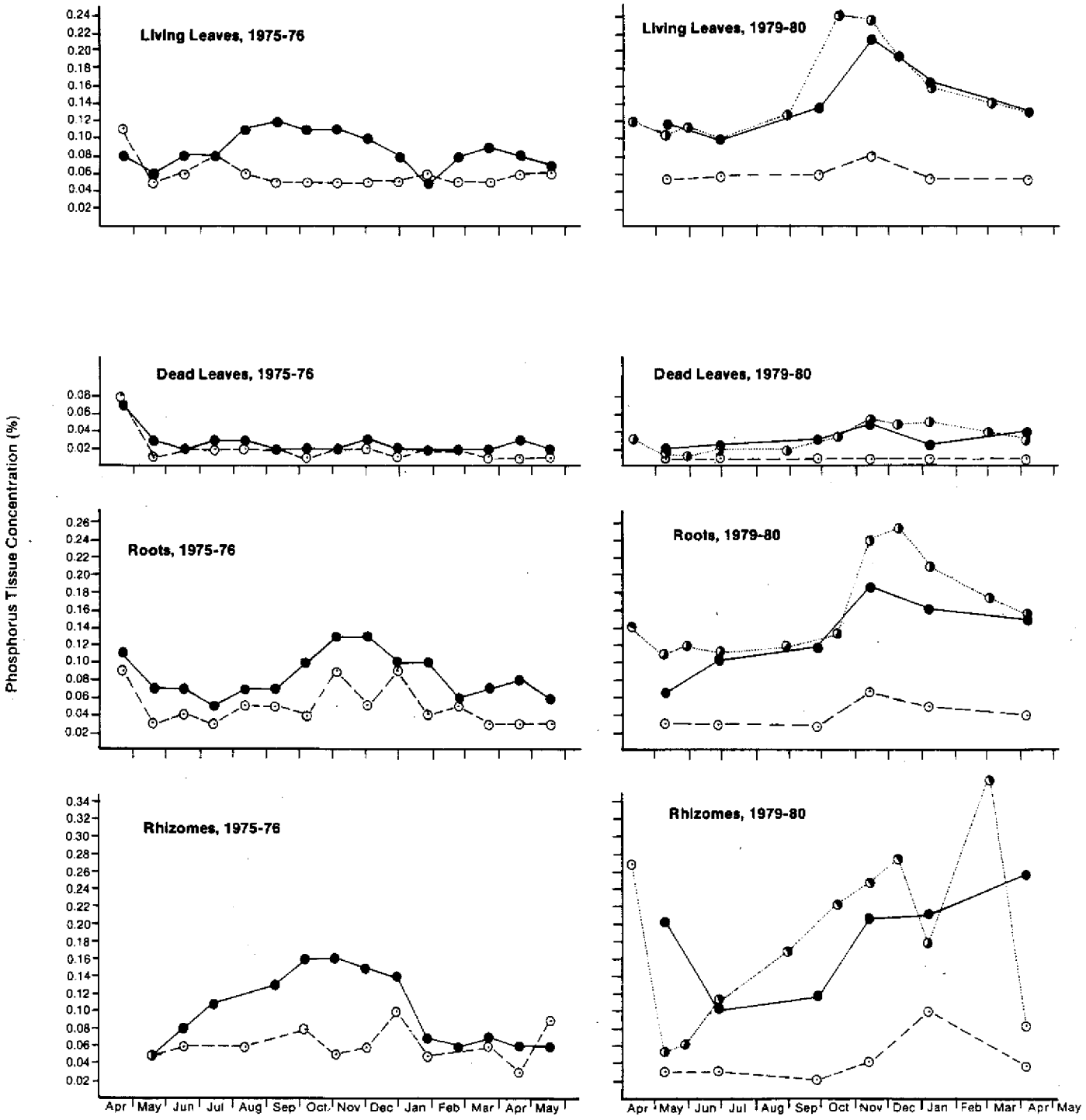


Figure 8 Phosphorus Tissue Concentrations (% dry weight) In Cattail From WCA2-A

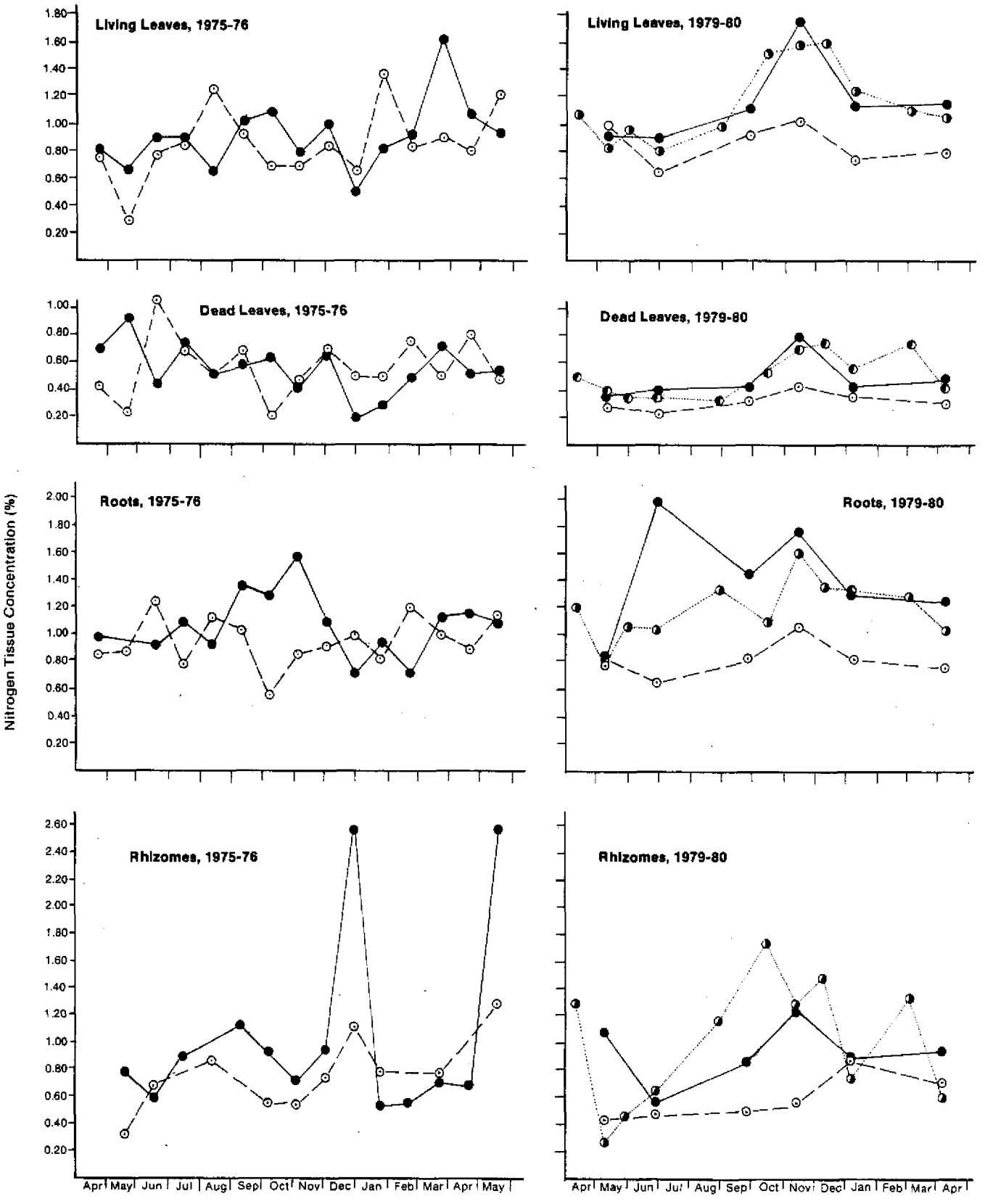


Figure 9 Nitrogen Tissue Concentrations (% dry weight) In Cattail From WCA2-A.

Seasonally fluctuating phosphorus and nitrogen concentrations in cattail leaves failed to produce discernible seasonal patterns in the storage (g/m^2) of these elements. Monthly P and N storages more closely followed fluctuations in leaf standing crop, which showed no seasonal pattern.

Concentrations and storages of phosphorus and nitrogen in living cattail leaves were significantly higher ($p = 0.01$) at nutrient-enriched sites in comparison to the background site during 1979-80 (Tables 7 and 8). However, only P appeared to be elevated at nutrient-enriched sites during 1975-76. Similar site differences were evident for P concentrations in roots and rhizomes. In comparison to living plant parts, dead leaves and flower stalks contained low P and N concentrations and showed little site-to-site variation.

The second study year yielded higher nutrient levels and storages than the first at enriched Site B (Tables 7 and 8). Mean concentrations and storages of both P and N increased between the two years in living leaves. Increases also were evident for P concentrations in roots and rhizomes and for N concentrations in roots. Higher tissue concentrations and storages at Site B during the second year corresponded to larger S-10D discharges. However, tissue concentrations and storages at background Site D were similar both years.

Mean annual P concentrations in cattail were strongly correlated with OPO_4 (Figure 10). Ortho PO_4 accounted for 91% of the variation in living leaf P concentration, 90% of the variation in root P concentration, and 95% of the variation in rhizome P concentration. In contrast, tissue N concentrations were not strongly correlated with NO_3.

Leaf P storage was significantly correlated with both OPO_4 and NO_3; however, correlations with NO_3 were stronger (Figure 11). NO_3 accounted for 96% of the variation in leaf P storage, while OPO_4 accounted for only 64%. Leaf N storage was correlated only with NO_3, which accounted for 88% of the

variation. The factor that appeared to most strongly affect leaf nutrient storages, NO_3, was the same one which influenced leaf standing crop.

TABLE 7. MEAN ANNUAL PHOSPHORUS AND NITROGEN TISSUE CONCENTRATIONS (% DRY WEIGHT) IN CATTAIL.

		PHOSPHORUS				
		Site A	Site B	Site C	Site D	Site E
Living Leaves	1975-76	---	0.09	0.10	0.06	0.07
	1979-80	0.15	0.14	---	0.06	---
Dead Leaves	1975-76	---	0.02	0.03	0.02	0.02
	1979-80	0.03	0.03	---	0.01	---
Roots	1975-76	---	0.08	0.07	0.05	0.06
	1979-80	0.16	0.13	---	0.04	---
Rhizomes	1975-76	---	0.10	0.08	0.06	0.07
	1979-80	0.18	0.18	---	0.04	---
Dead Stalks/ Spikes	1975-76(1)	---	0.04	0.03	0.02	0.02
		NITROGEN				
		Site A	Site B	Site C	Site D	Site E
Living Leaves	1975-76	---	0.94	1.04	0.91	0.96
	1979-80	1.00	1.18	---	0.86	---
Dead Leaves	1975-76	---	0.53	0.64	0.61	0.63
	1979-80	0.52	0.50	---	0.33	---
Roots	1975-76	---	1.09	0.86	0.98	0.92
	1979-80	1.21	1.45	---	0.84	---
Rhizomes	1975-76	---	1.08	0.56	0.81	0.87
	1979-80	1.01	0.94	---	0.60	---
Dead Stalks/ Spikes	1975-76	---	0.42	0.50	0.48	0.57

(1) Dead stalks and spikes were not analyzed for nitrogen during 1979-80

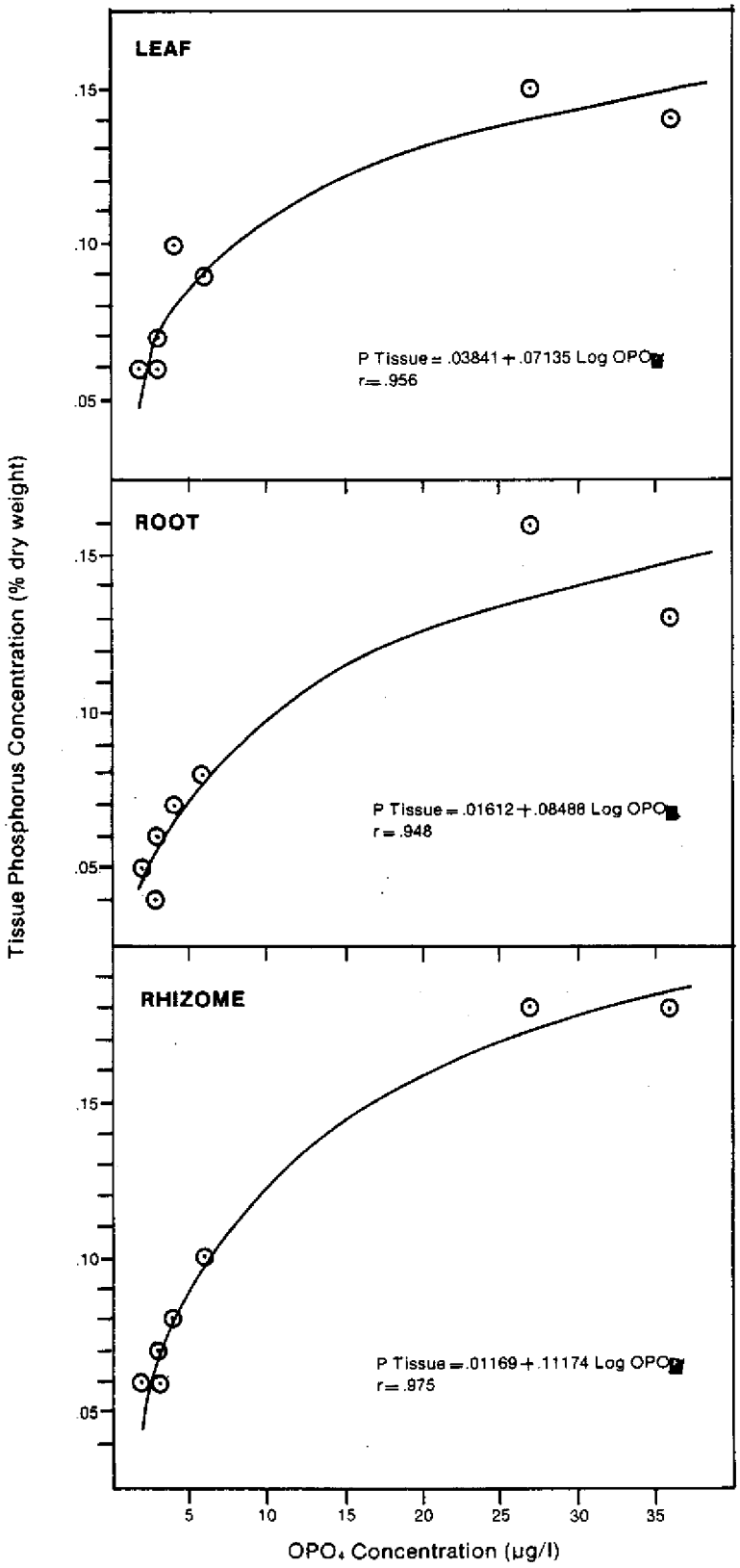


Figure 10 Mean Annual Tissue Phosphorus Concentrations In Relation To Mean Annual OPO_4 Concentration In Water

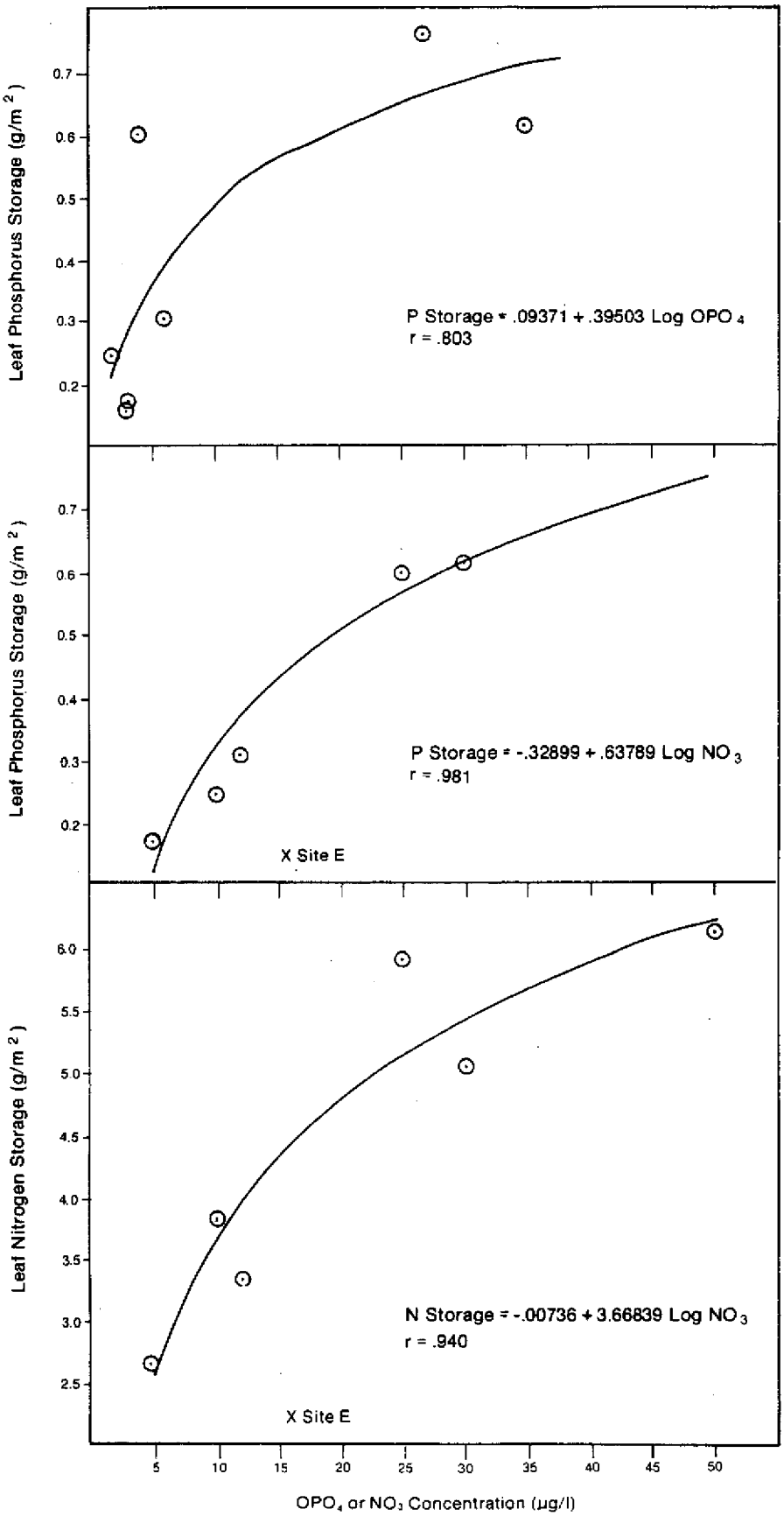


Figure 11 Mean Annual Phosphorus and Nitrogen Storages In Cattail Leaves In Relation To Mean Annual OPO_4 and NO_3 Concentrations In Water

TABLE 8. MEAN ANNUAL PHOSPHORUS AND NITROGEN STORAGES (g/m^2) IN LIVING CATTAIL LEAVES.

	Site A	Site B	Site C	Site D	Site E
PHOSPHORUS					
1975-76	-----	0.311	0.600	0.249	0.161
1979-80	0.761	0.618	-----	0.176	-----
NITROGEN					
1975-76	-----	3.346	5.919	3.845	2.316
1979-80	6.112	5.063	-----	2.640	-----

Nutrient Flux During Production and Mortality

Since annual phosphorus and nitrogen uptakes resulting from leaf growth were calculated from leaf P and N storages, site differences and relationships of uptakes to environmental variables were similar to those for storages. Annual leaf uptakes in the enrichment zone exceeded those at background sites during both years for P and during the second year for N (Table 9). Uptakes of both elements at nutrient-enriched Site B were greater during the second year of larger S-10D discharges. Annual P uptake significantly correlated with both NO_3 and OPO_4; however N uptake was correlated only with NO_3.

Much of the phosphorus and nitrogen that growing cattail leaves accumulated was lost from the leaves by the time they died (Table 9). Leaves that had recently died retained only 17-28% of the annual P uptake and 37-71% of the annual N uptake. Phosphorus retention in dead leaves was directly related to both OPO_4 and NO_3 (Figure 12); however, N retention was related to neither. Even though P uptake increased sharply with OPO_4 and NO_3, there was relatively little increase in P retention (Figure 12). The same pattern applied to N uptake and N retention in relation to NO_3. Therefore, the accelerated P and N uptake by growing leaves in the enrichment zone was also

accompanied by a larger loss of these elements from dying leaves. The net result of leaf growth and death in nutrient enriched areas differed little from that in non-enriched areas.

TABLE 9. ANNUAL UPTAKE, RETENTION, AND RELEASE ($g/m^2/yr$) OF PHOSPHORUS AND NITROGEN BY CATTAIL LEAVES.

	Site A	Site B	Site C	Site D	Site E
PHOSPHORUS					
Uptake by Living Leaves					
1975-76	-----	1.493	2.881	1.197	0.773
1979-80	3.651	2.968	-----	0.844	-----
Retention in Dead Leaves					
1975-76	-----	0.405	0.708	0.339	0.216
1979-80	0.930	0.756	-----	0.142	-----
Release During Mortality					
1975-76	-----	1.088	2.173	0.858	0.557
1979-80	2.721	2.212	-----	0.702	-----
NITROGEN					
Uptake by Living Leaves					
1975-76	-----	16.059	28.412	18.458	11.115
1979-80	29.339	24.303	-----	12.672	-----
Retention in Dead Leaves					
1975-76	-----	9.105	18.125	13.146	6.804
1979-80	14.654	11.810	-----	4.689	-----
Release During Mortality					
1975-76	-----	6.954	10.287	5.312	4.311
1979-80	14.685	12.493	-----	7.983	-----

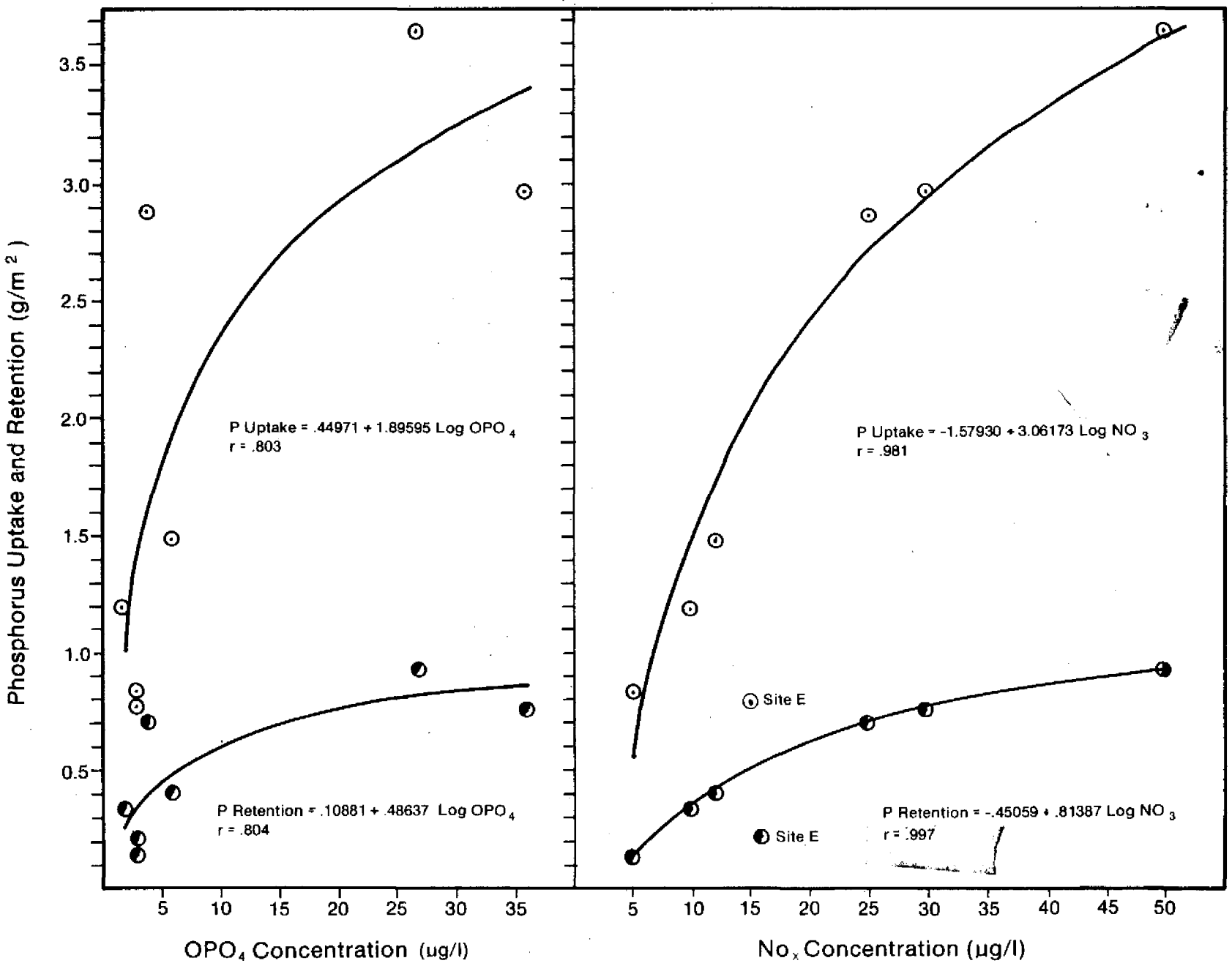


Figure 12 Phosphorus Uptake By Living Cattail Leaves and Phosphorus Retention In Dead Leaves In Relation To Mean Annual OPO_4 and NO_3 Concentrations In Water.

Phosphorus and nitrogen fluxes associated with cattail flowering (Table 10) were small in comparison to those resulting from leaf turnover. Flower stalks and spikes accumulated P and N from the beginning of their development in February until maximum storages were reached in April. Maximum annual accumulations (= uptakes) by stalks and spikes ranged from 0.02 to 0.19 g $P/m^2/yr$ and from less than 0.1 to 2.8 g $N/m^2/yr$. No flowering plants were collected during 1979-80 at Site B. Uptakes of P and N by flower stalks and spikes showed no significant correlation to water nutrient concentrations or depths. Much of the P and N that was accumulated by developing stalks and spikes was released during shoot senescence after flowering.

TABLE 10. ANNUAL UPTAKE, RETENTION, AND RELEASE ($g/m^2/yr$) OF PHOSPHORUS AND NITROGEN BY CATTAIL FLOWER STALKS AND SPIKES.

	Site A	Site B	Site C	Site D	Site E
PHOSPHORUS					
Uptake by Developing Stalks and Spikes					
1975-76	-----	0.030	0.188	0.104	0.042
1979-80	0.021	0	-----	0.028	-----
Retention in Dead Stalks and Spikes(1)					
1975-76	-----	0.014	0.065	0.040	0.015
Release During Mortality(1)					
1975-76	-----	0.016	0.123	0.064	0.027
NITROGEN					
Uptake By Developing Stalks and Spikes					
1975-76	-----	0.301	1.349	2.822	0.570
1979-80	0.139	0	-----	0.059	-----
Retention in Dead Stalks and Spikes(1)					
1975-76	-----	0.147	1.080	0.950	0.428
Release During Mortality(1)					
1975-76	-----	0.154	0.269	1.872	0.142

(1)Dead stalks and spikes were not analyzed for phosphorus and nitrogen during 1979-80

DISCUSSION

Year-round leaf turnover by Everglades cattail contrasts sharply with cattail growth in temperate latitudes. Temperate cattail growth typically involves shoot biomass increase during the growing season followed by shoot dieback with the onset of winter (Boyd, 1970a, 1971b; Bray et al., 1959; Bray, 1962; Jervis, 1969; Kvet, 1975; Mason and Bryant, 1975; Prentki et al., 1978). Cattail leaf production in the Everglades more closely resembles the continual turnover of Cyperus papyrus culms in Lake George, Africa (Gaudet, 1977).

Continual leaf turnover by Everglades cattail resulted in an average annual leaf production of 2080 g/m^2, which exceeded production estimates for cattail in temperate regions (Table 11). A partial explanation for this discrepancy is that maximum standing crops underestimate production because they do not account for plant mortality during the growing season (Wiegert and Evans, 1964). This mortality may be significant. Penfound (1956) noted that considerable plant turnover during the growing season in an Oklahoma stand of Typha latifolia resulted in a terminal standing crop which was less than the total production during the growing season. Peak standing crop of Typha angustifolia underestimated annual production by 23% in a stand bordering a eutrophic English lake (Mason and Bryant, 1975).

Everglades cattail also differs markedly from northern cattail populations in seasonal cycles of tissue nutrient concentrations. In temperate cattail stands, leaf nutrient concentrations peak in young, rapidly growing shoots shortly after their emergence early in the growing season (Boyd, 1970; Bayly and O'Neill, 1972; Klopatek, 1975; Prentki et al., 1978). These peaks coincide with declines in rhizome nutrient concentrations and apparently result from translocation of winter nutrient reserves from

rhizomes (Bayly and O'Neill, 1972; Prentki et al., 1978). In contrast, seasonal peaks in nutrient concentrations of Everglades cattail coincide neither with seasonal emergence of new shoots nor with a drop in rhizome concentration. Fluctuations in leaf, rhizome, and root tissue concentrations of WCA-2A cattails may be related to flowering and to seasonal availability of nutrients. Tissue concentrations declined during the spring flowering period and increased during the summer-fall wet season, when nutrient supplies from rainfall and S-10 discharges were greatest.

TABLE 11. ANNUAL PRODUCTION ESTIMATES ($g/m^2/yr$ DRY WEIGHT) FOR *TYPHA* FROM TEMPERATE LATITUDES BASED ON SEASONAL MAXIMUM STANDING CROP. ESTIMATES ARE FOR *T. LATIFOLIA* UNLESS OTHERWISE NOTED.

Location	Annual Production	Source
South Carolina	684	Boyd (1970a)
South Carolina infertile sites	520-1132	Boyd (1971b)
Minnesota	1360	Bray (1962)
Minnesota[1]	1680	Bray et al. (1959)
Long Island	1358	Harper (1918)
Long Island[1]	1731	Harper (1918)
New Jersey	1905	Jervis (1969)
Czechoslovakia	1600	Kvet (1975)
England[2]	1118	Mason and Bryant (1975)
South Carolina	574	Polisini and Boyd (1972)
South Carolina[3]	1483	Polisini and Boyd (1972)
England	1070	Pearsall and Gorham (1956)
Czechoslovakia	1657	Pelikan et al. (1970)
Oklahoma	1527	Penfound (1956)

[1] *T. latifolia/angustifolia* hybrid
[2] *T. angustifolia*
[3] *T. domingensis*

Leaf measurements indicated that individual cattail plants were highly variable in growth pattern, longevity, mean weight, and annual growth; however, water depth and water nutrient concentrations explained little of this variability. Thus, the growth/weight ratio derived from the individually measured plants represents an annual leaf turnover rate which

appears applicable to all the cattail stands which were sampled. While annual leaf turnover rates were not correlated with nutrient enrichment or water depth, leaf standing crops of the cattail stands increased with nutrient enrichment. Therefore, annual production and mortality were primarily functions of standing crop.

The strong correlation between leaf standing crop and NO_3 at four of the five sites suggests that nitrogen availability affects cattail production where the mean annual water depth exceeds 35 cm. The 20 cm depth at Site E apparently was inadequate for the potential cattail growth which could have occurred with a NO_3 concentration of 16 µg/l. Thus the response of cattail production to NO_3 appears to be suppressed where water depths are very shallow - somewhere between 20 and 35 cm. However, cattail production appears to be independent of water levels where the depth exceeds 35 cm. The suppressed cattail production at Site E may have resulted from factors which accompany a shallow mean water depth, such as increased frequency of drying or burning. The positive correlation of cattail annual production to NO_3 at Sites A-D and the abnormally low annual production at Site E suggest that both nitrogen enrichment and deeper water have augmented cattail colonization in WCA-2A.

The correlation between NO_3 and leaf standing crop and production indicates that inorganic nitrogen may limit cattail production even though concentrations of organic N are relatively high in surface water. The relationship of cattail standing crop to NO_3 in the Everglades is contrary to the findings of Boyd and Hess (1970) that Typha latifolia standing crop in southeastern North America was strongly correlated with dissolved water P and only weakly correlated with NO_3. This discrepancy may be explained by low water NO_3 concentrations which averaged 5 to 50 µg/l at Everglades sites, in comparison to water NO_3 concentrations of 10 to 450 µg/l at the

sites of Boyd and Hess. The lack of a significant correlation between cattail production and OPO_4 does not necessarily mean that cattail growth is independent of P supply in WCA-2A. Low concentrations of both OPO_4 and NO_3 at background sites would be expected to be insufficient for maximum cattail growth. However, cattail production apparently would be greater under existing OPO_4 concentrations if NO_3 concentrations were higher.

Annual P uptake due to leaf growth was a function of both annual production and P tissue concentration. NO_3 affected P uptake by influencing annual production, while OPO_4 affected P uptake by influencing P tissue concentration. Site differences in annual production were much greater than differences in tissue P concentration, which explains the stronger correlation of P uptake to NO_3 than to OPO_4. Standing crop and annual production were the predominant factors controlling annual P uptake.

In contrast to phosphorus, annual N uptake through leaf production was correlated only with water NO_3 concentration. This relationship appeared to depend largely upon the increase in standing crop with increasing NO_3, because N tissue concentration was not related to NO_3 or OPO_4.

Since dying cattail leaves released much of the phosphorus and nitrogen that they accumulated during their growth, cattail leaf production in the Everglades appears to function as a recycling mechanism more than as a sink for nutrients. The P and N that was lost from dying leaves possibly was recycled through two pathways. Rainfall probably leached organic P and N compounds from leaves back into the surface water (Tukey, 1970). Translocation of P and N from dying leaves to belowground roots and rhizomes is another likely pathway of nutrient recycling. Bayly and O'Neill (1972) demonstrated that Typha glauca from Ontario transferred P from dying leaves to rhizomes at the end of the growing season. Reallocation to belowground plant parts was shown by Prentki et al. (1978) to account for 23% of the P

loss from dying shoots in a Wisconsin Typha latifolia stand. The importance of roots and rhizomes as nutrient sinks would depend on the retention of P and N in these organs after death, decomposition, and conversion to organic soil. Similarly, any value of leaf production as a nutrient sink would depend upon the retention of P and N by dead leaf material during decomposition and eventual sediment accumulation. The roles of cattail leaf detritus and belowground roots and rhizomes in Everglades nutrient cycles are subjects of future publications in this series.

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