Limnology of a wetland complex in the Mississippi alluvial valley of southeast Missouri

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With 7 figures and 6 tables in the text

Abstract

Productive wetlands in southeast Missouri, U.S.A., characterized by low salinity, were studied from 1981–1983. Nutrient chemistry was related to water level management of individual sites. A permanently flooded reservoir had the lowest nutrient concentrations, periodically drained marsh sites contained moderate nutrient levels, and autumnally-flooded forest sites had the highest nutrient concentrations derived from leachate of leaf litter. Nutrient concentrations in these forested sites reached maximum values within a few months after inundation and decreased thereafter. Algal biomass was typically nitrogen-limited in the sites, but high macrophyte production in the largest sites did not depend on nutrients in the water. In addition, rates of community metabolism were related to relative dominance of phytoplankton, rooted macrophytes or duckweeds in the respective sites rather than to nutrient content of the water. Zooplankton concentrations in managed forested sites increased and decreased over time in patterns similar to changes in nutrient concentrations, which, together with results from other investigations, suggests that detritivore production in temporarily flooded forest is initially high and subsequently decreases with duration of flooding.

Introduction

The purpose of this paper is to document the large-scale chemical and biological limnology of a wetland complex in the Mississippi River alluvial plain of southeast Missouri, U.S.A. These wetlands have been studied mainly in relation to the life history of certain waterfowl species (Fredrickson 1979a), but their limnological characteristics were largely unknown. This information also contributes to the growing body of knowledge concerning wetland limnology (e.g., Kadlec 1979, Mitsch et al. 1979, Brinson et al. 1981), and provides basic ecological information for decisions on appropriate wetland management.

Site description

These wetlands are located in the contiguous public lands (ca 10,000 ha) of the Mingo National Wildlife Refuge (U.S. Fish and Wildlife Service) and Duck Creek Wildlife Management Area (Missouri Department of Conservation) in southeast Missouri, U.S.A. (FREDRICKSON 1979a, b). Study sites in the Duck Creek area were Pools 1, 2, and 3, which are shallow, diked man-made reservoirs of large surface area (Fig. 1). Pool 1 is a permanent reservoir, while Pools 2 and 3 are temporarily inundated sites forested mostly with lowland hardwoods, termed greentree reservoirs. In Pool 1 water inflows and outflows are controlled by a surrounding ditch system used to flood the adjacent greentree reservoirs each fall to attract waterfowl for hunting. Pools 3 and 2 are drained in early and late winter, respectively.

In the Mingo National Wildlife Refuge a variety of natural and man-made water bodies were studied (Fig. 1). Mingo Forest is a flooded forest of lowland hardwoods, the result of beaver impoundments which have killed trees in the center of this area, but rainfall temporarily floods bordering live forest. A shallow, diked impoundment termed Moist Soil Unit 7 (MSU), was managed for growth of herbaceous food plants for waterfowl by natural drawdowns dependent on rainfall patterns (FREDRICKSON & TAYLOR 1982). Monopoly and Rockhouse marshes are the largest wetlands on the Mingo Refuge (Fig. 1). Both marshes are shallow
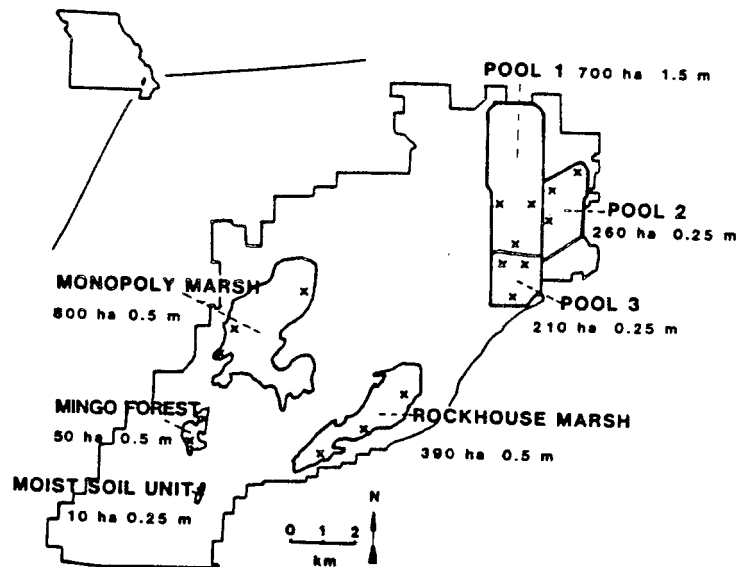

Fig. 1. Study sites in the Duck Creek Wildlife Management Area (Pools 1, 2, and 3) and the Mingo National Wildlife Refuge (remaining sites) in southeast Missouri. Sampling locations are denoted by x's.

(ca 0.5 m) with open water edged by a buttonbush-willow margin (*Cephalanthus occidentalis* and *Salix* spp). These sites are drained during alternate summers: during this study 1981 and 1983 for Rockhouse Marsh and 1982 for Monopoly Marsh. Drawdown was initiated in May and completed during summer; reflooding was sometime in fall, depending on precipitation.

Climatic description

Climate of the Mingo-Duck Creek area is temperate and continental with warm humid conditions (KRUSEKOPF 1966). Average rainfall is 112 cm and is generally greatest during winter. Precipitation during this study was erratic, and extreme rainfall events (ca 12 cm) occurred within most seasons. Monthly temperatures were usually within 3 °C of long-term means. In relation to long-term cycles, the period of this study was during an increase in yearly precipitation.

Materials and methods

Water chemistry

Surface water samples (0.2 m depth) were taken approximately biweekly from the sites (Fig. 1) during February 1981 through April 1983. Samples were preserved by refrigeration or acidification and analyses were done according to standard methods within recommended time limits (USEPA 1979).

A Radiometer PHM 26 meter was used to measure pH and redox potential (Eh), with glass and platinum probes, respectively. Values of Eh were corrected to pH 7 (STUMM & MORGAN 1970). Hach 16300 and Radiometer CDM2e meters were used to measure specific conductance (EC). Total alkalinity was determined by titration with 0.02 N sulfuric acid to pH of 4.8. Total and calcium hardness were measured by titration with 0.02 N CDTA; magnesium was estimated by difference (Hach Chemical Co. 1978). Seasonally, determination of sulfate was by the turbidimetric method and chloride by titration with 0.014 N mercuric nitrate (Hach Chemical Co. 1978). Organic color was determined by comparison of platinum-cobalt standards in matched Nessler tubes.

Total and volatile suspended solids (TSS and VSS) were determined by filtration, drying at 103 °C, and ashing at 550 °C. Total and volatile dissolved solids (TDS and VDS) were measured by drying 100 mL aliquots of the filtrates at 103 °C and ashing them at 550 °C. Total phosphorus (TP) was determined after persulfate oxidation and total dissolved phosphorus (TDP) was measured similarly from water filtered through a 0.45 μm membrane filter (MURPHY & RILEY 1962, MENZEL & CORWIN 1965). Ammonia and nitrate nitrogen were determined using a specific ion probe (Orion Research, Inc. 1977) and cadmium reduction, respectively. Total nitrogen (TKN) was analyzed by the micro-Kjeldahl procedure.

Plant biomass

Chlorophyll *a* concentrations were determined from subsamples of surface water filtered through Gelman Type A-E glass fiber filters which were stored up to 30 days frozen over desiccant. Chlorophyll *a* was extracted with 90% acetone and measured trichromatically (STRICKLAND & PARSONS 1972).

In summer 1982 and 1983 macrophyte biomass was sampled approximately monthly from Pool 1 and Monopoly and Rockhouse marshes with a sampler made of a wood frame in which plexiglass sheets were inserted to delineate a volume 0.5 m on each side and up to 2 m deep. Samples were taken along randomly selected transects within defined plant growth zones (Fig. 2). Plants within the sampler were removed above the sediment surface, and were washed, sorted to species, and dried at 80°C. Dry weight was determined and subsamples were prepared for ash, nitrogen, and phosphorus analysis by the Agricultural Experiment Station Chemical Laboratories at the University of Missouri-Columbia, using methods of LIKENS & BORMANN (1970). Surface area of the sites and plant growth zones were measured from aerial photographs using a compensating polar planimeter. Median biomass was calculated for each species in each sample period, and the maximum of these biomass values was interpreted as yearly production (WESTLAKE 1965).

Community metabolism

Aquatic community metabolism was estimated biweekly during summer using consecutive evening-morning-evening measurements of dissolved oxygen and pH, after WELCH (1968). Measurements of pH were determined within hours of sample collection, and dissolved oxygen samples (0.2 m depth) were fixed in the field and titrated the day of collection according to the modified Winkler method using Hach reagents (Hach Chemical Co. 1978). Oxygen values were corrected to mg/L at 25°C (MORTIMER 1956).

Zooplankton

In 1981 and 1982, zooplankton were sampled from Pools 1, 2, and 3 beginning when Pools 2 and 3 were filled in fall and ending when they were drained in winter. Zooplankton were sampled using a Schindler trap with an 80 µm mesh bucket. Samples were preserved with 90% ethanol, and zooplankton were classified and counted as no./L of cladocerans and copepods, the dominant taxa, to a standard error of 20% (ELLIOTT 1977).

Statistical treatment

For most analyses, data were combined across calendar seasons and years in an attempt to make large-scale comparisons among sites; however, seasonal effects are discussed when pertinent. Data were used in nonparametric correlation analysis (alpha = 0.05) and Kruskal-Wallis one-way analysis of variance (K-W ANOVA, alpha = 0.15) (DANIEL 1978, SAS 1982 a, 1982 b).

Canonical discriminant function analysis (SAS 1982 b) was used as an exploratory approach to summarize important differences and similarities of nutrient chemistry among the sites (COOLEY & LOHNES 1971). We took this approach because water chemistry of sites was dynamic, and values overlapped considerably among sites when each variable was compared separately. An assemblage of the least intercorrelated ($r < 0.5$) water chemistry variables representing P, N, and organic content were selected for the analysis: TDP, TKN, NH3-N, NO3-N, VSS, VDS, the proportion of suspended solids as organic (VSS/TSS), and the proportion of dissolved solids as organic (VDS/TDS). Values were transformed using log $(x+1)$ to satisfy normality assumptions, and analysis was done by season using mean daily values from each site. For each combination of season and site, data from all years were pooled prior to analysis.
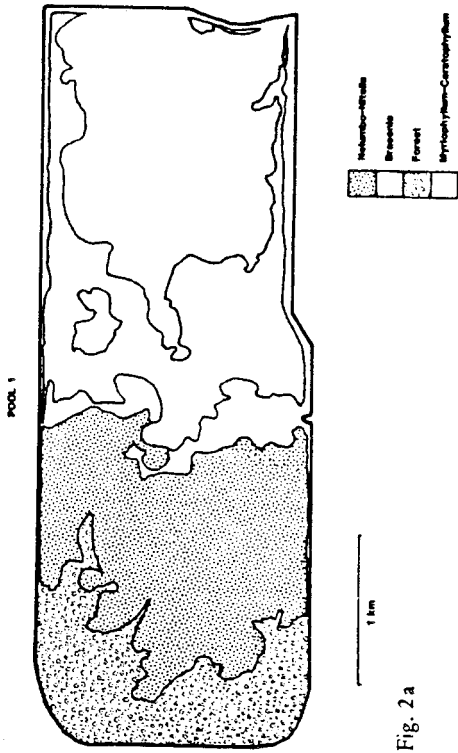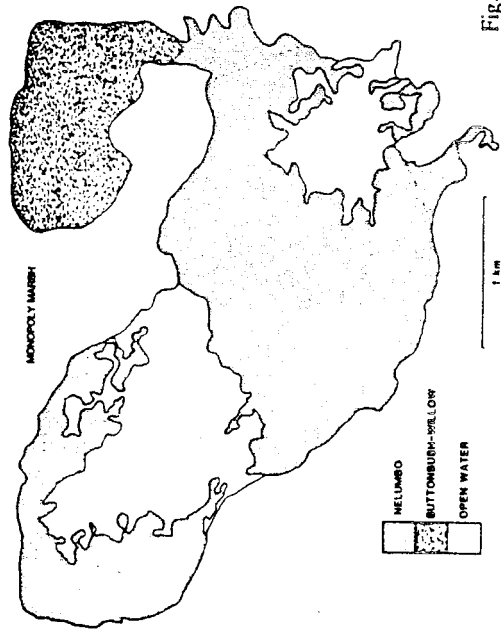
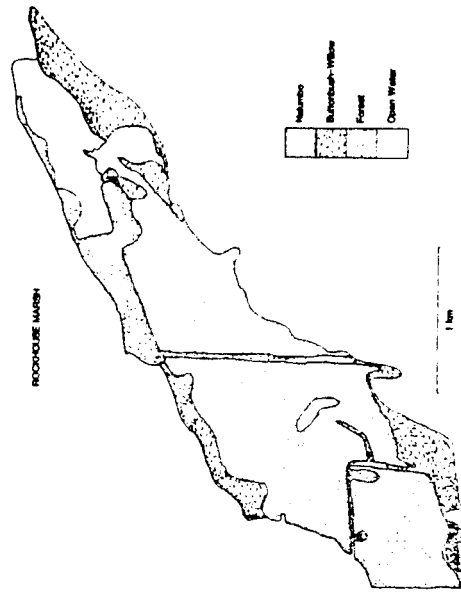Fig. 2. Plant growth zones in (a) Pool 1, (b) Monopoly Marsh, and (c) Rockhouse Marsh during summer.

Results and discussion

Water chemistry

Aquatic habitats in the Mingo-Duck Creek area generally contained soft, unbuffered water of low ionic strength. These characteristics are related to the weathered alluvial soil in the region underlaid by a shallow hardpan that prevents upward flow of groundwater (FREDRICKSON 1979b). Values of EC ranged from 50 to 110 μmhos/cm and pH values fluctuated around neutrality (Table 1). Median concentrations of total alkalinity were 40 mg/L or below, and concentrations of total hardness were 42 mg/L or below. These measurements were within criteria used to distinguish waters both low in alkalinity (MOYLE 1956) and soft (SAWYER & McCARTY 1979). Levels of Ca were about twice those of Mg in most sites and the carbonate system accounted for more than 50% of anion equivalents. Concentrations of SO_4 ranged from 2 to 15 mg/L and for Cl from 4 to 16 mg/L. Median values of Eh ranged from 410 to 490 mv in the sites (Table 1), near that of 500 mv determined for neutral, oxygenated water (STUMM & MORGAN 1970); values are within the Eh-pH limits of fresh waters compiled by BAAS & BECKING et al. (1960).

Among sites SO_4 was generally lowest in the greentree reservoirs, probably because of reduction of SO_4 to S in anaerobic flooded leaf litter. Ratios of Ca to Mg and most measurements of ionic content (alkalinity, hardness, and EC) were lowest in MSU and Mingo Forest, probably because their major water source was direct rainfall.

Concentrations of TDS ranged from 59 to 115 mg/L, and VDS ranged from 30 to 66 mg/L (Table 2). Color values ranged from 30 to 120 Pt units (Table 2) and were positively correlated with VDS concentrations ($r = 0.8$, $p < .001$); both parameters are measures of dissolved organic content. No relation between dissolved organic content and Eh was found among the sites, contrary to what might be expected (ALLGEIER et al. 1941). Anaerobic condition was the only characteristic that consistently changed (lowered) Eh.

Although salinity was low in these sites, suspended solids content was comparable to those of Missouri reservoirs with much higher salinity (JONES 1977, HOYER & JONES 1983). Total suspended solids concentrations ranged from 5.1 to 92.4 mg/L, and the volatile fraction ranged from 2.6 to 14.4 mg/L (Table 2). Among sites, those waters with the highest suspended solids content (both marshes and MSU) had the lowest proportion as organic solids (Table 2).

Concentrations of TKN ranged from 0.6 to 1.4 mg/L and were an order of magnitude higher than concentrations of inorganic nitrogen (Table 2). Values of NH_3-N and NO_3-N ranged from 0.01 to 0.04 mg/L and were frequently below detection limits (Table 2). Nitrogen concentrations were, however, in the range of values reported for other wetlands (KADLEC 1979). In wetland systems concentra-

Table 1. Median values and ranges of conservative water chemistry characteristics.

Site	pH	Eh mv ⱷ pH 7	EC μmhos/cm ⱷ 25 C	Total Alkalinity mg/L CaCO₃	Total Hardness mg/L CaCO₃	Ca mg/L	Mg mg/L	Cl* mg/L	SO₄* mg/L	Sample Size
Pool 1	7.4 (6.8–10.1)	430 (280–580)	77 (50–242)	29 (15–108)	31 (18–96)	7.2 (4.0–25.2)	3.2 (2.8–8.0)	11 (5–13)	10 (3–12)	163
Pool 2	7.0 (6.3–7.5)	460 (380–550)	102 (54–238)	40 (13–83)	42 (20–80)	9.8 (4.0–18.4)	4.3 (2.4–8.1)	16 (1–35)	2 (0–5)	66
Pool 3	6.8 (6.4–7.4)	430 (230–570)	110 (70–199)	33 (14–52)	36 (17–68)	8.8 (4.0–13.2)	3.4 (1.7–8.5)	14 (1–30)	2 (0–6)	29
Rockhouse Marsh	6.9 (6.3–7.5)	460 (390–560)	100 (43–312)	33 (9–67)	38 (16–91)	8.8 (3.2–23.2)	3.9 (2.0–8.0)	12 (8–15)	8 (0–25)	109
Monopoly Marsh	6.9 (6.1–8.6)	450 (360–520)	84 (50–179)	26 (8–59)	34 (15–58)	7.2 (4.0–13.6)	3.8 (1.2–5.8)	10 (1–15)	15 (0–30)	82
Moist Soil Unit	6.9 (6.1–9.0)	460 (330–520)	50 (28–73)	15 (8–30)	16 (8–29)	2.8 (1.6–7.2)	2.2 (1.0–2.4)	5 (1–6)	10 (0–15)	56
Mingo Forest	6.5 (5.8–7.6)	460 (380–550)	61 (20–136)	19 (4–39)	24 (15–56)	5.0 (3.2–12.8)	3.5 (1.7–5.8)	5 (1–10)	8 (0–20)	82

* Sample size was 24 for these measurements

Table 2. Median values and ranges of nutrient chemistry characteristics.

Site	TP (mg/L)	TDP (mg/L)	TKN (mg/L)	NO_3-N (mg/L)	NH_3-N (mg/L)	TSS mg/L	VSS mg/L	VSS/TSS ×100	TDS (mg/L)	VDS (mg/L)	VDS/TDS ×100	Color (Pt units)	Sample Size
Pool 1	0.04 (0.00–0.35)	0.02 (0.00–0.08)	0.6 (0.1–2.5)	0.02 (0–0.25)	0.02 (0.00–1.30)	5.1 (0.2–218.7)	2.6 (0.0–24.9)	59% (0–98%)	59 (29–157)	30 (9–100)	50% (18–88%)	30 (15–110)	160
Pool 2	0.35 (0.04–3.73)	0.20 (0.01–2.60)	1.1 (0.3–2.4)	0.01 (0–0.12)	0.02 (0.00–0.20)	6.4 (1.9–79.0)	3.3 (0.9–39.5)	51% (18–93%)	101 (46–200)	53 (20–144)	56% (26–87%)	90 (20–220)	60
Pool 3	0.33 (0.06–1.18)	0.20 (0.02–0.69)	1.4 (0.3–7.2)	0.01 (0–0.43)	0.04 (0.00–0.25)	6.2 (2.3–25.8)	4.0 (0.6–25.0)	69% (23–97%)	115 (44–549)	66 (30–492)	63% (29–90%)	120 (25–240)	29
Rockhouse Marsh	0.25 (0.05–1.08)	0.07 (0.01–0.60)	0.9 (0.1–3.2)	0.02 (0–0.67)	0.04 (0.00–0.67)	15.1 (2.9–86.0)	5.4 (0.7–20.8)	26% (4–88%)	103 (52–414)	48 (26–86)	47% (14–90%)	80 (50–250)	105
Monopoly Marsh	0.18 (0.04–0.64)	0.05 (0.01–0.31)	0.9 (0.1–4.4)	0.02 (0–0.20)	0.02 (0.00–0.20)	21.6 (1.7–388.4)	5.0 (1.6–72.7)	25% (5–94%)	96 (53–255)	44 (16–87)	47% (14–71%)	70 (50–280)	80
Moist Soil Unit	0.10 (0.03–1.31)	0.02 (0.00–0.13)	1.0 (0.1–3.3)	0.01 (0–0.17)	0.01 (0.00–0.50)	92.4 (5.8–463.6)	14.4 (1.4–75.7)	17% (1–48%)	113 (58–304)	42 (10–81)	34% (4–72%)	30 (5–200)	55
Mingo Forest	0.18 (0.01–1.21)	0.08 (0.00–1.08)	1.2 (0.3–3.8)	0.01 (0–0.19)	0.02 (0.00–0.83)	8.8 (2.0–236.3)	4.6 (0.8–44.5)	57% (8–96%)	82 (43–209)	57 (15–160)	67% (30–88%)	110 (20–500)	80

tions of inorganic nitrogen are typically low because of denitrification processes and assimilation in biomass of plants and decomposer organisms (PATRICK & TUSNEEM 1972, BRINSON et al. 1981).

Concentrations of TP ranged from 0.04 to 0.35 mg/L and of TDP from 0.02 to 0.20 mg/L (Table 2). In the forested sites, Pools 2 and 3 and Mingo Forest, more than 50% of TP was in dissolved form (Table 2). This high proportion of TDP to TP was attributable to large concentrations of dissolved organic matter from leaf leachate. In remaining sites, particulate P was greater than TDP (Table 2). As with nitrogen, phosphorus concentrations were in the range of values reported for other wetlands, but maximum concentrations exceeded reported maximum values (KADLEC 1979, HOYER & REID 1982).

In a multivariate comparison of nutrient chemistry among the sites, combined canonical R-square values of the first and second canonical variables explained 90% or more of the variation among sites in seasons combined across years (Table 3).

Table 3. Standardized canonical coefficients and cumulative canonical R-squares for canonical variables used to separate nutrient chemistry of sites by season.

Season	Variable	Can. var. 1 coefficients	Can. var. 2 coefficients	R^2	
Fall	VDS/TDS	1.70	−0.17	Can1	0.91
	VSS/TSS	1.59	−0.47	Can1+Can2	0.96
	TDP	0.84	1.07		
	VDS	−0.78	0.58		
	TKN	0.60	0.37		
	VSS	−0.20	0.11		
	NO3-N	0.08	−0.13		
	NH3-N	0.06	−0.20		
Winter	VDS	−1.75	0.53	Can1	0.87
	VSS/TSS	1.65	−0.28	Can1+Can2	0.96
	VDS/TDS	0.99	−0.24		
	TDP	0.79	1.11		
	TKN	0.54	0.24		
	NO3-N	−0.39	0.15		
	NH3-N	0.36	−0.52		
	VSS	0.02	−0.60		
Spring	VSS	1.56	−0.67	Can1	0.78
	VSS/TSS	−1.00	−0.22	Can1+Can2	0.92
	VDS	0.58	0.69		
	TKN	−0.37	0.49		
	NH3-N	−0.30	−0.02		
	NO3-N	−0.25	0.03		
	TDP	0.14	0.57		
	VDS/TDS	0.07	0.58		
Summer	VSS/TSS	0.91	−1.20	Can1	0.75
	VDS/TDS	0.84	0.55	Can1+Can2	0.92
	TKN	0.27	0.32		
	NH3-N	0.56	0.15		
	NO3-N	−0.35	−0.20		
	VDS	0.18	0.43		
	TDP	0.18	0.33		
	VSS	−0.15	0.70		

Of variables used in the analysis (Table 3) the most highly weighted were volatile solids content and the relative proportion of solids that were volatile. Phosphorus (TDP) was moderately weighted in discriminatory power, with TKN slightly less so. Inorganic nitrogen had poor discriminatory power.

Seasonal plots of the first canonical variable versus the second display site placement in canonical space based on nutrient chemistry variables used in the analysis (Fig. 3). Grouping of the sites can also be interpreted by examining inter-correlated variables that were not used. In general, both Pool 1 and MSU were uniquely placed in the canonical plots, while Monopoly and Rockhouse marshes were grouped together, and the flooded forest sites (Pools 2 and 3 and Mingo Forest) were grouped together.
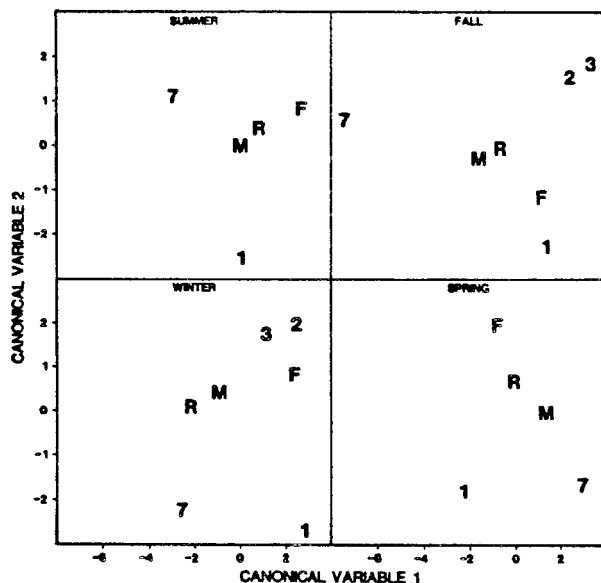

Fig. 3. Plots of the first canonical variable versus the second using seasonal nutrient chemistry values. Sites are identified by 1, 2, and 3 for Pools 1, 2, and 3, 7 for Moist Soil Unit 7, M and R for Monopoly and Rockhouse marshes, and F for Mingo Forest.

Unique nutrient chemistry of Pool 1 was due to its permanent inundation which restricted inflow of allochthonous nutrients. As a result, Pool 1 contained comparatively low concentrations of N, P, and solids (Table 2). Pool 1 supported extensive macrophyte growth and moderate phytoplankton biomass (discussed in a later section), so a relatively high percentage (50–59%) of solids were organic (Table 2) because of phytoplankton in the suspended solids and excretions from macrophytes (HOUGH & WETZEL 1975) in the dissolved solids.

Nutrient chemistry of MSU was distinct because of high clay turbidity (inorganic solids) and proportionately low organic content (VSS/TSS, VDS/TDS and color). These chemical characteristics resulted from the interaction of fluctuating shallow water levels (0.1–0.3 m) with the clay substrate exposed when this particular site was constructed. Moderate to high TP and TKN concentrations in MSU (Table 2) were related to high suspended solids ($0.41 < r < 0.52$, $p < 0.01$), but low TDP concentrations, used in the canonical analysis, were not affected ($p > 0.75$).

Drawdown of Monopoly and Rockhouse marshes resulted in the canonical grouping of these sites separately from others (Fig. 3). For example, during drainage of Monopoly Marsh in spring 1982 wind mixing increased suspended bottom sediments in the water column, which elevated concentrations of TP, TKN, TSS, and TDS 2–6 times normal values as the drawdown progressed; however, water formed small pools as drawdown neared completion, sediments settled from the water, and concentrations declined (Fig. 4). Bottom sediments added mostly inorganic particulate matter to the water column because concentrations of TDP, VSS, and VDS remained relatively stable (Fig. 6). Similar trends were seen in Rockhouse Marsh when it was drained in 1981 (WYLIE 1985). As a result, marsh water chemistry was characterized by relatively high concentrations of inorganic suspended solids and only moderate levels of dissolved organic matter (Table 2).
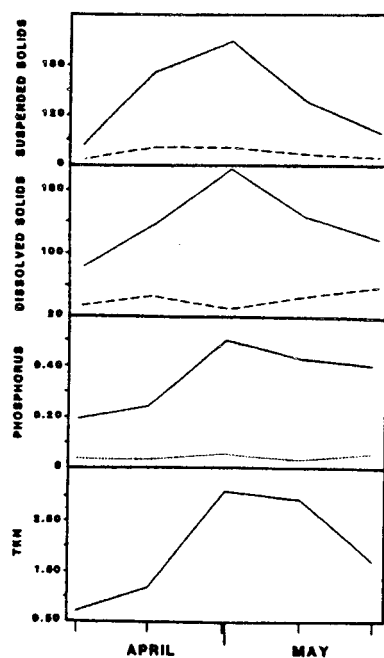

Fig. 4. Water chemistry changes in Monopoly Marsh during drawdown in spring 1982. Solid lines are total values, dashed lines are volatile solids values, and the dotted line is total dissolved phosphorus; chemical concentrations are in mg/L.

Nutrient chemistry of the greentree reservoirs and Mingo Forest was distinguished from other sites (Fig. 3) by high levels of color, VDS, P, TKN, and high VSS/TSS and VDS/TDS ratios (Table 2), which were likely the result of organic matter leached from leaf litter. In fall, precipitation was generally low and water in Mingo Forest was confined to an area where trees were dead, but in winter the live forest bordering the site was frequently flooded. Therefore, nutrient chemistry values from Mingo Forest during fall were different from the greentree reservoirs, but winter values were grouped closely (Fig. 3).

In Pools 2 and 3, chemical composition of water, originally from Pool 1, was markedly altered over time by organic matter from flooded leaf litter. For example, in fall 1982 most nutrients increased 2–15 times that of initial values within 2 months of inundation (Fig. 5). Similar results were obtained during the previous year as well (WYLIE 1985). Nutrient chemistry changes over time in both years resembled quadratic functions with peaks followed by declines. In Pool 2 most water chemistry measurements had slight peaks in late winter related to warming temperatures coupled with a gradual drainage of the site. The decline in nutrients from maximum values was probably due, in part, to flocculation of dissolved organic material and precipitation from the water column (LUSH & HYNES 1973). In the laboratory we found flocculation of dissolved organic matter transformed up
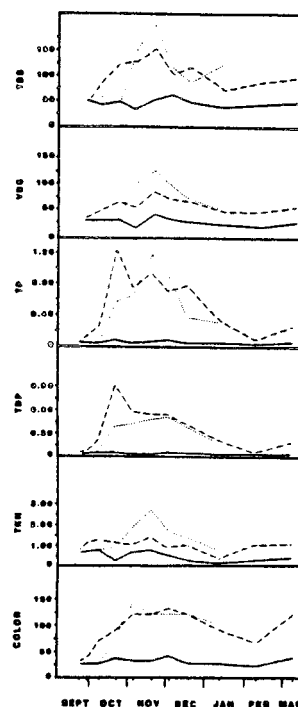

Fig. 5. Water chemistry changes in Pool 1 (solid line), Pool 2 (dashed line), and Pool 3 (dotted line) from fall 1982 through winter 1983. Chemical concentrations are in mg/L and color is in Pt units.

to 50% of the original TDP in filtered samples from Pools 2 and 3 into particulate P upon refiltration.

In summary, relative distinction of sites or groups of sites in the canonical discriminant function analysis could be traced to the influence of water regimes on nutrient chemistry. Because of permanent inundation, Pool 1 had comparatively low nutrient content, but proportionately high organic solids. Fluctuating shallow water levels in MSU interacted with a clay substrate and resulted in high inorganic solids content. Drawdown of the marshes also added inorganic solids to their water, but not to the extent of MSU. Temporary flooding of forest in the greentree reservoirs (managed) and Mingo Forest (natural) resulted in high organic nutrient content from leaf leachate.

Zooplankton

Concentrations of cladocerans and copepods, the dominant zooplankton taxa, dramatically increased in Pools 2 and 3 after fall flooding compared to populations in Pool 1, the original source of water. For example, in fall 1982 cladoceran and copepod concentrations increased an order of magnitude over those in Pool 1 (Fig. 6) with maximum concentrations occurring from late fall to early winter. Initial flooding of Pool 3 was 2 weeks later than Pool 2, and zooplankton concentrations increased more slowly than in Pool 2. Similar zooplankton dynamics were also observed in the previous year (WYLIE 1985). In the greentree reservoirs, ephippial (Cladocera) or encysted (Copepoda) eggs may hatch after inundation and augment numbers of zooplankton introduced from Pool 1. Rapid increases from initial densities can be attributed to the high productive capacity (biomass turnover times of 6–14 days) of many filter feeding zooplankton (WETZEL 1983).
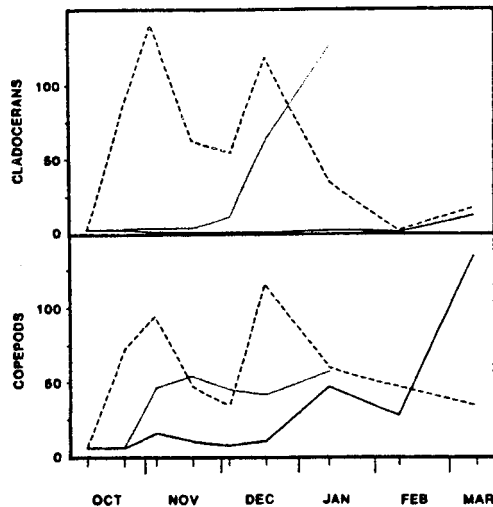

Fig. 6. Changes in zooplankton concentrations (no./L) in Pool 1 (solid line), Pool 2 (dashed line), and Pool 3 (dotted line) from fall 1982 through winter 1983.

Densities of zooplankton in both greentree reservoirs were comparable with those found in the Great Dismal Swamp (ANDERSON et al. 1977) and in forested temporary pools of southeastern Louisiana (MOORE 1970).

Detrital food, instead of phytoplankton, likely supported high zooplankton concentrations in the greentree reservoirs because changes in zooplankton concentrations were similar to changes in organic content of their waters (Fig. 7), while chlorophyll *a* values were usually lower than those from Pool 1 (Table 4). Zooplankton in a variety of habitats feed on detritus and its associated microbial biomass (SAUNDERS 1972, MANN 1972, PEDROS-ALIO & BROCK 1983), which, in these sites, was in the form of fragmented leaf litter or particles recoagulated from leaf leachate (LUSH & HYNES 1973).

In the greentree reservoirs the pattern of rapid increases in organic matter concentrations after inundation followed by gradual decreases (Fig. 7) was similar not only to changes in zooplankton concentrations, but also was paralleled by dynamics of macroinvertebrate detritivores measured in other studies of these sites (BATEMA et al. 1985, WHITE 1985). These results also complement macroinvertebrate dynamics in a greentree reservoir in Illinois (HUBERT & KRULL 1973) and zooplankton-chemistry data recorded from intermittent forested pools in Louisiana (MOORE 1970). Together, the phenology of change in nutrient chemistry and invertebrate populations suggests that the main pulse of detritus-based secondary production in flooded forest occurs within a few months of inundation, with production decreasing thereafter over time.

Phytoplankton biomass and nutrients

Chlorophyll *a* concentrations from the sites (Table 4) were variable and spanned the entire range of values in Missouri reservoirs (HOYER & JONES 1983). Chlorophyll *a* concentrations were 7 mg/m^3 or greater, which complements concentrations of N and P (above 0.02 and 0.50 mg/L, respectively) in classifying the sites as eutrophic (FORSBERG & RYDING 1980). During summer, however, the yield of chlorophyll *a* per unit TP was generally an order of magnitude less than might be estimated from a regression model developed for lakes (JONES & BACHMANN 1976). Two reasons may account for this low yield. First, algae may not be able to use P associated with high concentrations of inorganic solids as were found in both marshes and MSU (HOYER & JONES 1983). Second, TN/TP weight ratios were less than 10 in most sites (Table 4), suggesting that N was the limiting nutrient for planktonic algal standing crop (FORSBERG 1980). Low TN/TP ratios were likely the result of high denitrification rates from alternating dry-wet cycles in shallow, seasonally flooded sites (PATRICK & TUSNEEM 1972, REDDY & PATRICK 1976) in relation to relatively high P content of suspended sediments and detritus (BRINSON et al. 1981). Only in the permanent reservoir, Pool 1, where water was low in suspended solids and organic content, were TN/TP ratios generally above 10, and

summer TP and chlorophyll *a* values within the 95% confidence limits of the
JONES & BACHMANN (1976) regression (Table 4).

Table 4. Median values and ranges of chlorophyll *a* concentrations and TN/TP ratios for
the sites. Included also are ratios of chlorophyll *a* per unit TP based on medians of actual
summer values and predictions from the JONES & BACHMANN (1976) regression equation,
given summer TP concentrations.

Site	Chl. *a* (µg/L)	Sample Size	TN/TP	Summer chl. *a*/TP	Predicted Summer chl. *a*/TP
Pool 1	15.6 (2.0−719.5)	160	16.0 (2.1−103.3)	0.37	0.50
Pool 2	10.9 (0.9− 41.8)	60	3.2 (0.5− 23.8)	−	−
Pool 3	6.9 (0.6− 78.2)	29	3.7 (1.2− 39.0)	−	−
Rockhouse Marsh	15.8 (2.1−294.3)	105	3.9 (0.8− 15.8)	0.07	1.18
Monopoly Marsh	19.4 (1.0−533.0)	80	4.8 (0.6− 16.3)	0.05	0.88
Moist Soil Unit	39.8 (5.3−141.3)	55	6.7 (1.2− 29.6)	0.26	0.88
Mingo Forest	12.8 (0.5−331.2)	80	7.0 (1.3− 24.4)	0.11	1.00

Macrophyte biomass and nutrients

While plant nutrients in the water column may limit algal biomass, they
probably do not limit growth of aquatic macrophytes (BEST & MANTAI 1978,
CARIGNAN & KALFF 1980). Macrophytes covered most of the surface area of the
three largest sites, Pool 1 and Monopoly and Rockhouse marshes, during summer.
The American lotus, *Nelumbo lutea*, was the dominant macrophyte in both
marshes, and grew in nearly monospecific stands in more than half of their surface
area (Figs. 3 and 4). A variety of macrophytes grew over the entire surface area of
Pool 1 at locations differentiated by depth (Fig. 2). In shallow water (0.5 m) at
the north end of Pool 1 dominant macrophytes were *Nelumbo* with an understory
of *Nitella*. Watershield, *Brasenia schreberi*, grew in monospecific stands in 1 m
of water near the center of Pool 1 and bordering the perimeter of the borrow
ditch to the south. Extensive mixed beds of *Myriophyllum spicatum* and *Cerato-
phyllum demersum* grew in deeper water (1.5−2 m) at the southern end of Pool 1
and in the borrow ditch.

Maximum biomass for most macrophyte taxa was reached in August each year; senescence began in September and was complete by early October. Nutrient composition of macrophytes was consistent with literature values (BOYD 1970, POLISINI & BOYD 1972) and did not change appreciably from year-to-year or, in *Nelumbo*, from site-to-site (Table 5). Generally, submerged macrophytes contained higher percentages of N and P than the floating-leaved macrophytes. If these nutrient concentrations are extrapolated to estimated maximum standing crops of macrophytes, they represent an order of magnitude more N and P than contained in water volumes at the sites (Table 6).

Rapid drainage of Monopoly Marsh in summer 1982 killed *Nelumbo* foliage by early July from desiccation together with shading from terrestrial vegetation, mostly grasses, growing on exposed marsh soil. When the site was left flooded in 1983 *Nelumbo* biomass was twice that of the drawdown year (Table 5). In Rockhouse Marsh, however, a slow drawdown in summer 1983 prevented desiccation of *Nelumbo*, and may have allowed aeration and nitrification (REDDY & PATRICK 1976) of the marsh soil which increased *Nelumbo* maximum biomass compared to 1982, when water levels were normal (Table 5).

Growth of *Nelumbo* was less dense ($p < 0.05$) in the permanently inundated north end of Pool 1 than in the marshes (Table 5). In part, this difference may have been due to parasitism: about 10% of harvested *Nelumbo* petioles in Pool 1 were infested with *Donacia hypoleuca* larvae (Coleoptera:Chrysomelidae), while no larvae were observed in samples from the marshes. *Donacia* larvae have been

Table 5. Estimated maximum biomass (EMB) of macrophyte taxa, their nutrient content, and the surface area of their respective growth zones in Pool 1, Rockhouse Marsh, and Monopoly Marsh.

Site	Taxa	Growth Area (ha)	Sample Size	Year	EMB (g/m²)	% Dry Wt. N	% Dry Wt. P
Pool 1	Brasenia	144	16	1982	254	1.80	0.18
			20	1983	180		
	Myriophyllum	249	16	1982	107	2.60	0.26
			20	1983	80		
	Ceratophyllum	249	16	1982	39	3.70	0.35
			20	1983	181		
	Nitella	170	40	1982	115	3.80	0.70
			50	1983	85		
	Nelumbo	170	40	1982	320	1.80	0.26
			50	1983	400		
Rockhouse Marsh	Nelumbo	213	40	1982	408	1.80	0.26
			50	1983	614		
Monopoly Marsh	Nelumbo	420	25	1982	224	1.80	0.26
			50	1983	515		

Table 6. Total nutrient content by macrophyte taxa and water volumes in Pool 1, Rockhouse Marsh, and Monopoly Marsh.

| | Total Nutrient Content (Tonnes) | | | | | |
| | Pool 1 | | Rockhouse Marsh | | Monopoly Marsh | |
	N	P	N	P	N	P
*Brasenia**	6.0	0.60				
Myriophyllum	5.8	0.58				
Ceratophyllum	10.0	0.95				
Nitella	6.2	1.14				
Nelumbo	11.0	1.60	21.0	3.03	38.9	5.62
Water**	7.2	0.44	1.8	0.68	3.0	0.58
% of Total in Macrophytes	84%	92%	92%	82%	93%	91%

* Macrophyte nutrient content is based on averaged 1982 and 1983 EMB values and percentages of N and P from Table 5, except only 1983 data were used for Monopoly Marsh.
** Nutrient content of water is based on median of summer samples for water nutrient concentrations.

reported to inhabit a variety of floating-leaved macrophytes where they eat the leaves and pupate on the petioles under the sediments (McGAHA 1952), and have been observed to kill *Nelumbo* plants in the Tennessee River Valley (STEENIS & MITCHELL 1950).

Total macrophyte standing crop, however, was similar among the *Nelumbo* zones of Pool 1 and the marshes because *Nitella* grew in mats below *Nelumbo* in Pool 1, while shading prevented other plants from growing under the thick *Nelumbo* canopies in the marshes (LOW & BELLROSE 1944, BOLEN et al. 1975). Total macrophyte standing crop in Pool 1 was also increased by *Brasenia, Myriophyllum,* and *Ceratophyllum* (Table 5).

Estimated production of non-emergent macrophytes in the sites was comparable to those of a variety of fertile habitats (RICH et al. 1971, POLISINI & BOYD 1972, ADAMS & McCRACKEN 1974). Production of *Nelumbo* was relatively high because it has the advantage of growing in both floating and emergent habitats through its life history (SCULTHORPE 1967). In Monopoly and Rockhouse marshes *Nelumbo* production was within the upper 10% of values reported for submergent macrophyte productivity in temperate freshwater communities and was at the lower end of the productivity range for temperate emergent macrophytes (WESTLAKE 1982).

WELCH (1952) concluded that macrophyte production should be considered in evaluating total carbon fixation in aquatic ecosystems. Similarly, CANFIELD et al. (1983) proposed that trophic state assessment of lakes with extensive macrophyte biomass include nutrients in the plant tissue as well as those in the water column.

CANFIELD et al. (1983) based their proposal on observations of lakes in Florida which had high productivity due to macrophytes, but had low concentrations of nutrients and algae in the water column. Pool 1 and Monopoly and Rockhouse marshes would already be considered eutrophic according to concentrations of N, P, and chlorophyll a in their water columns (FORSBERG & RYDING 1980, FORSBERG 1980), but consideration of macrophyte biomass and nutrients (Tables 5 and 6) better represents productivity in these sites.

Frequently when macrophytes die and decay in aquatic systems, nutrient concentrations in the water column increase and growth of phytoplankton is stimulated (BOYD 1971, CARPENTER 1980, CANFIELD et al. 1983). In Pool 1 and in both marshes, concentrations of nutrients and chlorophyll a did not appreciably increase during fall and winter after macrophytes had senesced and decayed, even though macrophytes contained about 90% of the summer stocks of N and P above the sediments. Nutrient release from macrophyte detritus may have been gradual, so that N and P were reincorporated into macrophyte biomass of the next season (GODSHALK & WETZEL 1977) instead of stimulating phytoplankton growth during fall and winter (JEWELL 1971, CARPENTER 1980). Conservation of nutrients would result if N and P were immobilized in microbial biomass during decomposition (SAUNDERS 1979). Also, close proximity of sediments to decomposing plants in these shallow water bodies may have restricted the availability of N and P through denitrification and adsorption, respectively (BOSTON & PERKINS 1982, LANDERS 1982).

Community metabolism

Diel changes in dissolved oxygen content (DO) and pH of aquatic ecosystems have frequently been used as measures of aquatic community metabolism (ODUM 1956, VERDUIN 1956, WELCH 1968). This method has the advantage of integrating effects of photosynthesis from all plants with respiration from all biotic components of the water body, rather than having measurements limited to specific compartments of production and respiration. But physical processes, such as advection, convection, or diffusion, may add considerable error to calculation of production and respiration (KEMP & BOYNTON 1980, MELAK & FISHER 1983). Measurements of diel DO and pH changes from this study, therefore, were used as comparative rather than absolute representations of community metabolism.

In summer the significantly highest median daytime DO increase (Fig. 7) was 7.7 mg/L from MSU and the lowest increase was 2.2 mg/L from Mingo Forest (K-W ANOVA). Pool 1 and Monopoly and Rockhouse marshes had mid-range (4.9–5.2 mg/L) median DO increases (Fig. 9) that were not significantly different (K-W ANOVA). Nighttime decreases in DO from community respiration almost evenly balanced daytime increases from photosynthesis (Fig. 7).
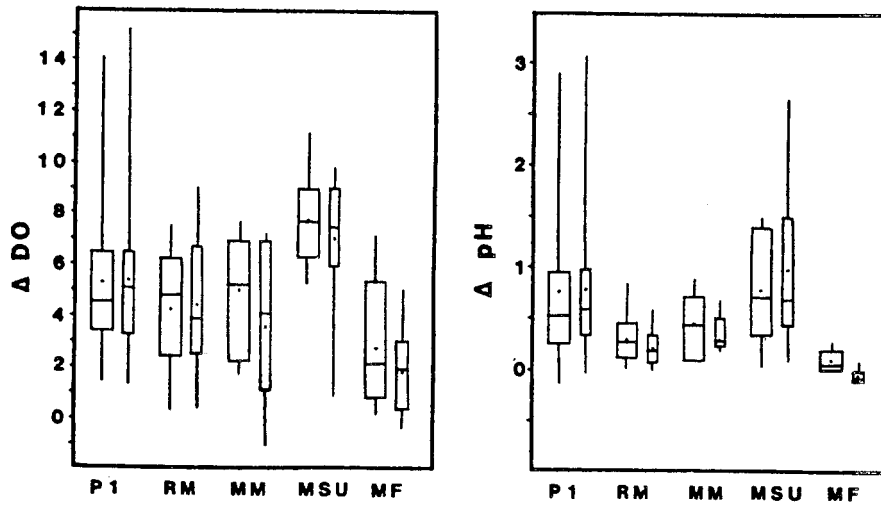
Fig. 7. Box plots of summer diel changes in mg/L of dissolved oxygen (DO) and units of pH in the sites. Sites are denoted by P1 (Pool 1), RM (Rockhouse Marsh), MM Monopoly Marsh), MSU (Moist Soil Unit 7), and MF (Mingo Forest). Morning to evening changes and evening to morning changes are represented by wide and narrow boxes, respectively. Respectively, top and bottom of each box are the 75th and 25th percentile values, lines and dots within each box are median and mean values, and extremes of box tails are minimum and maximum values.

Diel fluctuations of pH and DO were positively correlated ($r=0.67$, $p<0.001$), indicating that pH as well as DO responded to community metabolism in these soft water sites. The highest median increase in pH (Fig. 7) was 0.72 units from MSU and the lowest increase was 0.06 units from Mingo Forest (K-W ANOVA). Change of pH in remaining sites was not significantly different (K-W ANOVA), but greater buffering capacity of water in both marshes (Table 1) may have moderated their pH response (0.28–0.45 units) relative to Pool 1 (0.54 units). As with DO changes, nighttime decreases in pH balanced daytime pH increases (Fig. 7).

Rates of DO change were not significantly related to plant nutrient content of sites ($p>.26$), and pH changes were inversely related to N and P ($-.30<r<-.26$, $p<.03$). Instead, rates of community metabolism were likely related to whether production was influenced by algae, macrophytes, or duckweeds. In summer MSU had the highest rates of community metabolism attributable in the absence of macrophytes to large concentrations of phytoplankton (Table 4). Pool 1 generated rates of community metabolism comparable to Monopoly and Rockhouse marshes, which have much higher nutrient content (Table 2). These sites had similar standing crops of macrophytes (with associated epiphytes), whose production (Table 5) does not directly depend on nutrients in the water column. The importance of macrophyte-epiphyte effects on community metabolism was also described by

FONTAINE & EWEL (1981) for a Florida lake. Although Mingo Forest had high nutrient content (Table 2), summer community metabolism was inhibited by duckweeds (*Lemna* spp.) covering the surface, a phenomenon similar to anoxic water under floating meadows of Amazon floodplain lakes (MELAK & FISHER 1983) and under water hyacinth *(Eichhornia)* cover in a Florida pond (REDDY 1981).

Community metabolism occasionally produced large daily changes of pH and DO in some sites. For example, periods of high photosynthetic rates added to morning values 10–14 mg/L DO and increased pH 2.2–2.9 units in Pool 1, and, in MSU, 9–11 mg/L DO and 1.5 pH units. Nighttime respiration reversed these daytime shifts, and often reduced DO concentrations to less than 1.0 mg/L at dawn. Large fluctuations of DO and pH in productive aquatic ecosystems have frequently been documented (DUNN 1967, DYE et al. 1980, REDDY 1981), although high pH values may be maintained in some well-buffered systems (HALSTEAD & TASH 1982). Some organisms may be excluded by extreme DO and pH levels, but many survive these conditions through physiological adaptations or migration to favorable sub-habitats (HASLER & JONES 1949, STEEMAN NIELSEN 1952, MOORE & BURN 1968). Fish in Pool 1 (STEWART 1983) were apparently able to survive these extremes.

The extent of daily pH fluctuations in sites may have been related to differential physiology of macrophytes and algae. Whereas most aquatic vascular plants can utilize HCO_3 as their carbon source in photosynthesis, many phytoplankton species require CO_2 (STEEMANN NIELSEN 1946, HOUGH & WETZEL 1977). Very little free CO_2 exists in water of pH greater than 8.0 (WETZEL 1969), and in MSU, with high phytoplankton biomass (Table 4) and no submerged macrophytes, pH seldom exceeded this value. In Pool 1, however, photosynthesis by abundant submerged macrophytes (Table 5) often raised afternoon pH values to greater than 8.5. Tolerance of high pH and low CO_2 availability may be a physiological adaptation of macrophytes which allows them to compete with phytoplankton (HASLER & JONES 1949, WETZEL 1969), which may otherwise establish dominance in the system (JONES et al. 1983).

Daytime increases in DO were directly correlated with nighttime decreases ($0.77 < r < 0.82$, $p < 0.001$), as were day and night pH changes ($0.68 < r < 0.87$, $p < 0.001$). This balancing of community respiration with photosynthesis indicates, within the resolution of our measurements, that the sites experienced little or no net gain from primary production. These results were similar to diel measurements of metabolism in other aquatic habitats (VERDUIN 1956, WELCH 1968, DYE et al. 1980, FONTAINE & EWEL 1981, REDDY 1981), which suggests that biotic components of aquatic ecosystems tend to adapt to exploit all generated primary production (ODUM 1969).

Conclusions

Wetlands of the Mingo-Duck Creek area had soft, unbuffered water of low ionic strength, but nutrient concentrations were generally high. Conservative water chemistry characteristics are probably the result of local edaphic conditions that contribute few ions to standing water, which was further diluted by direct rainfall on the limited watershed of the area (FREDRICKSON 1979b). Relative amounts of nutrients were linked in a multivariate analysis to water regimes: temporary flooding of forest leached organic nutrients from leaf litter to result in the highest nutrient concentrations, temporary drawdown of marsh sites mixed water with sediments to result in high levels of inorganic nutrients, and permanent inundation resulted in the lowest nutrient concentrations. The wetland complex in the Mingo-Duck Creek area combines characteristics of closed-basin swamps and alluvial swamps (SCHLESINGER 1978) because water chemistry depends both on local edaphic factors and allochthonous nutrient inputs.

Many sites were productive because they were shallow and essentially functioned as littoral zones. This assessment is consistent with the direct relationship in lakes between productivity and surface area of sediments in contact with the epilimnion (FEE 1979). Because sites were shallow, processes of community metabolism during summer acted on the low buffer capacity of these waters to produce large daily DO and pH changes. Rates of community metabolism were not related to nutrient content of sites because macrophyte production, important in three sites, did not depend on nutrients in water, and duckweed cover in a site high in nutrients inhibited metabolism beneath it.

Macrophyte production was high in Pool 1 and both marshes because most sediment surface area was colonizeable by macrophytes. Most of this production was from Nelumbo lutea, a plant well adapted to shallow aquatic systems because it tolerates a wide range of environmental conditions and rapidly dominates macrophyte growth through shading of other macrophytes and spreading by rhizomes (BELLROSE 1941, BOYD 1971, JOHNSTON et al. 1983). The area is managed to attract waterfowl, however, and Nelumbo has little food value for waterfowl (BELLROSE 1941, LOW & BELLROSE 1944). In addition, few organisms were observed to use it for food or shelter during this study. Management efforts should probably be directed to control Nelumbo populations and promote production of more desirable wetland plants (MEEKS 1969, FREDRICKSON & TAYLOR 1982).

Overall wetland productivity is also based on detrital inputs as well as nutrient-plant relations. Flooding the two greentree reservoirs established aquatic habitat rich in detrital food. Organic matter was rapidly leached from the leaf litter, but nutrient concentrations were gradually reduced from maximum values after a few months. This pattern seems to be the limnological illustration of detritivore response to temporary flooding of these sites as seen in changes of zooplankton concentrations during this study and population dynamics of macroinvertebrate

detritivores from other studies of the area (BATEMA et al. 1985, WHITE 1985). Furthermore, these results complement dynamics of macroinvertebrate detritivores in a greentree reservoir in Illinois (HUBERT & KRULL 1973) and are similar to invertebrate-chemistry data from some temporary pools in lowland forest of Louisiana (MOORE 1970). Collectively, these studies suggest that the trophic response of detritivore communities to temporary inundation of forested wetlands is initially dramatic, but short-lived.

In wetlands zooplankton and macroinvertebrates act as a functional link in the transfer of energy and nutrients from detritus to higher trophic levels, including fish and waterfowl. Fish endemic to wetlands of lowland forest, such as top-minnows *(Fundulus)* and mosquitofish *(Gambusia)*, were found to rapidly inhabit flooded forest in the Mingo-Duck Creek area as it became available, presumably because of high densities of invertebrate detritivore prey in these sites (STEWART 1983). In addition, waterfowl overwintering in the area fed on invertebrates in flooded forest to elaborate protein necessary in their molt and reproductive cycles (HEITMEYER 1985). Dynamics of invertebrate production in temporarily flooded wetlands may partially explain high initial use by waterfowl of newly-flooded management areas followed by declining use (MacNAMARA 1957, KADLEC 1962). Management plans for forested wetlands should consider that the main pulse of detritivore production may occur within the first several months of site inundation with benefits of temporary inundation diminishing afterwards.

Acknowledgments

Summary

Wetlands in the Mingo-Duck Creek area are eutrophic soft water habitats with variable nutrient chemistry characteristics that segregated differentially managed sites in a multivariate analysis. Pool 1 was permanently inundated and had minimal interaction with terrestrial areas, which resulted in the lowest nutrient concentrations of the sites. Water from Pool 1 was used to flood two greentree reservoirs, and initial water chemistry was dramatically altered by release of nutrients from inundated leaf litter. Nutrient concentrations in the greentree reservoirs decreased after a few months, however. Flooded forest in the Mingo Refuge also had high nutrient content from flooding of forest leaf litter. Rockhouse and Monopoly marshes and MSU, were periodically drawn down which resulted in moderately high nutrient concentrations from interactions of water with the sediments.

Concentrations of zooplankton in the greentree reservoirs rapidly increased and then diminished over time in a pattern similar to both concentrations of nutrients in the water and population changes of macroinvertebrate detritivores measured in other studies (BATEMA et al. in press, HUBERT & KRULL 1973, WHITE 1985). This pattern suggests that inundation of lowland forest rapidly makes nutrients available for secondary production, but this effect diminishes after a few months.

Phytoplankton biomass was usually N-limited in most sites, but extensive growth of macrophytes in Pool 1 and Monopoly and Rockhouse marshes did not depend on nutrients in the water column. Also, rates of aquatic community metabolism depended on the relative importance of phytoplankton versus macrophyte growth in sites, rather than nutrients in the water. Macrophyte production in Pool 1 and both marshes was similar to other productive habitats, and N and P content of above-sediment plant tissue was an order of magnitude greater than N and P in water of these sites. Estimates of macrophyte production (dry wt.) were on the order of 500 g/m^2 for *Nelumbo*, 200 g/m^2 for *Brasenia*, and 100 g/m^2 for *Myriophyllum*, *Ceratophyllum*, and *Nitella*.

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