

The Production, Nitrogen, and Phosphorus Dynamics
of Elodea sp., Potamogeton sp., and
Nitella sp. in Sam Rayburn
Reservoir, Texas

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ABSTRACT

The 1977 annual maximum biomass of Elodea sp., Potamogeton sp., and Nitella sp. was found to be 1013.6 g m^{-2} , 168.4 g m^{-2} , and 327.6 g m^{-2} , respectively. Combined, these plants produce $80,528.16 \text{ kg dry wt lake}^{-1} \text{ year}^{-1}$. However, this value is only 0.289% of phytoplankton production. Production of the macrophytes may have been greater had a severe draw-down not occurred.

The seasonal changes in ash weight and nutrient concentrations did not conform to the typical curves; nor did the seasonal change in biomass conform to the expected sigmoid curve (Westlake, 1965b). The atypical patterns were due to the effects suffered from the water level change.

Nitrogen and phosphorus concentrations in the plant tissues were not found to be indicative of environmental concentrations of nitrogen and phosphorus. This occurrence may have been due to neither nitrogen nor phosphorus of waters or sediments being limiting.

Evidence for secretion of phosphorus by Elodea sp. was found. Diffusion gradients of phosphorus were found between the interior and exterior of the Elodea sp. stands.

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I. INTRODUCTION

There were three primary objectives in this study: first, to describe seasonal trends of biomass, ash weight and tissue concentration of nitrogen and phosphorus of plants in a reservoir, second, to assess the relationship existing between productivity and the concentration of nitrogen and phosphorus in the tissues, ambient waters, and sediments, and third, to determine whether tissue nutrient concentrations are indicative of environmental nutrient concentrations. Of secondary interest was the investigation of nutrient loss from macrophytes to surrounding waters. All data were compared to other such information typical of submerged macrophytes in natural lakes.

Macrophytes have only in the last decade and a half begun to be recognized as important producers contributing to the eutrophication of a lake or reservoir (Wetzel, 1964). Because of this lack of understanding, there are only a few quantitative studies that describe the seasonal flux and interaction of macrophyte production with nutrient concentrations of plant tissues, waters, and sediments. After performing numerous studies of emergents, Boyd (1970) pointed out that data on submergents are needed for comparison of emergent and submergent plants.

The lack of data for submergent plants is primarily due to the inaccessibility of these organisms. Many devices such

as rakes, dredges, and mechanical samplers have been developed to collect submergents, but even at their best, the results these techniques yield are not quantitative. The refinement of self contained underwater breathing apparatus (SCUBA) equipment has made it possible to sample submergent plant populations accurately. Wood (1963), Schmid (1965) and Fager, et al. (1966) have described the advantages of SCUBA and the equipment needed for sampling and censusing submerged plant beds.

Many studies have established seasonal trends regarding production, percent ash weight and the nutrient concentrations of the plant (Penfound, 1956; Caines, 1965; Boyd, 1969; Boyd and Hess, 1970; Boyd and Vickers, 1971; Adams and McCracken, 1974; Klopatek, 1975; Nichols and Keeney, 1976), but these studies have predominantly been confined to lakes. Because lakes and reservoirs are vastly different, specifically in terms of stability and constant water levels, comparative data between macrophytes inhabiting lakes and reservoirs are needed.

The interaction between productivity of submerged plants and the concentrations of nutrients in water, tissues, and sediments needs to be clarified. Phosphorus and nitrogen are two of the most important factors governing phytoplankton production; perhaps, the same holds true for submerged vascular plants. Boyd and Vickers (1971) found that no correlation existed between the productivity of emergents and the inorganic nutrient concentrations of surrounding waters or underlying sediments. No such data have been published for submergents.

There is some argument as to whether tissue concentrations

of nutrients are reliable estimates of environmental concentrations of the same nutrients. Gerloff and Krombholz (1966) have demonstrated, in the laboratory, that up to a specific concentration, tissue and water nutrient concentrations are similar. Beyond a certain nutrient concentration, luxuriant uptake becomes important. Boyd and Hess (1970) reported that low, but significant correlations existed between the concentration of nutrients in emergent plant tissues and the environment, however, none of the correlations accounted for more than 32% of the variability in tissue concentrations of an element. Boyd (1970b) reported that the ratios of tissue nutrients of emergents in Par Pond, S. C. were not similar to the ratios of nutrients in the water, because of the accumulation of the nutrients in the plant tissues. In other studies of emergents, Boyd observed large accumulations of nutrients in plants (Boyd and Lawrence, 1966; Boyd, 1967). A proportional relationship has yet to be substantiated fully, or negated, between the external and internal nutrient concentrations, relative to the submerged plant. The submergent is more dependent on nutrient absorption from the water by foliage than the emergent; thus, the concentration of a particular nutrient in water may be directly related to the concentration of the same nutrient in submergent plant tissues.

The reason for attempting to determine whether submerged macrophytes act as "nutrient pumps" is because of the possible detrimental effects the aquatic ecosystem would suffer under such conditions. Adding sediment nutrients, which are

normally unavailable to phytoplankton, would presumably increase phytoplankton production tremendously and consequently accelerate eutrophication. DeMarte and Hartman (1974) established that, in the laboratory, Myriophyllum exalbescens is capable of releasing phosphorus to the surrounding waters. The amount of nutrient loss that occurs in the freshwater environment needs to be investigated. DeMarte and Hartman (1974) suggested that the excreted phosphorus in the environment follows a substrate-root-stem-leaf pathway. McRoy and Bardstate (1970) estimated that the saltwater macrophyte, Zostera minor, loses 33% of absorbed phosphorus to the ambient water. McRoy, et al., (1972) later estimated that $166 \text{ mg P m}^{-2} \text{ day}^{-1}$ was absorbed from the sediment by Zostera minor, and that 62 mg of that was excreted to the water.

The following definitions are presented to familiarize the reader with ambiguous, but essential, terminology used in the text of this paper. The fact is recognized that some of the definitions are debatable, and differences between some definitions slight; however, in this manuscript these definitions will apply:

Primary Production- the increase in biomass over a period of time plus all losses; thus, production is the quantity of new organic matter created by photosynthesis (Westlake, 1963, 1965; Wetzel, 1975).

Primary Productivity- the rate of production (Wetzel, 1975). If production is Q and the time T, then the productivity is

Q/T (Penfound, 1956; Westlake, 1965a). The difference between production and productivity is analogous to the difference between distance and velocity. Obviously, to travel any distance takes time in the same way as production of organic matter takes time. In the case of travel the distance is the concern, but in the case of production one conducts experiments for a particular time and then finds the production. A given distance, or a given production, corresponds to different periods according to the velocity or productivity (Westlake, 1965a). Productivity may or may not include losses through the time interval, as discussed below.

Gross Productivity- the observed change in biomass plus all losses, including respiration, divided by the time interval (Westlake, 1965a).

Net Productivity- the rate of production of new organic matter minus respiration divided by the time interval (Westlake, 1965a).

Standing Crop- the weight of plant material that can be sampled or harvested by normal methods at any one time (Westlake, 1963, 1965a; Wetzel, 1975). As applied to macrophytes, standing crop refers to only the above substrate tissue.

Biomass- the weight of all living material present in a unit area at a given time (Westlake, 1963, 1965a; Wetzel, 1975). As applied to macrophytes, biomass includes root and shoot structures.

II. LITERATURE REVIEW

A. Introduction

Aquatic vascular plants are an important component of aquatic ecosystems. Macrophytes provide habitat for microscopic plant life and for a wide variety of invertebrate and fish life (Nichols and Keeney, 1973, 1976). They are also important producers of organic matter that may be used by higher trophic levels in the aquatic ecosystem. Despite these positive ecological roles, large plant beds have in many instances become hindrances to the activities of man, e.g., obstructing the navigation and flow of water; hampering the use of water for recreational activities; interfering with hydroelectric production; and becoming potential health hazards (Smith, et al., 1967; Holm, et al., 1969). Because of these problems, present day investigations of aquatic macrophytes center around methods of controlling and containing weed growth.

Although the problems caused by excessive plant growth are pressing, the need for basic physiological and growth data still exists. The factors, or interaction of factors, governing plant production need to be quantified and their roles clarified. Data are needed on rates of production "...among varying climates, floral composition and community structure, and a host of community parameters." (Wetzel and

Hough, 1973). Questions concerning the relationships between the plant and its physical-chemical environment, the site of nutrient absorption among differing taxa, and an array of physiological problems need to be answered. These kinds of data can then be beneficial to those searching for a means of regulating macrophyte growth.

B. The Production of Aquatic Macrophytes

Estimates of primary production in aquatic ecosystems have, until recently, centered on that production contributed by phytoplankton. However, assessment of total production in aquatic systems may prove to be misleading if production due to aquatic macrophytes and periphyton is excluded. This oversight is especially true in shallow transparent waters (Straskraba, 1963; Wetzel, 1964b).

Average biomass values for phytoplankton and macrophytes on fertile sites vary between 0.01 - 0.1 kg dry wt m^{-2} and 0.2 - 10 kg dry wt m^{-2} , respectively (Westlake, 1963). Although this difference in biomass per unit area is large, total annual production of phytoplankton in an entire lake or reservoir may be greater than that of macrophytes. This phenomenon is due to the occurrence of a larger amount of suitable habitat and faster turnover rates for phytoplankton. Illustrating this point, Wetzel (1964b) reported total annual productivities of 101 and 1.36 kg C lake $^{-1}$ day $^{-1}$ for phytoplankton and macrophytes, respectively. However, in a large, clear shallow lake with an abundance of suitable habitat, macrophyte production could conceivably equal or exceed

phytoplankton production. As a result, any assessment of the trophic status of an aquatic ecosystem should include macrophyte production estimates.

Comparisons between the seasonal productions of macrophytes and terrestrial producers (Table 1) show emergent autotrophs (reedswamp) to be the most productive plants in temperate regions, and worldwide, second only to certain tropical communities (rainforest). However, submerged plant production is low, as compared to that of terrestrial and emergent communities.

Submerged communities exhibit low production because of rapid attenuation of light (Westlake, 1963) and the sluggish diffusion of carbon dioxide (Gessner, 1960). Submerged plants, despite these drawbacks, do have the advantage of a stable environment, e.g., temperature fluctuations are generally slow, water shortage problems do not exist, and the plants are well protected from winds, rains and wave action.

High production of emergent communities is the result of the plants being able to derive benefits from both the terrestrial and aquatic environments. Emergents are provided with an abundant supply of water and nutrients from the aquatic environment, while exposed to optimum light conditions and fast diffusion rates as a result of aerial shoots. Wave action poses the greatest threat to emergent vegetation.

Production rates and biomass values are extremely variable among aquatic macrophytes. These values vary from season to season, location to location, and species to species (Penfound,

Table 1. Probable annual net primary productivity of fertile sites (modified from Westlake, 1963).

approx. organic productivity (m.t. ha ⁻¹ yr ⁻¹)	range ± %	climate	type of ecosystem
1	50	arid	desert
2	50	—	ocean phytoplankton
2	50	temperate	lake phytoplankton
3	50	—	coastal phytoplankton
6	50	temperate	polluted lake phytoplankton
6	20	temperate	freshwater sub- merged macrophytes
12	25	temperate	deciduous forest
17	25	tropical	freshwater sub- merged macrophytes
20	25	temperate	terrestrial herbs
22	15	temperate	agriculture-annual plants
28	25	temperate	coniferous forest
29	15	temperate	marine submerged macrophytes
30	20	temperate	agriculture-peren- nial plants
30	20	—	salt marsh
30	20	tropical	agriculture-annual plants
35	15	tropical	marine submerged macrophytes
40	15	sub-trop.	cultivated algae
45	30	temperate	reedswamp
50	20	tropical	rain-forest
75	15	tropical	agriculture-peren- nial plants & reed swamp

1956). This is substantiated by the reported biomass and productivity values listed in Table 2.

Comparisons of plant production (Table 2) do not indicate a north-south trend in temperate climates. Rather, biomass values vary as much within regions of similar latitude as between regions of differing latitudes. The variable production values presumably indicate differences in individual lakes, rather than climate or latitude, as being responsible for the magnitude of production. As a result, studies should be designed toward discovering what factors are most important in determining production of aquatic plants within individual bodies of water.

Comparisons between plant types do show that emergent vegetation is generally more productive than submersed and floating vegetation; however, Eichornia crassipes (floating) does exhibit productivities and biomass values comparable to those of emergents.

Thus far, plant studies have been conducted primarily in northern waters. I feel more studies are needed throughout the United States before accurate conclusions regarding trends in plant production can be made.

C. The Nutrition of Aquatic Macrophytes

1. The Role of the Root in Nutrient Absorption.

In the latter part of the last century, it was believed that aquatic angiosperms derived all of their nutrients from the surrounding waters by foliar uptake (Hutchinson, 1975). The roots were perceived as simply holdfasts.

Table 2. Reported maximum seasonal biomass values (dry wt.) or standing crop values (dry wt.) and productivities (Modified and expanded from Wetzel, 1975 and Sculthorpe, 1967).

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Lake	Submergent Plant Species	Standing Crop or Max. Biomass	Productivity	#
L. Mendota, Wis.	<u>Chara</u> sp. and <u>Nitella</u> sp.	92.92 g C m ⁻²	—	1
Green L., Wis.	<u>Chara</u> sp. and <u>Nitella</u> sp.	81.88	—	2
Little John L., Wis.	<u>Chara</u> sp. and <u>Nitella</u> sp.	00.23	—	3
Muskellunge L., Wis.	<u>Chara</u> sp. and <u>Nitella</u> sp.	00.21	—	3
Sweeney L., Wis.	<u>Chara</u> sp. and <u>Nitella</u> sp.	00.80	—	4
Trout L., Wis.	<u>Chara</u> sp. and <u>Nitella</u> sp.	00.03	—	5
Weber L., Wis.	<u>Chara</u> sp. and <u>Nitella</u> sp.	7.72	—	6
Lawrence L., Mich.	<u>Chara</u> sp.	50.60	71.3 g C m ⁻² yr ⁻¹	7
West Blue L., Manitoba	<u>Chara vulgaris</u>	80.96	2.1 mg C m ⁻² day ⁻¹	8
River Yare, England	<u>Potamogeton</u> sp.	174.80	—	9
Lowes L., Scotland	<u>Potamogeton</u> sp.	14.72	—	10
Spiggie L., Scotland	<u>Potamogeton</u> sp.	46.09	—	10
River Colne, England	<u>Potamogeton pectinatus</u>	55.20	—	11
Chautaugua L., N.Y.	<u>Potamogeton crispus</u>	120.01	—	12
L. Maggiore, N.Y.	<u>Potamogeton crispus</u>	—	3.32 mg C g (dry wt.) ⁻¹ hr ⁻¹	13
L. Maggiore, N.Y.	<u>Potamogeton lucens</u>	—	4.42 mg C g (dry wt.) ⁻¹ hr ⁻¹	13
West Blue L., Manitoba	<u>Potamogeton richardsonii</u>	14.40 g C m ⁻²	2.4 mg C m ⁻² day ⁻¹	8
West Blue L., Manitoba	<u>Potamogeton pectinatus</u>	1.3	0.2 mg C m ⁻² day ⁻¹	8
L. Osby, Sweden	<u>Myriophyllum verticillatum</u>	110.40	—	14
Chautaugua L., N.Y.	<u>Myriophyllum</u> and <u>Anacharis canadensis</u>	41.70	—	12
L. Maggiore, N.Y.	<u>Myriophyllum spicatum</u>	—	6.64 mg C g (dry wt.) ⁻¹ hr ⁻¹	13
West Blue L., Manitoba	<u>Myriophyllum alterniflorum</u>	5.60	0.8 mg C m ⁻² day ⁻¹	8
L. Wingra, Wis.	<u>Myriophyllum spicatum</u>	92.00	379 mg C m ⁻² day ⁻¹	15
L. Grasvarpet, Sweden	<u>Ceratophyllum demersum</u>	128.80	—	16
L. Osby, Sweden	<u>Ceratophyllum demersum</u>	312.80	—	14

Table 2 - Cont'd.

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<u>Lake</u>	<u>Submergent Plant Species</u>	<u>Standing Crop or Max. Biomass</u>	<u>Productivity</u>	<u>*</u>
Doodhadhari L., India	<u>Ceratophyllum & Hydrilla</u>	48.57 g C m ⁻²	—	17
Chautaugua L., N.Y.	<u>Vallisneria americana</u> & <u>Anacharis canadensis</u>	44.90 50-200	—	12
River Test, England	<u>Ranunculus sp.</u>	174.80	—	18
Bere Stream, England	<u>Ranunculus pinnatifidus</u>	27.60	—	19
Borax L., California	<u>Ruppia sp.</u>	238.74	29.4 g C m ⁻² yr ⁻¹	20
River Ivel, England	<u>Berula erecta</u>	—	4.32 mg C g (dry wt) - 1 hr ⁻¹	18
L. Maggiore, N.Y.	<u>Loganosiphon major</u>	—	0.30 mg C g (dry wt) - 1 hr ⁻¹	13
L. Maggiore, N.Y.	<u>Trapa natans</u>	—	2.08 mg C m ⁻² day ⁻¹	17
West Blue L., Manitoba	<u>Megalodonta beckii</u>	14.80 g C m ⁻²	—	13
Doodhadhari L., India	<u>Najas minor</u>	57.45	—	8
				17
<u>Lake</u>	<u>Floating Plant Species</u>	<u>Standing Crop or Max. Biomass</u>	<u>Productivity</u>	<u>*</u>
New Orleans, La.	<u>Eichornia crassipes</u>	289.80-627.12 g C m ⁻²	690-2530 g C m ⁻² yr ⁻¹	21
Czechoslovakia	<u>Lemna minor</u>	23.00 g C m ⁻²	—	22
	<u>Lemna gibba</u>	69.00	—	22
Par Pond, S.C.	<u>Nymphaea odorata</u>	117.76	—	23
	<u>Nuphar advena</u>	84.00	—	23
<u>Lake</u>	<u>Emergent Plant Species</u>	<u>Standing Crop Max. Biomass</u>	<u>Productivity</u>	<u>*</u>
Minn. wetlands	<u>Carex sp.</u>	391.00	339.4 g C m ⁻² yr ⁻¹	24

Table 2 - Cont'd.

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<u>Lake</u>	<u>Emergent Plant Species</u>	<u>Standing Crop or Max. Biomass</u>	<u>Productivity</u>	<u>*</u>
Surlingham Broad, England	<u>Glyceria sp., Typha sp., Phragmites sp.</u>	368-506 g C m ⁻²	—	25
Opatovicky Pond, Czechoslovakia	<u>Phragmites sp.</u>	3266-4949 g C m ⁻²	—	26
Cedar Creek, Minn.	<u>Typha sp.</u>	2134.40 g C m ⁻²	1150 g C m ⁻² yr ⁻¹	27
Par Pond, S.C.	<u>Scirpus domingensis</u>	682.18	—	23
	<u>Scirpus validus</u>	639.86	—	23
	<u>Eleocharis quadrangulata</u>	333.50	—	23
	<u>Pontederia cordata</u>	329.36	—	23
	<u>Typha latifolia</u>	264.04	—	23
	<u>Scirpus americanus</u>	188.60	—	23
	<u>Eleocharis equisetoides</u>	173.42	—	23
Steel Pond, S.C.	<u>Juncus effusus</u>	732.32	—	28
L. Ogletree, Ala.	<u>Justicia americana</u>	1130.68	—	29
	<u>Alteranthera philoxeroides</u>	386.86	—	29
Silver Springs, Fla.	<u>Sagittaria subulata</u>	285.66	—	30
Southeast U.S.	<u>Typha latifolia</u>	1035.92	—	31
Ladoga L., USSR	emergents	0.18-4.92 g C m ⁻²	—	32
Onega L., USSR	emergents	0.05-15.18 g C m ⁻²	—	32
Polish Lakes	emergents	202.4-381.8 g C m ⁻²	—	33

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- (2) Rickett, (1924)
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Table 2 - Cont'd.

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 (32) Raspopov, (1971).
 (33) Szczepanska, (1973).

The first major study attempting to determine whether the root functions as an absorption organ was performed by Pond (1905). By rooting Elodea canadensis, Potamogeton perfoliatus and Myriophyllum exalbescens in sand and natural sediments, Pond observed that better growth occurred on the natural sediment. Growth was measured as increase in length of the shoot. He thus concluded that the sediments contained essential elements supplied to the plant via the root.

Snell (1908) performed a similar experiment using Groenlandia densa, as well as Elodea canadensis, and observed best growth on natural substrate. Snell also found that removing the roots from the floating Lemna minor and Spirodela polyrhiza did not curtail growth. Accordingly, he concluded the roots to be of no value in absorbing nutrients.

Additional data supplied by Pond (1905) and Snell (1908) showed Elodea sp., Potamogeton sp. and Ranunculus sp. as being capable of absorbing lithium chloride and potassium ferricyanide through the roots and translocating them to other plant parts. These data gave further credence to the idea that roots were instrumental in providing nutrition to the plant.

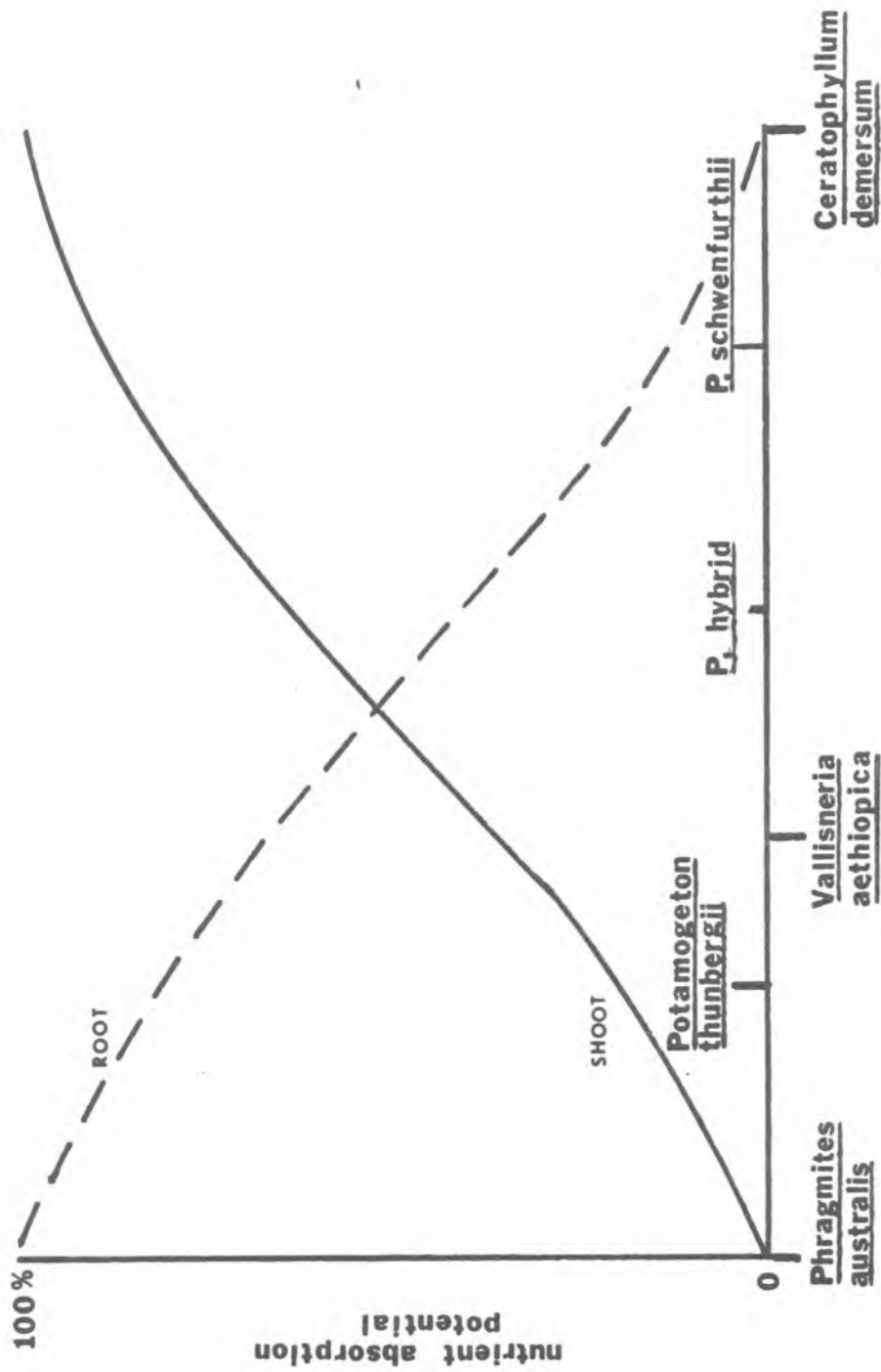
Brown (1913), using Elodea canadensis, copied Pond's and Snell's work. The results obtained showed that differences in growth rates between plants rooted in sand and natural soil could be eliminated by bubbling with CO₂. He concluded that the soil was only providing CO₂ for photosynthesis through the decomposition of organic matter. However, as Hutchinson

(1975) points out, the two experiments are not comparable. Brown was using soft water and was probably seeing a CO₂ limitation long before the limitation of other materials became important.

Over the next forty years studies were continued which confirmed that rooted angiosperms grew better on natural sediment than on sand (Moyle, 1945; Mulligan and Baranowski, 1969). Although the work of Pond (1905) and Snell (1908) and each of their successors did establish that plants grow better when rooted in a natural substrate, no conclusion could be drawn as to whether or not the benefit was due to nutrient absorption by the roots.

The work of Denny (1972) established that sediments, as well as water, could supply nutrients via the roots. In this study, six taxa including three species of Potamogeton, were planted in artificial ponds with either nutrient-rich mud or nutrient-poor sand as a substrate. The Potamogeton species provided the key by demonstrating a trend from great dependence on root absorption to very little dependence. The degree of root absorption was positively correlated with trends toward emergence, complexity of shoot structures (vascular tissue) and an increasing root-shoot ratio on sand substrates. With these correlations Denny (1972) constructed a schematic diagram of the factors that possibly contribute to a tendency for root or shoot absorption (Fig. 1). Submergence and simple anatomy, with little differentiation of plant tissues, probably indicates foliar uptake. Vascular differentiation and high root-shoot ratios reflect nutrient uptake by the roots.

Fig. 1. A schematic diagram of factors which could contribute towards a tendency for root or shoot nutrient absorption. The taxa are arranged in a linear order of shoot absorption potential but their actual position on the x-axis is arbitrary (redrawn from Denny, 1972).



SUBMERGED
 DIRECT SUBSTRATE EFFECT (MUD/SAND GROWTH RATE RATIO)
 SIMPLICITY OF ANATOMY
 ROOT/SHOOT RATIO ON POOR SUBSTRATE
 VASCULAR DIFFERENTIATION

McRoy and Barsdate (1970), in laboratory experiments, found Zostera minor capable of absorbing phosphate by either roots or foliage. However, they believed that in natural surroundings the sediment was probably the main source of phosphate.

Radioisotopes have been used successfully to elucidate the role of the root. Bristow and Whitcomb (1971) cultured three aquatic species in a two-compartment apparatus which allowed the upper and lower portions of the plant to be kept in different nutrient solutions. ^{32}P was supplied to either compartment. The radioactivity of the phosphate-labeled tissue was determined in axillary shoots after a 10-day growing period. With the exception of Myriophyllum spicatum, most of the phosphate was absorbed in the lower compartment by the roots (90% in Myriophyllum brasiliense, 50% in M. spicatum and 74% in Elodea densa).

Toetz (1974), using a modified Bristow and Whitcomb apparatus, measured the uptake of $^{15}\text{NH}_4$ in Potamogeton pectinatus, Scirpus sp., Elodea densa and Ceratophyllum demersum. E. densa absorbed $^{15}\text{NH}_4$ via the roots and translocated it to the shoots. $^{15}\text{NH}_4$ uptake and translocation occurred in P. pectinatus, but was slow, taking 3 days. Scirpus sp., surprisingly, exhibited no translocation to shoots. C. demersum was found to take in $^{15}\text{NH}_4$ equally well in basal and apical tips.

DeMarte and Hartman (1974), using an apparatus which again isolated root and shoot systems, obtained direct evidence that ^{32}P , ^{59}Fe and ^{45}Ca were absorbed by the roots of

of Myriophyllum exalbescens and translocated to shoot tissues. The experiment showed that uptake varied depending on the substrate type (sand or ooze) and the element being traced, e.g., ^{32}P translocation occurred equally well in either sediment type, ^{45}Ca exhibited the greatest translocation rate when plants were rooted in sand, and ^{59}Fe translocation occurred mainly when the plants were rooted in ooze.

Nichols and Keeney (1976b) using a two-compartment apparatus found foliar uptake in Myriophyllum spicatum to supply about twice as much nitrogen to new shoots and about five times as much nitrogen to the old shoots as did root uptake. However, they believed that plant nitrogen requirements could be met by the roots alone. Interestingly, foliar uptake of $\text{NH}_4\text{-N}$ was found to be several times faster than that of $\text{NO}_3\text{-N}$ when both forms of nitrogen were present in the water.

Other studies searching for sites of nutrient absorption have been done. Arisz (1963) established that Vallisneria aethiopica can absorb nutrients through the leaves. Littlefield and Forsberg (1956) have shown that nonvascular Chara sp. is capable of absorbing phosphorus in all parts.

No doubt exists, from this discussion, that some aquatic plants are capable of absorbing nutrients through roots. However, additional data are needed for a much wider variety of plants and for all the macro and micro nutrients. Trends or keys to sites of absorption, such as hypothesized by Denny (1972), e.g., no vascular differentiation, should also be looked for in any such analysis.

2. The Secretion of Dissolved Organic Compounds, Nitrogen and Phosphorus

Interest has recently been focused on the excretion of dissolved substances from plants to ambient waters. From the minimal research that has been done on vascular plants, the plants which obtain their nutrition from the sediment are the most likely to excrete dissolved compounds. It has been suggested that the loss of substances follows a substrate-root-stem-leaf pathway (DeMarte and Hartman, 1974). The effect of addition to the water of otherwise unavailable sediment nutrients is accelerated eutrophication. Eutrophication would be increased by stimulation of phytoplankton production by the added nutrients.

Wetzel (1969), using Najas flexilis in a laboratory study, simultaneously measured the excretion of dissolved organic compounds, photosynthetic rates and nutrient concentrations of the water. With increasing concentrations of Ca^{++} in the range of 10 - 20 mg l^{-1} , photosynthetic rates increased while the excretion of dissolved organic carbon decreased. Above 20 mg l^{-1} Ca^{++} photosynthetic rates and excretion of dissolved organic carbon decreased. Wetzel credited the decreased excretion of organic compounds to the reduction in cytoplasmic permeability and dehydration that accompany increasing concentrations of calcium. Contrary to these results, excretion of organic compounds increased with most increases in Mg^{++} and Na^+ , while photosynthetic rates decreased. A strong interaction between photosynthetic rates, excretion rates and light intensity was also observed.

Under low light conditions, dissolved organic compound loss was enhanced and photosynthesis was reduced. The opposite was true for high light intensities. From these results it seems that a negative relationship exists between dissolved organic compound loss and light intensity or photosynthesis.

Working with phosphorus absorbed by the roots, McRoy and Barsdate (1970) observed a phosphorus loss from Zostera marina to surrounding waters. They estimated that 33% of the phosphate absorbed by the roots was released to the water. In a later study, McRoy, et al., (1972) estimated that $166 \text{ mg P m}^{-2} \text{ day}^{-1}$ was absorbed from the sediments by Zostera marina, and that 62 mg of that was excreted to the water.

DeMarte and Hartman (1974) found Myriophyllum exalbescens capable of absorbing ^{32}P by the roots and releasing a portion to the water. The excreted ^{32}P was then absorbed by the foliage of Elodea canadensis. Evidence also indicated that the release of absorbed ^{32}P could be increased by injury to shoots. Contrary to the results of DeMarte and Hartman (1974) and McRoy and Barsdate (1970, 1972), Bristow and Whitcombe (1971) did not observe the loss of ^{32}P in their studies of Myriophyllum sp. and Elodea sp.

The release of nitrogen is not as well documented as that of phosphorus. Nichols and Keeney (1976b) stated that 1% of nitrogen taken up by the roots was released to the water by foliage of Myriophyllum sp. Wetzel and Manny (1972a) found a fraction of the dissolved organic matter secreted from Najas flexilis to contain nitrogen.

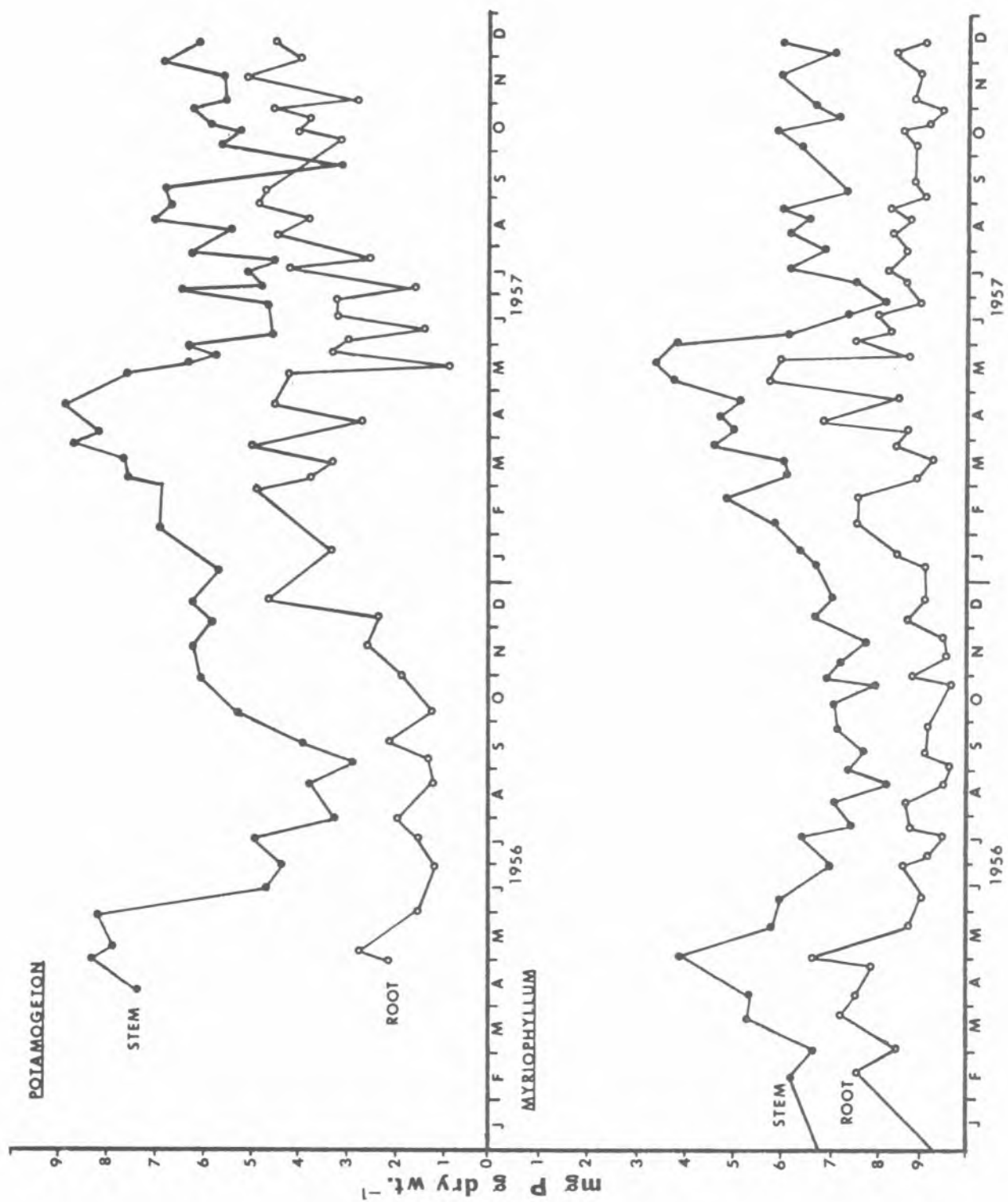
3. Seasonal Fluctuations in the Nutrient Content of Macrophytes.

Caines (1965), investigating the phosphorus content of Myriophyllum sp. and Potamogeton sp., found that phosphorus fluctuations were cyclic (Fig. 2). Maximum tissue concentrations occur in April and May, followed by a rapid decline through June, July, and August. The late summer minimum is followed by slow accrument, until a high concentration is again obtained.

Caines explains the initial spring maximum concentration to be the result of increased nutrient absorption due to accelerated metabolic activities. The summer low is credited to the increased demands of reproductive shoots and the subsequent translocation to such areas. However, no analysis of reproductive tissues was conducted to confirm this hypothesis. The fall accumulation of phosphorus is due to the end of flowering; thus, the demand for phosphorus is lessened.

Working with the emergent, Justicia americana, Boyd (1969) observed many of the macronutrients, especially nitrogen and phosphorus, to occur in high concentration early in the growing season and subsequently decline. Boyd also observed the highest absorption rates for several mobile nutrients to be early in the growing season, e.g., nitrogen, sulfur, and potassium. According to Boyd (1969), absorbing large quantities of nutrients in the spring, vascular plants lessen their competition with the phytoplankton. However, phytoplankton normally exhibit increased photosynthesis early and late in the growing season; therefore, macrophytes and phytoplankton would be in direct competition for available nutrients in the spring.

Fig. 2. Seasonal variation in the P content (mg P/g dried plant material) of Myriophyllum alterniflorum and Potamogeton praelongus (redrawn from Caines, 1965).



Because of this phenomenon Boyd's hypothesis is less tenable.

Boyd (1970a) and Boyd and Hess (1970) investigated the seasonal cycle of nutrients in the emergents, Scirpus americanus and Typha latifolia. Again the spring maximum and summer minimum concentrations were observed. In the T. latifolia stand attempts were also made to correlate tissue nutrient content with concentration in the water and sediment. Although some significant positive correlations were derived, e.g., phosphorus in waters, $r=0.44$; potassium in waters, $r=0.50$; sodium in waters, $r=0.56$; magnesium in sediments, $r=0.46$, and sodium in sediments, $r=0.53$, none of the correlations accounted for more than 32% of the variability in tissue concentrations of an element. Boyd (1970b) found that the ratio of nutrients in tissues was different from the ratio of the same nutrients in the water due to the accumulation of nutrients in the plants. Large concentration factors for phosphorus and manganese have also been reported for filamentous algae (Boyd and Lawrence, 1966) and Justicia americana Boyd (1967). These results are contrary to those obtained by Gerloff and Krombholz (1966) who suggested that tissue nutrient analyses can be used as an index of available nutrients in waters. The discrepancy is probably because Gerloff and Krombholz varied only one nutrient under controlled conditions and kept all other nutrients in adequate supply. This type of experiment may result in erroneous data because "... many interrelationships exist between the concentration and ratios of ions in the environment and uptake of these ions by plants." (Sutcliffe, 1962).

In another study of emergents, Boyd and Vickers (1971) again observed the typical seasonal pattern of tissue nutrient content change in Eleocharis quadrangulata. This study established clearly that maximum growth and maximum nutrient uptake in an emergent do not coincide. It was also pointed out that although the highest tissue concentration of a particular ion is early in the growing season, the maximum value per area of lake does not occur until the maximum seasonal biomass is obtained or a point immediately preceeding it.

By coupling the concentration of nutrients in the plant (percent dry weight) with the amount of nutrients accrued by emergent vegetation (Fig. 3 & 4), Klopatek (1975) was able to divide the seasonal nutrient cycle into four phases. Phase I is characterized as occurring early in the season when tissue concentrations are at their highest and growth is in a lag phase. Phase 2 is the period of peak nutrient accumulation and maximum decline in tissue concentration per area. This phase exists until the maximum seasonal biomass is reached. Phase 3 begins with a major switching in the life cycle of the plant. In this phase root growth is increased and subsequent nutrient translocation to the below ground structures occurs. Phase 4 is the time of leveling off of tissue nutrient concentrations and the decline of nutrient levels per area, due to losses of tissue. This phase is best illustrated by Scirpus fluviatilis (Fig. 4).

The submergent, Myriophyllum spicatum, was found to exhibit a similar pattern for nitrogen concentration over

Fig. 3. Seasonal change in nitrogen and phosphorus content and the accumulation of nitrogen and phosphorus in Typha latifolia of Theresa Marsh in 1972; ● shoot, ○ roots and rhizomes, ■ total (Klopatek, 1975).

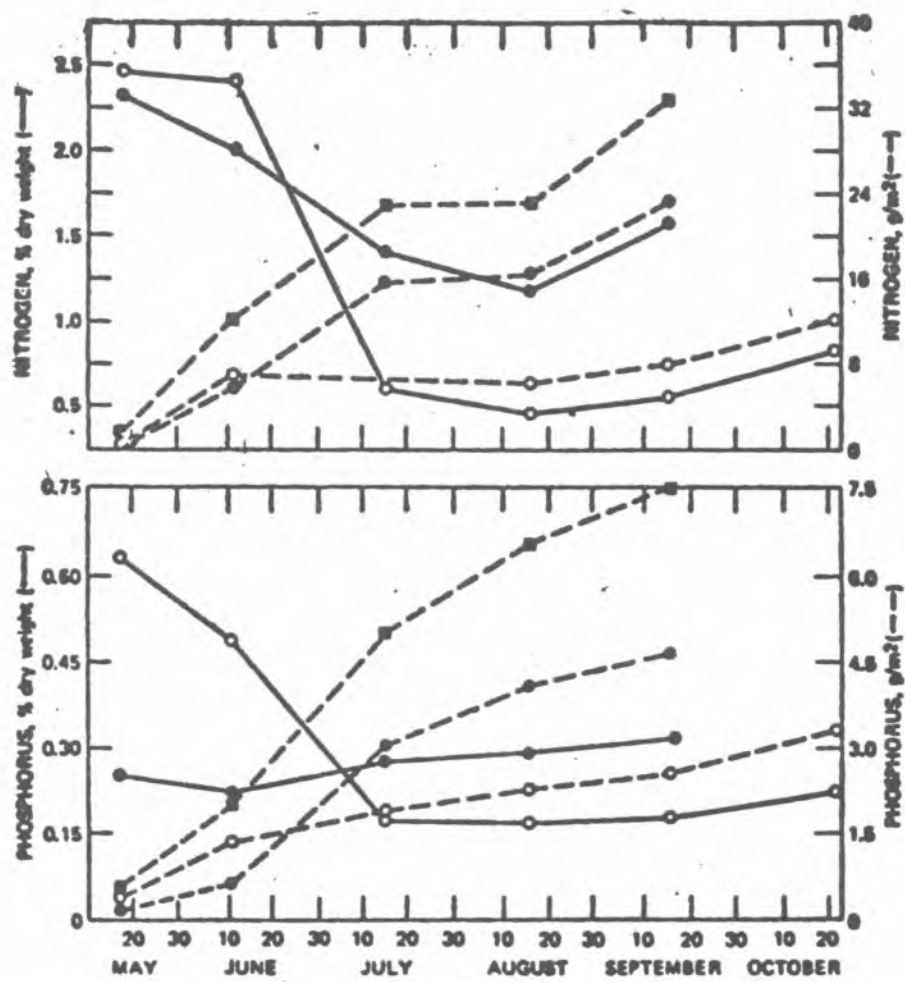
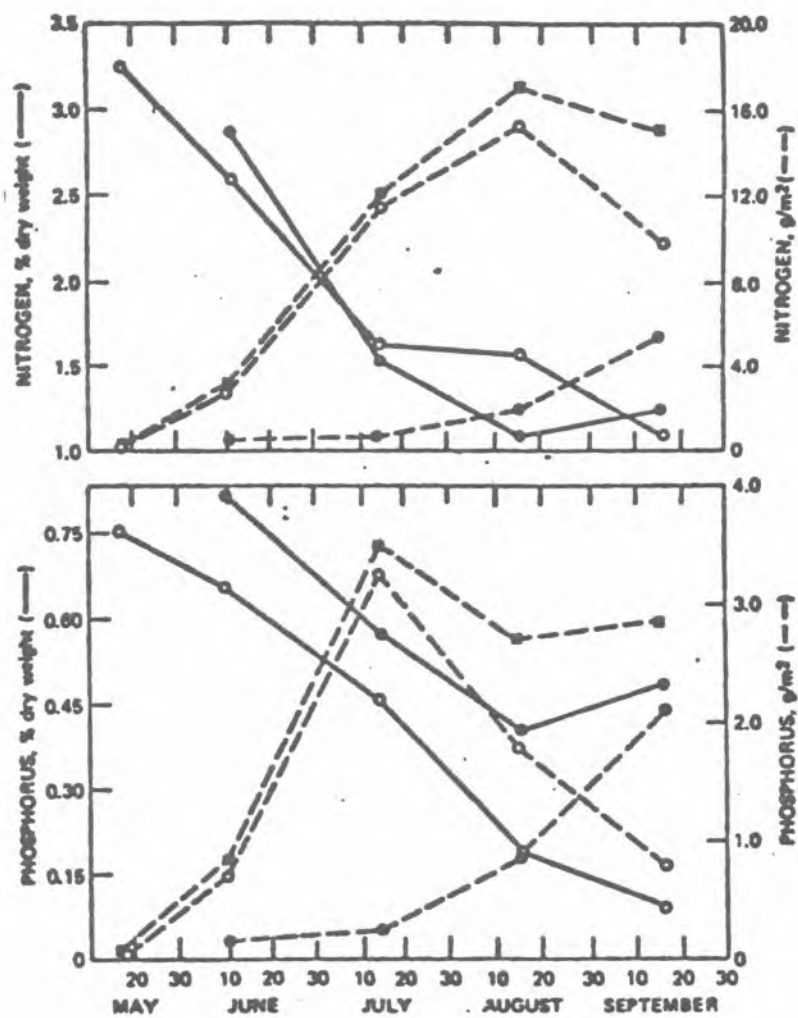


Fig. 4. Seasonal change in the nitrogen and phosphorus content and the accumulation of nitrogen and phosphorus in Scirpus fluviatilis of Theresa Marsh during 1972; ● shoots, ○ roots and rhizomes, ■ total (Klopatek, 1975).



the growing season, as compared to emergents (Nichols and Keeney, 1976). The authors credit the decreasing nitrogen concentrations during the summer to nitrogen uptake being less than nitrogen use, due to vigorous growth.

As can be seen, the seasonal cycle of nutrients among emergents is well established and has been thoroughly investigated. However, little knowledge of submergents is available, as emphasized by Boyd and Vickers (1971):

There appears to be little need for additional research of this type on emergent plants. However, studies of the dynamics of dry matter and chemical substances in populations of submerged species would be of interest because these plants have much different life habits than emergent macrophytes.

D. Important Factors Governing the Production and Distribution of Aquatic Macrophyte Beds

1. Effect of Controlling Factors.

A number of factors control the distribution and production of macrophytes, e.g., light quality and quantity, dissolved gases, nutrient levels, substrate composition, presence of phytoplankton, wave action, etc. Although these controlling factors are diverse, each affects plant growth in one of two ways; (1) a needed substance may not be present in sufficient amounts for maximum growth, such as light or one or more nutrients, or (2) the factors may be antagonistic to the growth of plants. Vigorous wave action (Wilson, 1941), adverse climate (Peltier and Welch, 1970), and presence of high concentrations of phytoplankton (Mulligan, et al., 1969, 1976; Jupp and Spence, 1977) can cause poor macrophyte pro-

duction or complete elimination of plant beds. Three factors important in regulating growth will be presented here. These are light, substrate type, and nutrient content of waters.

2. Light.

Light, quality and quantity, is the overriding factor regulating photosynthesis. Owens and Edwards (1961) stated that "... the growth of macrophytes is primarily determined by the amount of available solar radiation." Robel (1961) correlated low light with low production of plants. Peltier and Welch (1970) credited high light intensities for plant explosions. The vertical extinction of light within beds has even been used to estimate standing crops (Westlake, 1964).

Normally, aquatic vegetation can exist at light intensities as low as 1 - 4 percent of the surface intensity (Sculthorpe, 1967). The actual depth at which light becomes limiting and plants cease to exist varies with the color of the water and the concentration of organic and inorganic particles.

The maximum reported depth of vascular angiosperm occurrence is in Lake George, New York (Sheldon and Boylen, 1977). Elodea canadensis was reported at a depth of 12 m, Potamogeton robbinsii at 10 m, P. pusillus at 9 m and other Potamogeton species at 7 m. In this lake 10% of surface light was able to penetrate to 12 m. Until this discovery, vascular plants were thought to have been confined to the upper 10 m of a body of water (Sculthorpe, 1967). Arber (1920) reported Ceratophyllum sp. growing at 9 m, which is unusual, since

Ceratophyllum is rootless and generally considered a floating plant.

Under circumstances where light penetrates to great depths, factors other than light become limiting. These include temperature (Arber, 1920), hydrostatic pressure (Ruttner, 1963), and anerobic conditions.

Bryophytes and Charophytes have the ability to penetrate to greater depths than vascular angiosperms. The Charophyte, Nitella sp., has been found at 27 m in a volcanic lake in Japan (Jimbo, et al., 1955). Juday (1934) reported bryophytes and periphyton growing at 18 - 21 m in Crystal Lake, Wisconsin. Depths of 120 m have been reported for aquatic mosses in Crater Lake, Oregon (Hasler, 1938) and 175 m in Lake Tahoe, California and Nevada (Frantz and Cordone, 1967).

Water depth and turbidity are often positively correlated with photosynthesis (Robel, 1961; Peltier and Welch, 1969; Meyer, et al., 1941). Increasing quantities of light should yield higher photosynthetic rates. However, Meyer (1943) reported maximum photosynthesis to occur at light intensities less than that of full sunlight. Schomer (1934) asserted the optimum depth for photosynthesis of Elodea sp. and Ceratophyllum sp. to be 5 m.

Although photorespiration of aquatic plants is less than that of terrestrial plants, this phenomenon has been demonstrated to occur under high light and oxygen conditions (Hough and Wetzel, 1972; Hough, 1974), and may explain why Meyer (1943) and Schomer (1934) found maximum photosynthesis at lower light intensities.

Results contrary to those above have been reported. Manning, et al., (1938) did not see diminished photosynthetic rates at the surface for Potamogeton sp., Vallisneria sp., and Sagittaria s.p. Adams et al., (1974) found 56% of the total productivity for Myriophyllum spicatum to be within 20 cm of the surface. Light attenuation and depth distribution of photosynthetic tissues were cited as the major reasons for decreased photosynthesis with depth.

In addition to influencing the production of plants, light can also affect the diversity of aquatic plant life (Sheldon and Boylen, 1977). Diversity drops linearly with increased depth. Apparently, few species are adapted for very low light intensities. Because of less competition from other species, low-light adapted taxa can successfully fill the deeper niches.

Spence and Chrystal (1970) concluded that light might be as important as substrate or competition in controlling the zonation of macrophytes. Light, however, is the indirect cause of zonation. The amount of light may be responsible for restricting plants to specific areas, but only because certain species are better adapted than others for that particular light intensity. Because of this reasoning, competition is the fundamental factor determining zonation.

In summary, light affects aquatic plant life in three ways; (1) the production, (2) the depth to which plants will occur, and (3) the diversity of taxa existing in a single locality.

3. The Composition of the Sediment and Water

Many investigators have reported apparent relationships between the occurrence of aquatic plant beds and the underlying sediment composition (Brown, 1911; Pearsall, 1917, 1918, 1920, 1921; Welch, 1935; Misra, 1938; Potzger, et al., 1942; Boyd, 1967). Particle size, chemical composition and rate of sedimentation are the chief edaphic factors governing plant distribution. Not all plants exhibit maximum growth under the same conditions. Monodominant stands are the result.

Generally, best macrophyte growth occurs in sand. Minerals are supplied indirectly to the plant by the filtration of organic matter through the sand. Misra (1938), working with three soil types mixed in the laboratory, found good growth of some plants, e.g., Isoetes lacustris, in highly organic sediments. However, no such growth was found on organic soils in lakes. Misra concluded that the heavy sedimentation needed to form organic soils would not permit plant growth. Wilson (1937) reported large losses of plant material during periods of heavy organic matter decomposition.

Nitrogen, calcium, and potassium have been found to be supplied to plants via the sediment. Nichols and Keeney (1976a) found sediment nitrogen and tissue nitrogen in Myriophyllum spicatum to be related. Although some plants have the ability to absorb nutrients from the sediment, it has yet to be demonstrated how much absorption occurs in nature, and to what extent this governs submerged plant existence.

Many have cited the nutrient status of ambient waters

surrounding plants to be the most important factor governing plant distribution (Juday, 1942); Edwards and Owens, 1960; Seddon, 1965; Spence, 1967). Moyle (1945) was able to divide the lakes of Minnesota into three categories of floral composition on the basis of degrees of hardness. The pH has been found to control the distribution of macrophytes in the lakes of Denmark (Iverson, 1929). Metcalf (1931) observed a relationship between plant distribution and the dissolved mineral content of the water in North Dakota lakes. Salinity has also been shown to be important in governing plant distribution (Penfound and Hathaway, 1938). However, in terms of governing plant production, the chemistry of hard waters can support the heaviest growth.

Studies attempting to discern the role of specific macronutrients in the water have been performed by fertilizing replicated ponds. Mulligan, et al., (1969, 1976) enriched pond and lab samples with ammonium nitrate and triple super phosphate ($\text{CaH}_4 \cdot (\text{PO}_4)_2 \cdot \text{H}_2\text{O}$). These forms of nitrogen and phosphorus were determined, in greenhouse experiments, to be the most appropriate forms to support optimal growth of Potamogeton sp., Myriophyllum sp., and Elodea sp. The most significant fact to come from this work was the loss of plant material with continued enrichment of the water. Under such conditions, phytoplankton blooms formed immediately and outcompeted the macrophytes for light. Jupp and Spence (1977) also observed the inhibitory effects of phytoplankton on macrophytes in Loch Levin. Loch Levin waters have a phosphate-phosphorus concentration greater than 0.05 mg l^{-1} . Because this phosphate concentration is able to sustain large phytoplankton densities, the investigators concluded the

inhibitory effect of algal blooms to be due to "... attenuation of irradiance and an increase in pH."

Moore (1952) and Hasler and Jones (1949) credited low phytoplankton production to luxuriant growth of submerged macrophytes. In the study of Mulligan, et al., (1976), Elodea canadensis was able to survive the high phytoplankton densities, but growth was less than the control. The fact that macrophytes and phytoplankton apparently compete for nutrients and light lends support to Boyd's (1969) hypothesis that macrophytes absorb the majority of their nutrients during the spring, before the maximum concentration of phytoplankton.

Obviously, many factors interact to determine the existence of plants. Chemical components, both sediment and water, may interact among themselves (Sutcliffe, 1962) or with other components of the ecosystem, e.g., phytoplankton, to regulate plant growth. Therefore, efforts should be made to measure many parameters and their interaction as they affect macrophytes. This approach can provide considerable information on the ecology of macrophytes.

E. Methodolgy

1. The Measurement of Production.

The primary production of aquatic macrophytes has been most commonly estimated by one of three techniques; change in biomass, ^{14}C assimilation, or O_2 production. The latter two have the advantage of being applied in situ, while biomass changes represent a more static approach. Change in biomass and ^{14}C assimilation are different estimates of net production

(organic matter produced minus that lost by respiration). Oxygen techniques yield an estimate of gross production (organic matter produced including that respired).

Since excellent reviews and descriptions of techniques are presented elsewhere (Wetzel, 1964a, 1964b, 1965; Westlake, 1963, 1965b), it would be redundant to describe the methods in detail. Therefore, I will discuss the advantages and disadvantages of each technique as they affect the attainment of accurate results.

a. O_2 evolution.

The measurement of in situ primary production of aquatic macrophytes can be estimated from diurnal oxygen curves as described by Odum (1956). Studies using this technique for macrophyte production estimates are few (cf. Wetzel, 1964b). The technique is based on the assumption that for each mole of inorganic carbon dioxide reduced to organic carbon, one mole of oxygen is released (Ryther, 1956). This occurrence is rarely the case. Most studies in which the photosynthetic quotient is derived (oxygen evolved to carbon dioxide assimilated) yield values above one.

As applied to aquatic vascular plants, this method contains inherent errors. In such in situ experiments, the dissolved oxygen concentration is influenced by all biotic components of the ecosystem. The density of epiphytic algae and bacteria is considerable on aquatic macrophytes and may bias measurements. Thus, diurnal oxygen curves are more accurately a measure of community metabolism.

The lacunal systems of macrophytes represent a second source of error in this technique. Hartman and Brown (1966) proved that during photosynthesis, oxygen concentration increases rapidly within the lacunae, but diffuses slowly to the surrounding waters. Thus, the diffusion of oxygen out of the plant is not proportional to the degree of photosynthesis.

Because of both errors mentioned, the data from studies of macrophytes where oxygen techniques have been employed as a measurement of production should be discarded or used with extreme caution (Wetzel, 1964b, 1965).

b. ^{14}C Assimilation

The assimilation of CO_2 is equal, mole for mole, to the production of organic carbon. Thus, it is the most direct approach to the measurement of primary production (Ryther, 1956). The ^{14}C techniques for the measurement of in situ productivity are described by Wetzel (1964a, 1964b). The technique and calculations for macrophytes are similar to those for phytoplankton.

The greatest difference between the ^{14}C technique of vascular plants and phytoplankton is the conversion of plant organic carbon to CO_2 for radioassay in the gas phase. ^{14}C in phytoplankton is usually determined from intact, filtered cells.

The validity of the ^{14}C for macrophytes is weakened if CO_2 builds up in the lacunal systems. However, CO_2 diffusion rates are much greater than those of oxygen. Because of this phenomenon, the error is probably minimal.

The ineffective removal of periphyton from plant surfaces may cause overestimates of net production due to their uptake of ^{14}C . Another potential source of error is the loss of photosynthetically fixed organic material. Wetzel and Manny (1971) demonstrated that 1 - 10% of photosynthetically fixed material may be excreted.

c. Change in Biomass.

Seasonally, macrophyte biomass changes follow a sigmoid growth curve (Fig. 5), culminating in a late summer maximum biomass. Net production in such cases is equal to the seasonal maximum biomass minus the biomass initially present at the start of the growing season (Fig. 6, curves A, B, and C; Westlake, 1965b; Wetzel, 1975). Estimation of net production is complicated when losses (damage, grazing, etc.) of a portion of the initial biomass or current year's production occurs (Fig. 6, curves D and E). Reedswamp plants (Westlake, 1966) and some submerged plants, e.g., *Chara* sp. (Rich, et al., 1971), have been found to lose portions of both.

In figure 5, gross productivity reaches a plateau and declines while respiration continues to climb with the increase in biomass. Because of the increase in respiration net productivity decreases and becomes negative. The seasonal maximum biomass is reached when net productivity equals zero.

Production rates (productivity) of macrophytes will typically have maximum rates in the spring and autumn. This phenomenon is probably due to maximum rates of photosynthesis occurring at lower temperatures than maximum rates of respira-

Fig. 5. Hypothetical growth and metabolism curves for an annual plant; — Biomass, X Current gross productivity, □ Current net productivity, o Current respiration rate, + Death losses (Westlake, 1965).

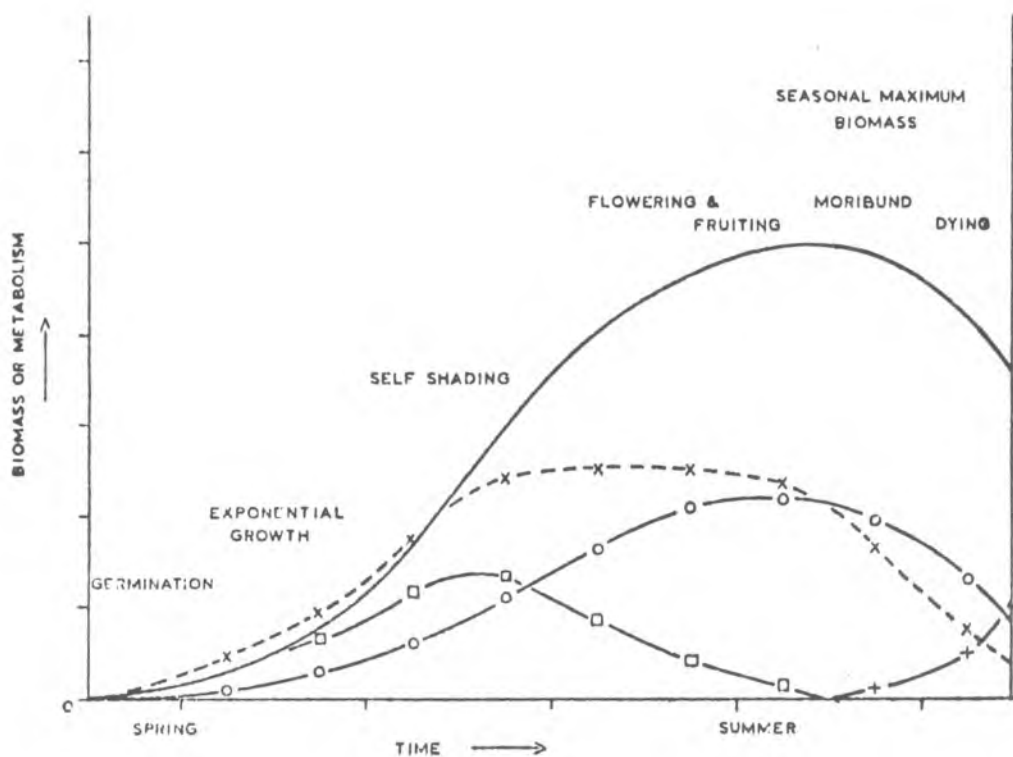
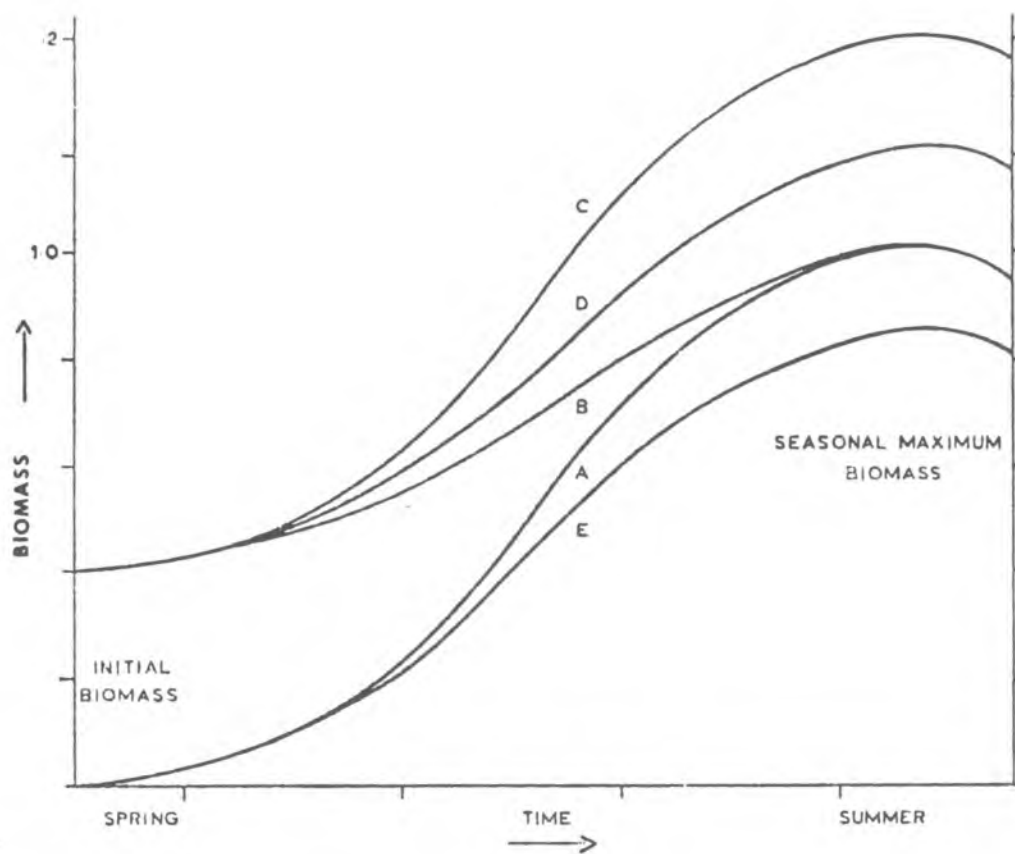


Fig. 6. Types of growth curves. A. True annual or plant with manifest annual regrowth. B. Plant with obscured annual regrowth. C. Plant with spring biomass persisting until seasonal maximum. D. Plant with only part of spring biomass persisting until seasonal maximum. E. Plant with annual regrowth, losses from current year's biomass before seasonal maximum (Westlake, 1965).



tion (Penfound, 1956). This hypothesis is supported by the fact that respiration rates are often higher than photosynthetic rates during periods of hot days and nights in midsummer.

The measurement of production by change in biomass has been criticized by some authors (Forsberg, 1959; Penfound, 1956; Wetzel, 1964b). However, as expressed by Westlake (1965b), these works are not condemnations of the technique, with the condition that the technique is applied conscientiously by a dedicated researcher. The change of biomass over a short period of time is an acceptable estimate of net productivity, if no losses (damage, grazing, etc.) in plant material occur. If losses do occur, efforts must be made to account for that material lost.

Comparing the biomass and ^{14}C techniques, Love and Robinson (1977) found productivities derived from ^{14}C uptake to be far in excess of those productivities determined by changes in biomass. They suggest that the discrepancy may have been due to the depression of biomass productivity values because of the occurrence of unobserved losses of plant material during the growing season. Alternatively, ^{14}C assimilation could have been increased by the presence of periphyton on plant surfaces; thus, yielding higher productivity values.

The existing techniques for estimation of macrophyte production are less than perfect. However, if one is familiar with the limitations and sources of error involved, he should not hesitate to use either the biomass or ^{14}C technique.

Each method will produce acceptable results. The accuracy of the data depends on the ability of the researcher to apply the technique and interpret the results.

2. Sampling and Censusing of Aquatic Vegetation.

Emergent vegetation has typically been sampled by the use of variously sized quadrats. Submergent macrophytes, due to their inaccessibility, have been sampled by an array of devices, e.g., rakes, dredges, corers, etc. (cf., Wetzel, 1964b). The quantitative accuracy of such methods is of some doubt because the accuracy of such techniques is dependent on taking numerous samples and homogeneous plant coverage (Forsberg, 1959).

With the refinement of self-contained underwater breathing apparatus (SCUBA), the ability to accurately sample submersed vegetation has improved. The advantages of SCUBA and equipment needed for sampling of vegetation have been described by Wood (1963), Fager, et al., (1966), and Sheldon and Boylen (1977). SCUBA has been used successfully for sampling submersed vegetation (Lind and Cottom, 1969).

In many bodies of water the distribution of plants is nonrandom and related to gradients, such as increasing depth (Vollenweider, 1969). This situation may make it necessary to take samples along transects parallel to the gradients. If the plant distribution is random, plant sampling should be random.

The sampling of rooted macrophytes should always include underground root and rhizome structures. Some plants may

have no roots, e.g., Ceratophyllum sp., or only a few, but many plants, especially emergents, have significant portions of underground structures. Ivlev (1945) reported that root stock weights of reeds and rushes can exceed that of erect shoots. Many studies have confirmed this (Table 3).

Submergent plants are no exception to the fact that underground structures may be significant portions of biomass. Ozimek, et al., (1976) reported underground biomass to be between 28 - 72% for Potamogeton lucens and 36 - 51% for Potamogeton perfoliatus. A positive correlation between the biomass of above and underground structures was also reported. Best and Nicholson (1974) examined the root-shoot ratios for several submerged plants (Table 4). Borutskii (1950), as cited in Westlake (1965), reported a value of 2.6% of total biomass for underground structures of Elodea canadensis.

To estimate the production of organic material per square meter of lake surface, the percent coverage of aquatic vegetation for a lake must be known. Siegler (1941, 1943) outlined a technique to determine plant coverage in very small ponds. This technique is performed by using linear and transect counts of paces. This technique is of no value for bodies of water of any appreciable size.

In large bodies of water where vegetation is emergent or only slightly below the surface, aerial photography can be used to estimate the plant coverage (Edwards and Brown, 1960; Benton and Newman, 1976; Steffensen and McGregor, 1976). When submersed beds are too deep to be detected by aerial

Table 3: The relative weights of parts of perennial reedswamp plants (% biomass; modified from Westlake, 1965)

Species, time of sampling and ash or dry wt.		Green shoots Tops-Stubble	Underground Rhizomes-Roots	
(1)	<u>Alisma plantago-aquatica</u> , July-August, fresh	60	40	
(2)	<u>Butomus umbellatus</u> , August, fresh	< 64	> 36	
(3)	<u>Carex riparia</u> , August, fresh	< 76	> 30	
(1)	<u>Equisetum fluviatile</u> , July-August, fresh	17	83	
(3)	<u>Glyceris maxima</u> , July, fresh	49±15	51	
	dry	61	39	
	September, fresh	33±16	67	
	dry	45	55	
(1)	<u>Phragmites communis</u> , July-August, fresh	17	83	
(2)	<u>Scirpus lacustris</u> , August, fresh	< 54	> 46	
(1)	<u>S. lacustris</u> , July-August, fresh	10	90	
(4)	<u>S. lacustris</u> , October, fresh	17	8	47 28
	dry	25		75
(2)	<u>Sparganium erectum</u> , August, fresh	< 70	> 30	
(1)	<u>Sparganium ramosum</u> , July-August, fresh	33	66	
(2)	<u>Typha angustifolia</u> , August, fresh	< 48	> 52	
(4)	<u>T. angustifolia</u> , October, fresh	20	31	34 25
	dry	43		57
(5)	<u>T. hybrid</u> , September, dry	37		64
(2)	<u>T. latifolia</u> , August, fresh	< 54	> 46	
(1)	<u>T. latifolia</u> , July, fresh	50	50	

(1) Aario (1933).

(2) Hejny (1960).

(3) Biomass samples taken by River Frome, Kingston Maurward. Stubble included in underground. $\pm$ range.

(4) Plants sampled at Velky Palenec, Czechoslovakia. Stubble included in dry green shoots.

(5) Bray, et. al., (1959).

Table 4: Root:shoot ratios of macrophytes species in Chautauque Lake (derived from dry wts.; Best and Nicholson, 1974).

<u>Species</u>	<u>No. of Samples</u>	<u>Mean $\pm$ S.D.</u>
<u>Nuphar variegatum</u>	5 ^P	2.09 $\pm$ 1.29
<u>Pontederia cordata</u>	3 ^P	1.99 $\pm$ 0.68
<u>Vallisneria americana</u>	30 ¹	0.89 $\pm$ 0.68
<u>Heteranthera dubia</u>	12 ^P	0.23 $\pm$ 0.11
<u>Potamogeton richardsonii</u>	43 ¹	0.14 $\pm$ 0.09
<u>Myriophyllum</u> sp.	14 ^P	0.11 $\pm$ 0.05

¹ Individual plants sampled.

^P Populations sampled.

photography, an underwater survey method using SCUBA may be used (Schmid, 1965). This technique involves the laying of markers around the periphery of plant beds.

Rough estimation of plant distribution and bed size may be determined by using modern depth sounders (Lind, personal communication). Although this equipment can be extremely useful, accurate estimations of coverage are not possible.

In lakes of large size and extensive coverage of vegetation, it may be possible to use a combination of the available techniques. The values can then be added when deriving the percentage of cover.

3. Proper techniques for the estimation of production by change in biomass.

Typically, biomass data are expressed as g dry wt. m^{-2} , g ash free wt. m^{-2} , or mg C m^{-2} . When production is expressed as a rate, the time factor is usually per day.

Dry weight should be determined by drying to a constant weight at 105°C or 60°C. Plants should not be allowed to cool because moisture is rapidly absorbed from the air. Absorption of moisture from the air can cause weights to be 5 - 10% higher than the true oven-dry weight (Westlake, 1965b).

Ash-free weights can be determined by igniting a sample of known weight at 550°C. The residual is then subtracted from the sample weight to obtain ash-free weight. Error may occur because of the decomposition of carbonates. Magnesium carbonate decomposes above 350°C, but is usually insignificant. If large amounts of magnesium carbonates are present initially, they should be dissolved in acetic acid. The dissolved car-

bonate can then be determined and added to the residual. Above 550°C , calcium carbonate begins to decompose.

Ash weights normally vary between 10 - 30% of dry weight (Table 5). Submergent plants typically have a higher percentage of ash than emergent plants. In very calcareous waters, ash weights may soar to values above 38.8%. Wetzel (1960) found marl incrustations to approach a weight equal to the supporting plant material.

Contrary to Westlake's (1965b) opinion that there is little evidence of seasonal variation in percent ash weight of dry weight, Boyd (1969) has demonstrated seasonal variations (a decline) in ash content of the shoots of emergent plants. The decline was presumably due to the utilization of inorganic substances during accelerated periods of photosynthesis. Percent ash of dry weight may increase if calcareous deposits accumulate on photosynthetically active plant organs during periods of rapid growth.

The organic carbon content can be estimated from the ash-free weight. The organic carbon content is limited in range in aquatic plants, varying between 43 and 48% of ash-free weight (Westlake, 1965b). Analysis of organic carbon is most accurately determined by dry combustion of plant samples. The problems confronted by wet oxidation procedures are discussed by Westlake (1963).

Table 5. The proportion of inorganic matter in certain aquatic vascular plants (taken from Sculthorpe, 1967).

Species	Inorganic (ash) weight (as % of total dry weight)
Emergent:	
<u>Arundo donax</u>	2.5-7.4
<u>Typha</u> sp.	8.0-10.0
<u>Mentha aquatica</u>	16.0
<u>Sparganium</u> sp.	18.0
<u>Myosotis scorpioides</u>	20.0
Floating-leaved:	
<u>Nuphar advena</u>	8.0
<u>Nymphaea odorata</u>	11.2
Free-floating:	
<u>Salvinia auriculata</u>	28.0
Submerged (mainly or exclusively):	
<u>Groenlandia densa</u>	12.0
<u>Ranunculus pseudofluitans</u>	12.0-21.9
<u>Potamogeton pectinatus</u>	13.0-19.0
<u>Potamogeton praelongus</u>	14.0
<u>Hippuris vulgaris</u>	15.0
<u>Ceratophyllum demersum</u>	15.7-23.7
<u>Myriophyllum verticillatum</u>	16.5-20.7
<u>Rorippa nasturtium-aquaticum</u>	17.0-23.0
<u>Myriophyllum spicatum</u>	17.1-20.3
<u>Najas flexilis</u>	17.3-23.9
<u>Potamogeton amplifolius</u>	18.3-38.8*
<u>Potamogeton zosteriformis</u>	18.4
<u>Callitriche obtusangula</u>	19.2
<u>Elodea canadensis</u>	22.0-30.7
<u>Littorella uniflora</u>	24.0
<u>Berula erecta</u>	24.0-27.0
<u>Thalassia testudinum</u>	24.8
<u>Myriophyllum alterniflorum</u>	25.0
<u>Vallisneria spiralis</u>	25.2-28.6
<u>Heteranthera graminea</u>	28.4
<u>Potamogeton richardsonii</u>	30.2
<u>Potamogeton lucens</u>	32.0

* High value obtained from material encrusted with calcareous deposits.

III. HABITAT DESCRIPTION

Sam Rayburn Reservoir is located in the Angelina River Basin and receives drainage from the acid soils of the surrounding East Texas Timber Land Resource Area. Although the reservoir is surrounded and sheltered by a hill topography, a north-west wind can cause considerable wave action. Despite the vulnerability to a north-west wind and a shallow depth (mean depth = 3.5 m), the reservoir is monomictic (one complete turnover per year). During the summer stratification, a complete hypolimnetic oxygen depletion occurs.

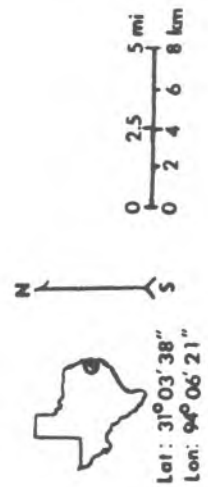
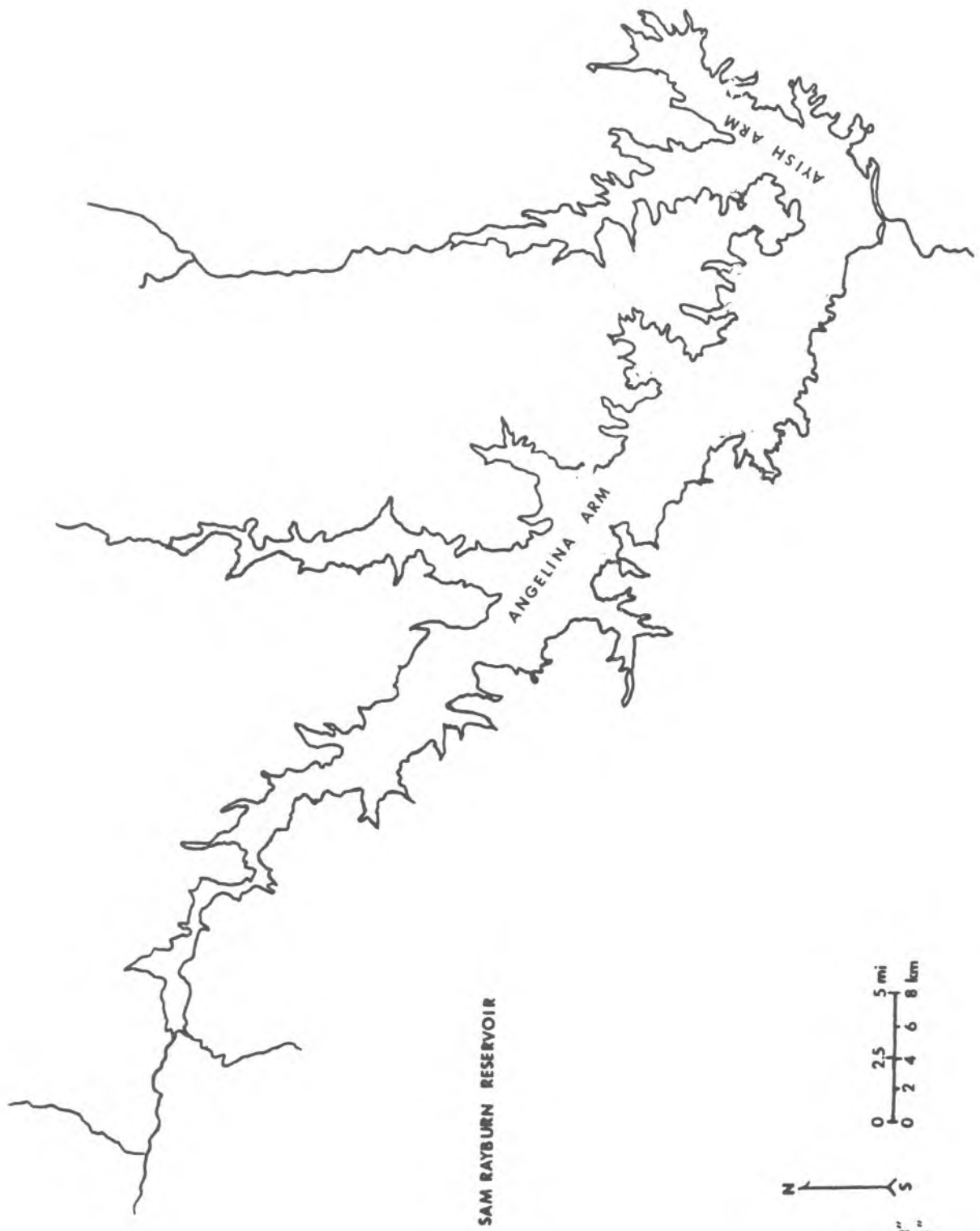
The reservoir water is tinted brown by decomposing vegetation, but has little turbidity due to organic or inorganic matter. Only microgram quantities of nitrogen and phosphorus are present in the water. The dissolved silica concentration is approximately 3 mg l^{-1} . The water is also characterized by low alkalinity (max. value = 35 mg l^{-1}) and calcium hardness (max. value = 40 mg l^{-1}).

Sam Rayburn Reservoir supports a wide variety of macrophytes: Potamogeton sp., Elodea sp., Nitella sp., Vallisneria sp., Myriophyllum sp., Nymphaea sp., and two species of Sagittaria. In the past, large floating beds of Eichornia crassipes (water hyacinth) have existed in the reservoir, but are no longer present. Of the above plant types, only three occur in the reservoir in significant quantities. These are Elodea sp., Potamogeton sp., and Nitella sp.

In bays where the three main plant taxa are present together, they form concentric bands around the shoreline. Nitella sp. occurs at depths of 0.5 to 1.5 m, Potamogeton sp. occurs at depths from 1.0 to 2.5 m, and Elodea sp. exists at depths of 2.5 to 5.0 m. Often Potamogeton sp. and Nitella sp. stands overlap; however, Elodea sp. and Potamogeton sp. stands never overlapped.

Potamogeton sp. and Nitella sp. occur in all vicinities of the reservoir. Elodea sp. is restricted primarily to the western shore of the Angelina arm of the reservoir and both shorelines of the Ayish arm of the reservoir (Fig. 7).

Fig. 7. Sam Rayburn Reservoir and the location of the Ayish and Angelina arms.



IV. METHODS

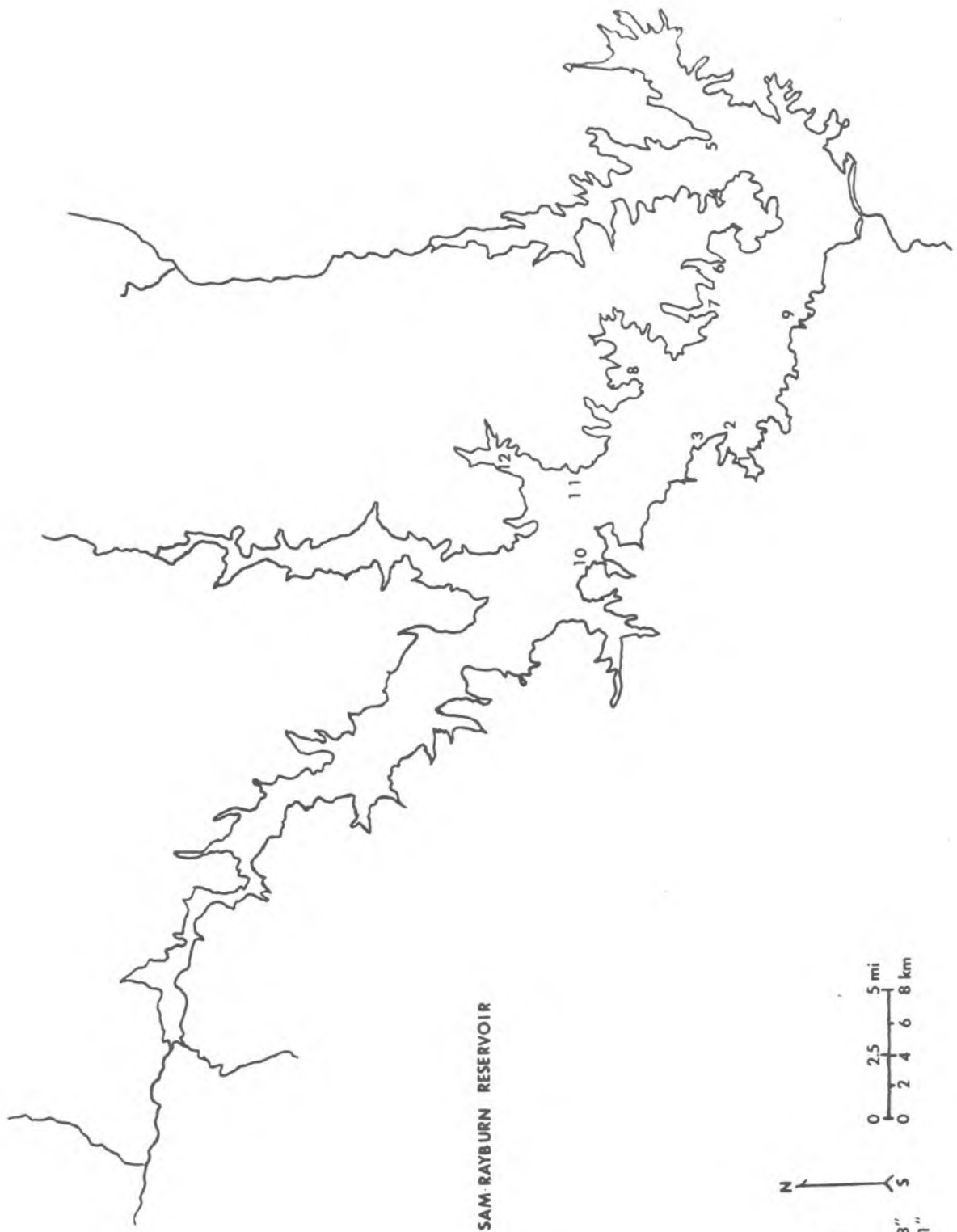
A. Sampling

Three macrophyte taxa, Elodea sp., Potamogeton sp., and Nitella sp., were quantitatively sampled from the littoral zone of Sam Rayburn Reservoir using SCUBA. Also, included in the sampling were specimens of the underlying sediments and surrounding waters. The plant samples were analyzed for biomass, percent ash weight, phosphorus concentration, and nitrogen concentration. Nitrogen and phosphorus concentrations were determined from the water and sediment samples.

Plant, water and sediment samples were collected from 12 sites (Fig. 8 - three Elodea sp. sites and nine Potamogeton and Nitella sp. sites) at monthly intervals between April, 1977 and November, 1977, inclusive. Because Potamogeton sp. and Nitella sp. beds overlapped, one water and sediment sample was taken to represent both plant types. All plant samples were taken from an area of homogeneous vegetative cover judged to be typical of the entire bed.

Standing crop per square meter was estimated by harvesting all above-substrate plant material within a 0.25 m^2 quadrat. The quadrat frame was designed with two modifications (Fig. 9). The design included corner spikes to hold the quadrat firm when sampling and tall corner posts which supported a cloth bag. Because of the length of Elodea sp.

Fig. 8. The location of collection sites for macrophytes of Sam Rayburn Reservoir (Elodea sp. - 3, 4, & 5 and Nitella sp. and Potamogeton sp. - 1, 2, & 6 - 12).



SAM RAYBURN RESERVOIR

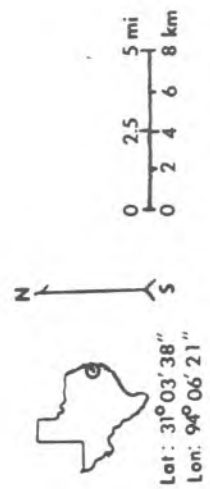
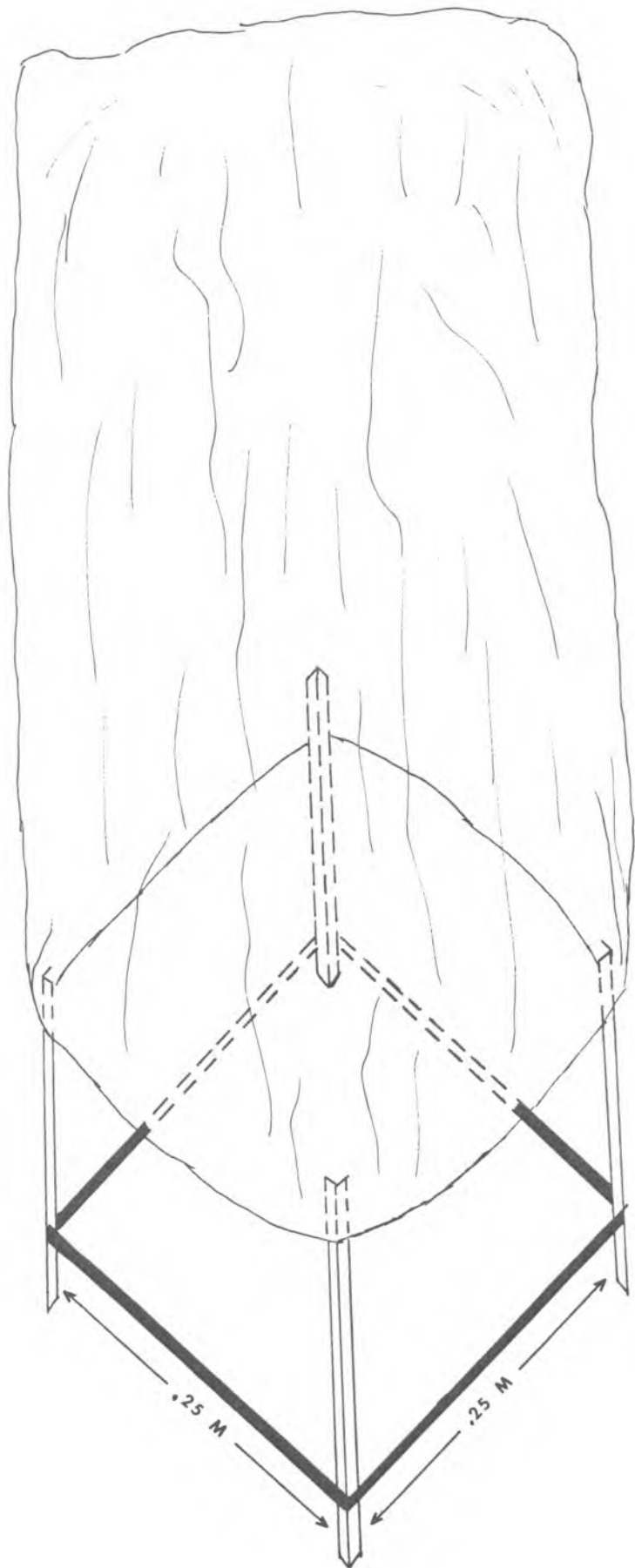


Fig. 9. Modified quadrat used in the sampling of the submerged macrophytes of Sam Rayburn Reservoir.



plants (1-2 m), the bag was designed to serve as a receptacle for the plants as they floated up after their detachment. The bag was removed underwater and closed by a drawstring and taken to the surface. The sample was removed from the bag in the boat and placed in a plastic trash bag for transportation to the laboratory.

To determine the precision of sampling with the quadrat frame, multiple samples were taken within a plant bed at the first sampling. The maximum variation from the mean weight of the samples was 30%. The mean variation from the mean weight of the samples was 16%.

Because root and rhizome structures are often a significant portion of plant biomass, entire, intact, single plants were carefully removed at each monthly sampling. A root-shoot ratio was obtained from these plants. Using this ratio, the standing crop was corrected to include the weight of below ground tissue; thus, yielding biomass (root + shoot, Wetzel, 1975). Surprisingly, no appreciable difference in root - shoot ratios occurred through the season.

Sediment samples were taken from the macrophyte beds by coring approximately 10 cm into the substrate. Two water samples (one for phosphorus analysis and one for nitrogen analysis) were taken within each plant bed, halfway between the top of the plants and the substrate.

It has been pointed out that some macrophytes have the ability to excrete phosphorus (DeMarte and Hartman, 1974). Because of this report, at the Elodea sp. beds, two extra

water samples were taken. The first sample was taken 2 m outside the periphery of the bed and the second 4 m outside the periphery. These samples were used to determine whether a concentration gradient of phosphorus existed between the interior of the bed and an area outside the bed.

Before transportation, one water sample was acidified with concentrated H_2SO_4 (0.8 ml conc. H_2SO_4 l of sample⁻¹) to prevent the loss of NH_3 (conversion of NH_3 to NH_4). The other water sample was preserved by addition of HgCl_2 (40 mg HgCl_2 l of sample⁻¹). Soil samples were preserved with concentrated H_2SO_4 . After preservation, the samples were transported in an insulated cooler to the laboratory. All samples were refrigerated (5°C) until analysis.

In the laboratory, dry weight of plant samples was determined by drying for 24 hours at 105°C and weighing to the nearest 0.1 g. The percent ash weight of dry weight was determined by ashing sub-samples weighed to the nearest 0.00001 g at 550°C for one hour. A portion of the remainder of the dried sample was stored in a seal lock plastic bag for later nitrogen and phosphorus analysis.

B. Water Analysis

The water sample preserved with H_2SO_4 was analyzed for NH_3 , NO_3 , and organic nitrogen. Kjeldahl distillation was used to determine the NH_3 and organic nitrogen concentrations (Amer. Public Health Assoc., 1976). This procedure allows for the separation of NH_3 and organic nitrogen. The NH_3 was first distilled into a boric acid trap. The remaining organic

nitrogen was then digested and oxidized to NH_3 . This NH_3 was distilled into a second boric acid trap. The nitrogen in each boric acid solution was determined by the phenate method of Stainton, Capel, and Armstrong (1974). The common method of titration with standard acid, using a mixed indicator solution, was not used because nitrogen concentrations were below the detectability of this technique. Nitrate analyses were made using the cadmium-reduction technique (Amer. Public Health Assoc., 1976).

Concentrations of orthophosphate phosphorus, dissolved, and total phosphorus were determined from the water sample preserved in HgCl_2 . All phosphorus analyses were done according to Murphey and Riley (1962).

Orthophosphate phosphorus was determined from a 200 ml aliquot of the original sample. The Murphey and Riley technique for orthophosphate was modified by extraction with 20 ml of butyl acetate (Lind, in press). This modification enhances the sensitivity of the technique by concentrating the phosphorus into the butyl acetate.

The phosphorus in two 50 ml aliquots was digested and oxidized in the autoclave at 15 lb in^{-2} for 30 minutes using 5% potassium persulfate. Before digestion, one sample for dissolved phosphorus was filtered through an acid washed glass fiber filter. The second unfiltered digested sample was analyzed for total phosphorus.

C. Tissue Analyses

Total nitrogen in each plant sample was assessed using

Kjeldahl digestion and distillation (Amer. Public Health Assoc., 1976). The oxidized nitrogen in the digest was distilled into boric acid and subsequently titrated with 0.02 N H_2SO_4 using a mixed indicator solution of methylene blue and methyl red. One replicate of each sample was analyzed.

Total phosphorus in plant tissues was measured using the unmodified Murphey and Riley (1962) technique after digestion with potassium persulfate. Tissues were first ground to a powder using a mortar and pestle. Each ground specimen was suspended in 50 ml of deionized water and 8 ml of 5% potassium persulfate. This sample was digested in an autoclave at 15 lb in^{-2} for 1 hr. The digested solution was filtered using 0.8 μm Millipore filters. Since these filters are reported to leach phosphorus (Rigler, 1964), each filter was rinsed twice with 0.1 N HCL and twice with deionized water before use.

Since the potassium persulfate procedure is not described in the literature for plant tissues, the accuracy of the technique was determined. After the initial determination, three ground tissue samples were resuspended in deionized water and shaken for approximately one minute. The ground tissue was then separated from the water by centrifuging. This washing procedure was repeated three times to remove all phosphorus adhering to the ground tissue. After washing was complete, the samples were redigested and reanalyzed. The entire procedure was then repeated again. The results are given in Table 6. The initial digestion yielded between

Table 6. Phosphorus recovery from plants using potassium persulfate digestion.

<u>Sample</u>	<u>Initial Digestion</u>		<u>Second Digestion</u>		<u>Third Digestion</u>	
	<u>$\mu\text{g g}^{-1}$</u>	<u>%</u>	<u>$\mu\text{g g}^{-1}$</u>	<u>%</u>	<u>$\mu\text{g g}^{-1}$</u>	<u>%</u>
1	1145.2	85.6	168.0	12.6	23.8	1.8
2	1096.4	83.0	223.5	17.0	0.0	0.0
3	1563.4	<u>90.0</u>	177.5	10.0	0.0	0.0
	$\bar{X} = 86.0$					

83 - 90% of the total phosphorus. Because of the underestimation each phosphorus value was corrected by 14% (derived from the mean of the three).

D. Sediment Analysis

The soil samples were analyzed for total nitrogen and total phosphorus using the same methods as described for the plants. The phosphorus technique had not been reported for sediments; therefore, three samples were resuspended after filtering, washed, digested and analyzed three times.

Between 65 - 69% of the phosphorus was recovered in the initial digestion of the sediment (Table 7). Each soil sample was corrected by 33% (derived from the mean of the three samples).

E. The Interaction Between Productivity, External Nutrient Supplies, and Internal Nutrient Supplies

The seasonal net production per square meter was estimated by subtracting the weight of overwintering plant tissues from the seasonal maximum biomass (Westlake, 1965).

Total net macrophyte production in Sam Rayburn Reservoir was determined by multiplying the seasonal net production by the approximate total coverage of plant beds. Coverage of plant beds was measured by planimetry of aerial photographs and hand measurement of selected beds from different areas of the lake. This value was multiplied by 2.6 (the ratio of non-measured plant bed shoreline to measured plant bed shoreline as determined by a cartometer) to obtain an approximate value for the entire reservoir.

Table 7: Phosphorus recovery from sediments using potassium persulfate digestion.

<u>Sample</u>	<u>Initial Digestion</u>		<u>Second Digestion</u>		<u>Third Digestion</u>	
	<u>$\mu\text{g g}^{-1}$</u>	<u>%</u>	<u>$\mu\text{g g}^{-1}$</u>	<u>%</u>	<u>$\mu\text{g g}^{-1}$</u>	<u>%</u>
1	66.9	65.8	34.8	34.2	0.0	0.0
2	48.2	66.9	23.8	33.1	0.0	0.0
3	61.8	<u>69.1</u>	23.8	26.6	3.8	4.3
	X = 67.3					

The relationship of phosphorus and nitrogen to productivity was determined by computing product-moment correlation coefficients (Zar, 1974). Significance of all correlations was examined using the Student's T test (Zar, 1974). Correlations were calculated between all phosphorus and nitrogen concentrations in the water and the succeeding periods of productivity (approximately 1 month). Correlations were also calculated between mean Kjeldahl nitrogen and mean total phosphorus concentrations and the following periods of mean productivity for each plant type. Both analyses were performed to determine if productivity is dependent on external concentrations of nitrogen and phosphorus. A high positive correlation would indicate that the external nutrient in question is limiting.

The effect of internal (tissue) nitrogen and phosphorus on productivity was examined by deriving a correlation between the two. The correlation was calculated between the mean nitrogen and phosphorus concentration and the following periods of mean productivity for each plant type. A positive correlation would be an indication that productivity is directly related to the tissue concentration of nitrogen and/or phosphorus.

To determine whether tissue nutrient concentrations are indicative of the environmental concentrations of the same nutrients, correlation coefficients were calculated between the mean concentrations of tissue nitrogen and phosphorus and the mean concentration of nitrogen and phosphorus in

the water and the sediment. The tissue concentration of total nitrogen and phosphorus was correlated with all forms of nitrogen and phosphorus in the water. Only total nitrogen and phosphorus concentrations were used in the calculation between tissue and sediment concentrations.

The hypothesis that increased productivity might cause increased secretion of nutrients was investigated. Such a relationship would be reflected by increased concentrations of phosphorus and/or nitrogen concentrations in the water, following a period of high productivity. To test this hypothesis, correlations were calculated between periods of productivity and the concentrations of phosphorus and nitrogen in the surrounding waters at the end of the growth period.

V. RESULTS

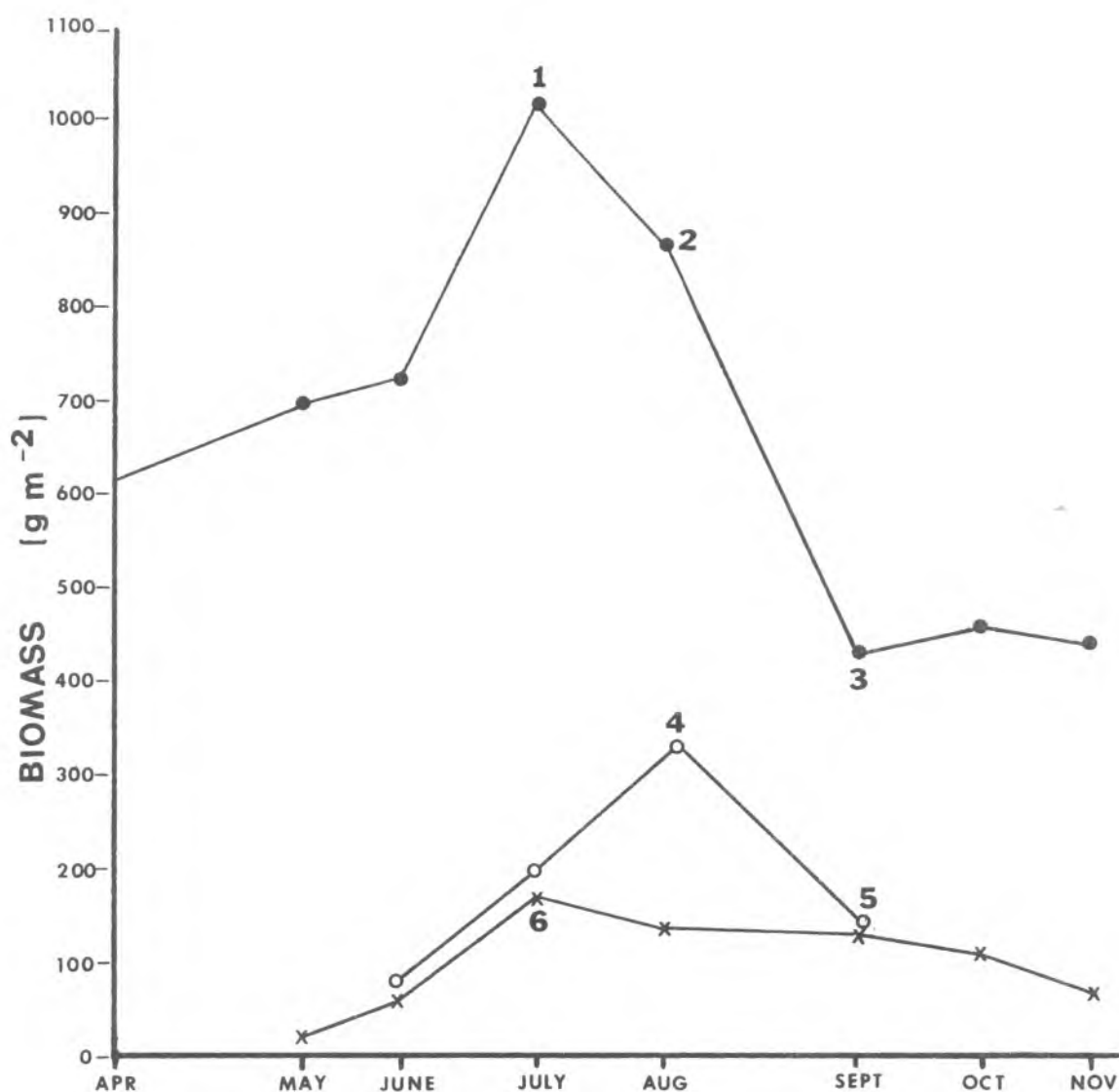
A. Seasonal Change in Biomass and Productivity

Elodea sp., Potamogeton sp. and Nitella sp. each exhibited an approximation of the typical sigmoid pattern of seasonal change in biomass (Fig. 10). However, Nitella sp.'s and Elodea sp.'s biomass patterns were atypical, in that the decline of biomass was much more abrupt than would normally be expected, based on Westlake's (1965b) seasonal growth curve. Potamogeton sp.'s biomass declined at a rate that is slower than Westlake's representation.

The seasonal maximum biomass of Elodea sp. and Nitella sp. occurred in July and August, respectively. At this time, the apical stem tips were exposed at the surface, due to the draw-down (Fig. 10 footnotes). At the next sampling, all apical tissues were rotting severely and fouling the water. The seasonal maximum biomass of Potamogeton sp. occurred in July, but no deterioration was evident through the rest of the season.

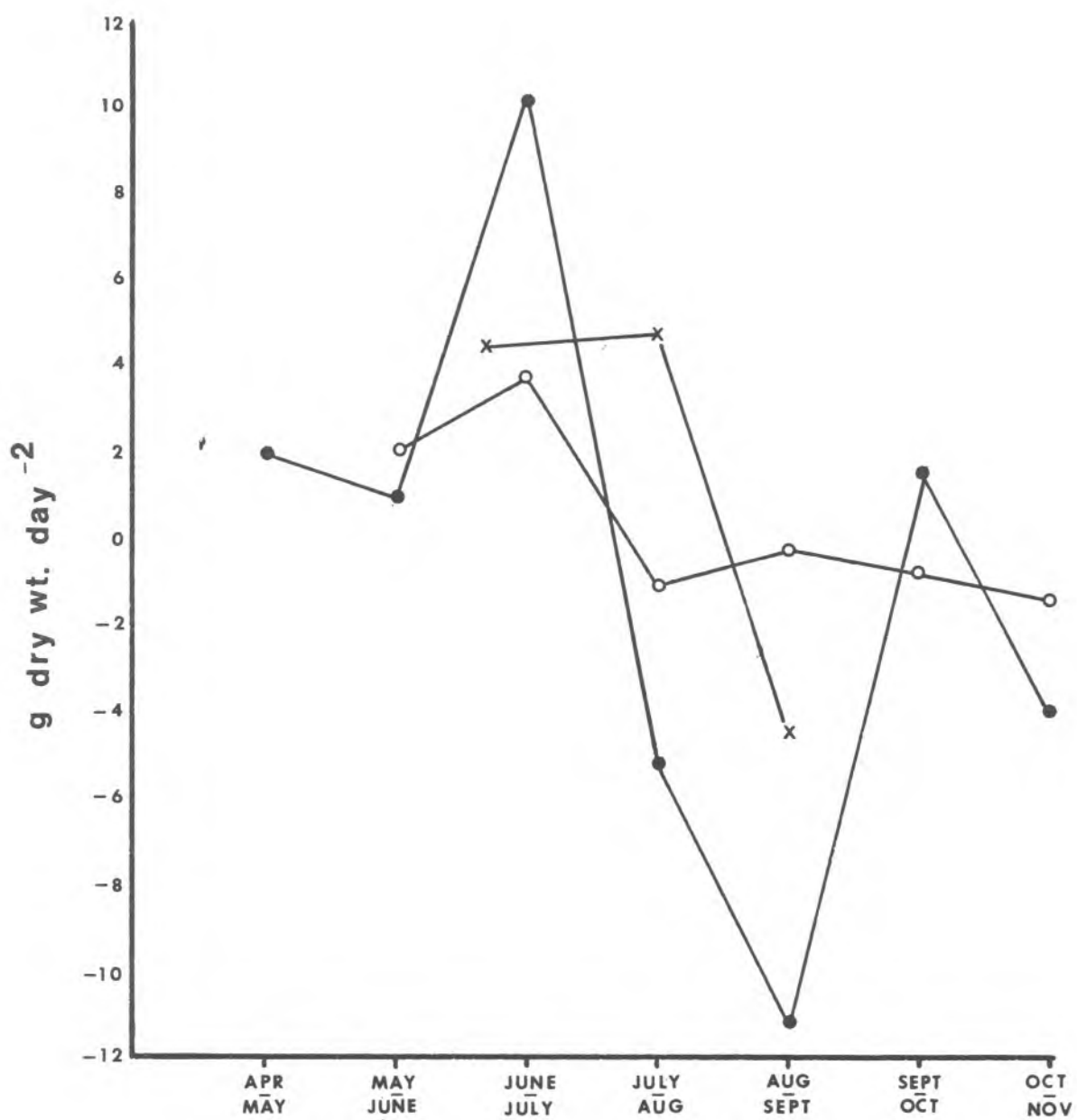
The pattern of productivity of the taxa was highly variable through the season (Fig. 11). The maximum rates of photosynthesis ($\text{g dry wt m}^{-2} \text{ day}^{-1}$) for Elodea sp. and Potamogeton sp. occurred from June to July, directly before the seasonal maximum biomass. Maximum productivity of Nitella sp. was from July to August, again directly preceding the

Fig. 10. Mean monthly change in biomass of Elodea sp. (●), Potamogeton sp. (o), and Nitella sp. (x). The intervals between months on the x-axis are based on the number of days between samplings. Exact values and standard deviations are presented in Appendix 1.



- 1). The plants were at the surface and the color was brown.
- 2). The plant organs near the surface were deteriorating.
- 3). The plants had deteriorated back to 0.3 - 0.5 m below the surface.
- 4). The plants were at the surface.
- 5). The plants were deteriorating.
- 6). The area of the plant bed was decreasing.

Fig. 11. Mean productivity of Elodea sp. (●), Potamogeton sp. (○), and Nitella sp. (x). Exact values and standard deviations are presented in Appendix 2.



seasonal maximum biomass. Since all plants were growing vigorously before their decline, the seasonal maximum biomass might have been 1 to 2 months away had the draw-down not occurred.

B. The Seasonal Net Production

The annual maximum biomass of Elodea sp. occurred in July. Because a portion of the plant overwinters, the mean biomass of the last three sampling dates was assumed to be the overwintering condition (because of the stability of biomass from Sept. to Nov., Fig. 10). The mean of the last three samples was subtracted from the seasonal maximum to obtain the seasonal net production of 572.4 g m^{-2} (Table 8). Only insignificant portions of Potamogeton sp. overwinter, e.g., less than 2% as root structures. Thus, nearly all material existing at the July seasonal maximum biomass represents the seasonal net production of 168.4 g m^{-2} (Table 8).

The annual maximum biomass of Nitella sp. occurred in August. This value represents the seasonal net production of 327.6 g m^{-2} (Table 8).

The total net production values of each taxon per lake per year are presented in Table 9. Although large variations of biomass occurred among sampling sites of each taxon (Appendix 1), all samples were given equal status in determining the total production of macrophytes in the entire reservoir, because the variation in biomass did not show trends within different areas of the reservoir. In other words, the variation in biomass within a particular arm of the

Table 8. Cumulative Seasonal Net Production of Elodea sp., Potamogeton sp., and Nitella sp. (g dry wt. m⁻²).

	Maximum Seasonal <u>Biomass</u>	<u>Residual</u>	Cumulative Net <u>Production</u>
<u>Elodea</u> sp.	1013.6	- 441.3	572.3
<u>Potamogeton</u> sp.	168.4	- 00.0	168.4
<u>Nitella</u> sp.	327.6	- 00.0	327.6

Table 9. Total production of selected macrophytes in Sam Rayburn Reservoir (kg lake⁻¹ year⁻¹).

<u>Elodea</u> sp.	54427.62
<u>Potamogeton</u> sp.	6036.87
<u>Nitella</u> sp.	<u>20063.67</u>
Total	80528.16

reservoir was as great as the variation in the entire reservoir.

C. Nitrogen and Phosphorus in Waters and Sediment

Mean total dissolved phosphorus and orthophosphate phosphorus of the waters in Elodea sp., and Potamogeton sp., and Nitella sp. plant beds exhibited a gradual decline through the summer (Fig. 12 and 13). The mean total phosphorus concentration within the Elodea sp. beds rapidly increased during the early summer. This rise was followed by a plateau during the late summer and early autumn. In late autumn (Sept. - Oct.), the mean total phosphorus concentration dropped back to near the early summer concentrations (Fig. 12). The mean total phosphorus concentration of waters within Potamogeton sp. and Nitella sp. beds was variable, but gradually accumulated through the fall (Fig. 13).

The mean organic nitrogen concentration of the waters of all plant beds was initially high in May (Fig. 14 and 15). The value rapidly declined during the next two months for Elodea sp. beds and the next month for Potamogeton sp. and Nitella sp. beds (Fig. 15). During midsummer, the mean organic nitrogen concentrations of waters of all plant beds increased drastically, possibly as a result of nitrogen release from decaying tissues. After August the organic nitrogen declined to values lower than were present at the beginning of the season; thus, an absolute decline occurred over the entire season.

$\text{NO}_3\text{-N}$ concentration in the waters of all plant beds exhibited an absolute decline through the summer and fall

Fig. 12. Mean phosphorus concentration of the waters from Elodea sp. collection sites (● total phosphorus, o total dissolved phosphorus, and x orthophosphate phosphorus). The intervals between months on the x-axis are based on the number of days between samplings. Exact values and standard deviations are presented in Appendix 3. The dissolved phosphorus and orthophosphate phosphorus concentrations for Aug. and Oct. were not found to be statistically different.

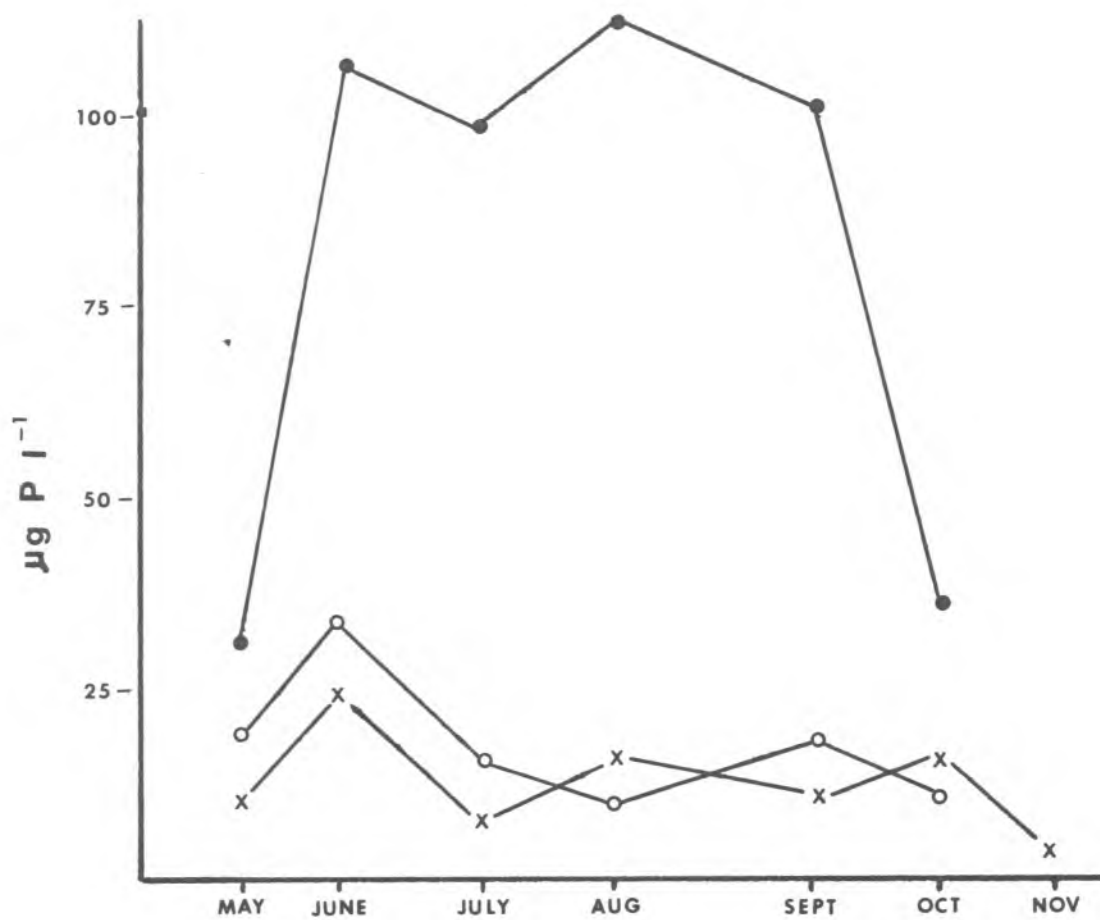


Fig. 13. Mean phosphorus concentration of the waters from Potamogeton sp. and Nitella sp. collection sites (● total phosphorus, o total dissolved phosphorus, and x orthophosphate phosphorus). The intervals between months on the x-axis are based on the number of days between samplings. Exact values and standard deviations are presented in Appendix 3. The dissolved phosphorus and orthophosphate phosphorus concentrations in May and August were not found to be statistically different.

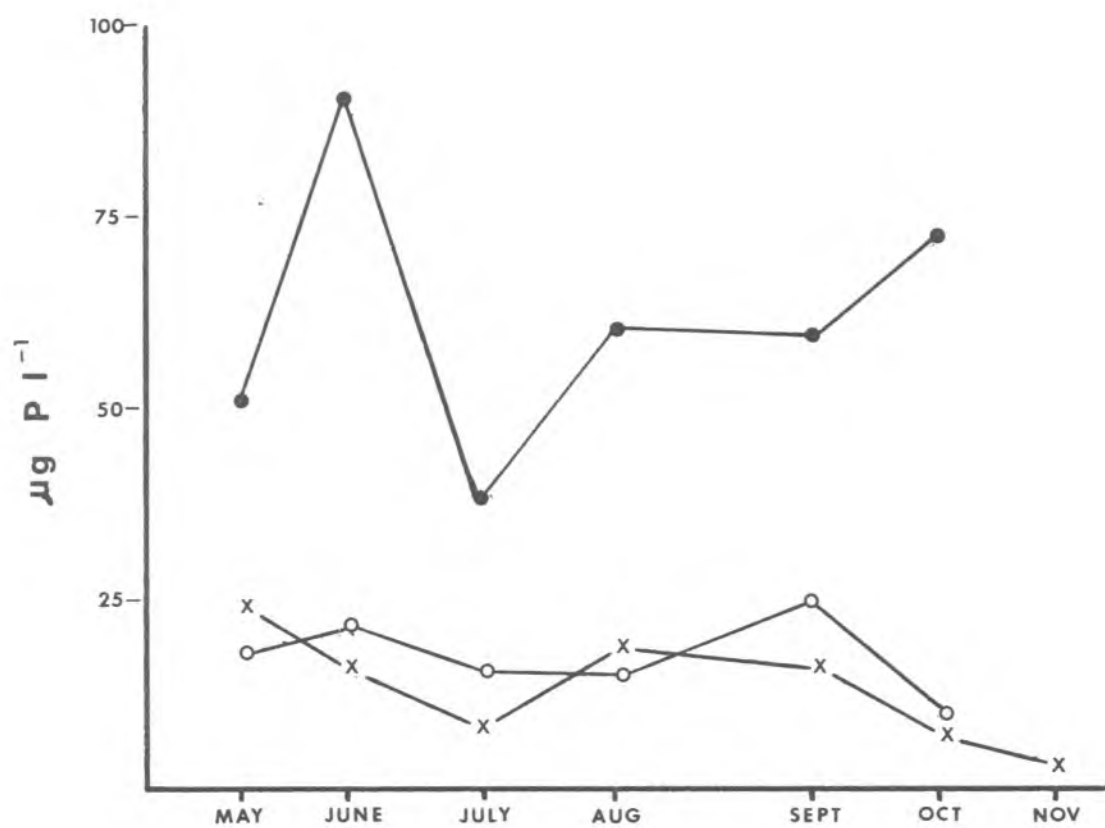


Fig. 14. Mean nitrogen concentration of the waters from Elodea sp. collection sites (● organic nitrogen, o $\text{NH}_3\text{-N}$ and x $\text{NO}_3\text{-N}$). The intervals between months on the x-axis are based on the number of days between samplings. Exact values and standard deviations are presented in Appendix 3.

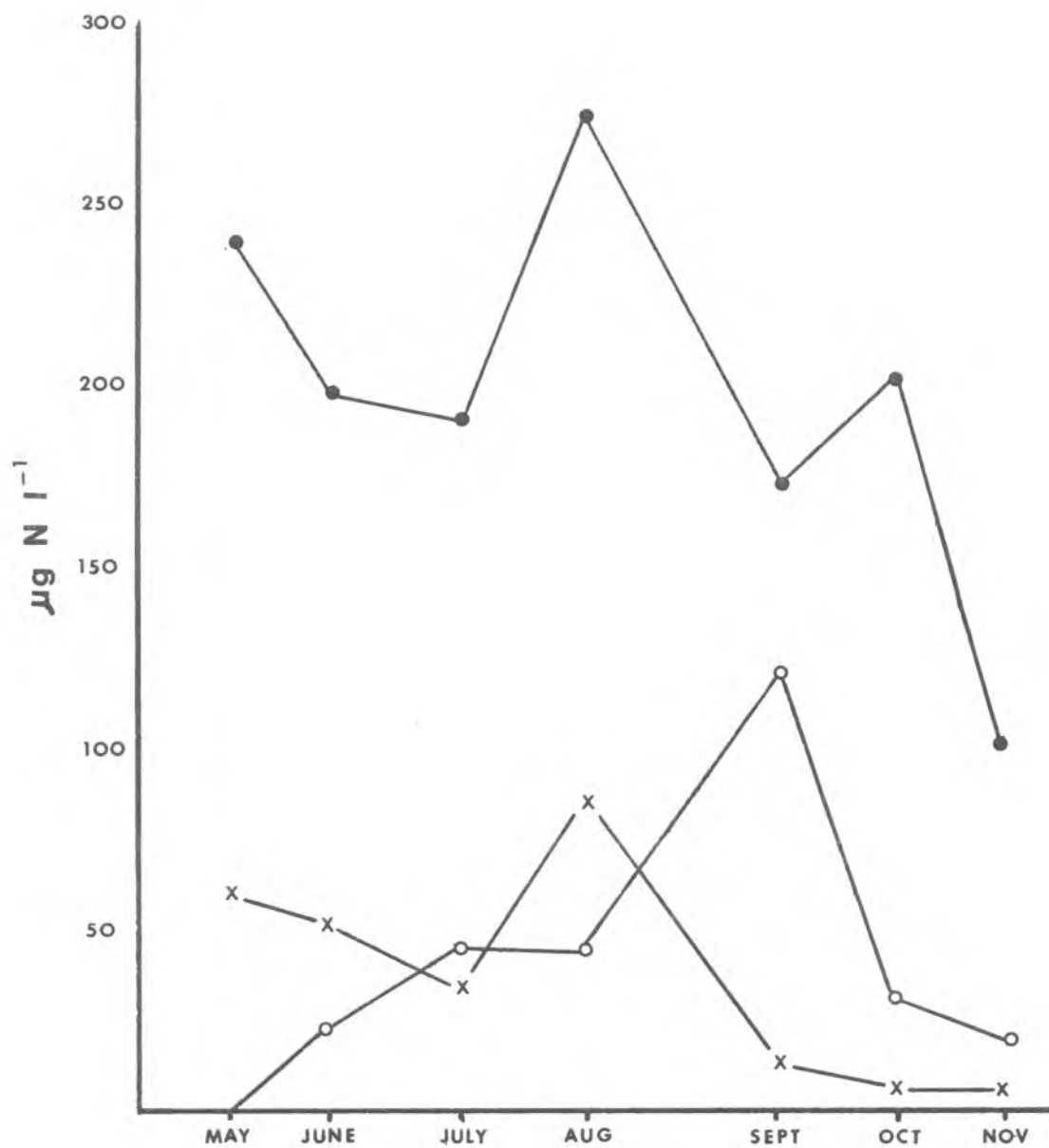
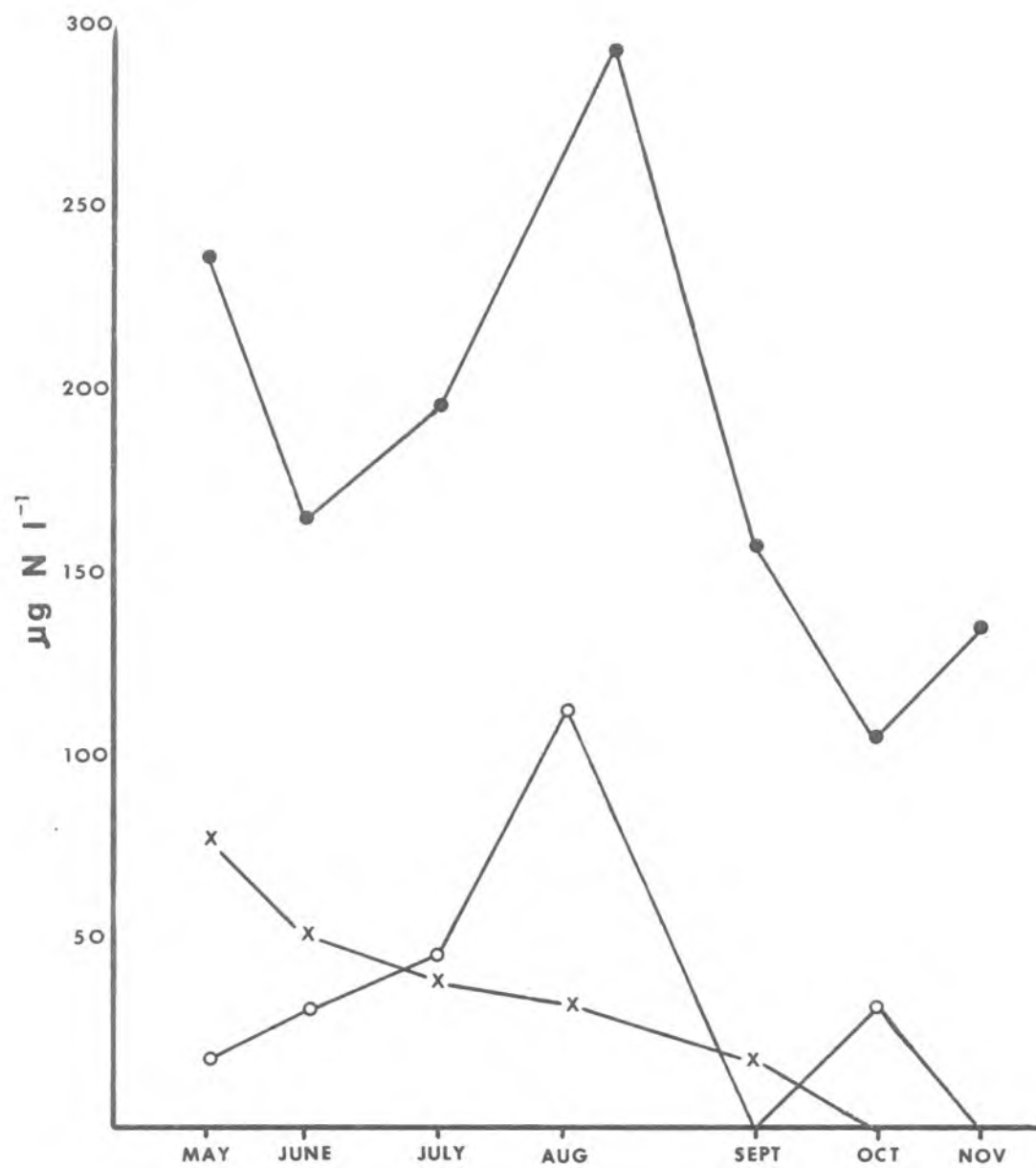


Fig. 15. Mean nitrogen concentration of the waters from Potamogeton sp. and Nitella sp. collection sites (● organic nitrogen, ○ $\text{NH}_3\text{-N}$, and x $\text{NO}_3\text{-N}$). The intervals between months on the x-axis are based on the number of days between samplings. Exact values and standard deviations are presented in Appendix 3.



(Fig. 14 and 15). $\text{NH}_3\text{-N}$ was variable through the season, but exhibited an erratic climb through the summer and a sharp decline during the autumn for all plant beds.

Total phosphorus and orthophosphate phosphorus concentrations of the waters within, 2 m from, and 4 m from an Elodea sp. bed indicated a diffusion gradient during July, September, and October. The August concentrations indicated a gradient for orthophosphate phosphorus; however, not total phosphorus. The total dissolved phosphorus concentrations were erratic, showing no definite gradient (Table 10).

The mean total phosphorus concentration of the sediment beneath Elodea sp. plant beds was variable through the summer, but exhibited an absolute increase (Fig. 16). The late summer maximum was followed by a sharp autumnal decline. The mean total phosphorus concentration of the sediments beneath the Potamogeton sp. and Nitella sp. plant beds was erratic during the early portion of the growing season, before reaching a high in August, and declining in the autumn (Fig. 16).

The mean Kjeldahl nitrogen concentration of the sediment beneath Potamogeton sp. and Nitella sp. plants beds was inconsistent, but an overall decline occurred from a spring maximum (Fig. 17). After an initial increase, the sediment nitrogen concentration of Elodea sp. beds exhibited an absolute decline through the rest of the growing season (Fig. 17). The June drop may be due to erroneous data because of only one sample analysis. The early maximum of both plant beds was probably obtained through winter accumulation, however, because no samples were taken from November to April, this hypothesis cannot be substantiated.

Table 10. Phosphorus concentration ($\mu\text{g l}^{-1}$) within, 2 m from, and 4 m from an Elodea sp. bed.

PO_4			
	<u>Within</u>	<u>2 m</u>	<u>4 m</u>
July	5.2	2.2	2.0
Aug.	8.9	3.5	6.0
Sept.	9.9	8.9	10.3
Oct.	13.5	9.9	5.6
Total Dissolved			
	<u>Within</u>	<u>2 m</u>	<u>4 m</u>
July	10.9	10.9	10.9
Aug.	10.6	5.5	51.3
Sept.	15.7	11.6	11.9
Oct.	11.6	18.7	10.6
Total			
	<u>Within</u>	<u>2 m</u>	<u>4 m</u>
July	44.4	20.5	10.9
Aug.	41.1	51.3	10.6
Sept.	56.4	49.3	35.0
Oct.	51.3	41.2	20.7

Fig. 16. Mean total phosphorus concentration of the sediments beneath Elodea sp. (●) and Potamogeton sp. and Nitella sp. (○) collection sites. The intervals between months on the x-axis are based on the number of days between samplings. Exact values and standard deviations are presented in Appendix 5.

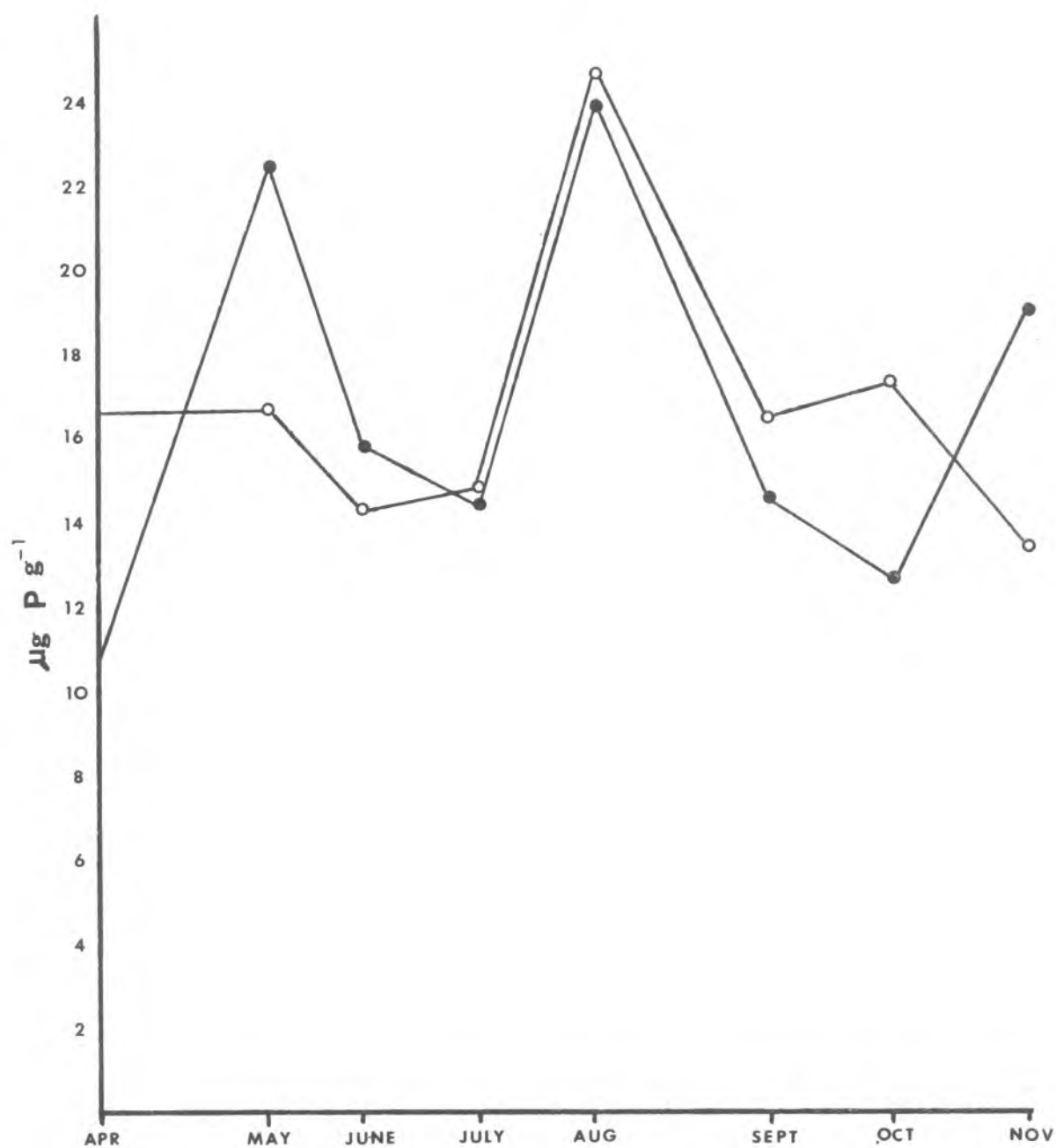
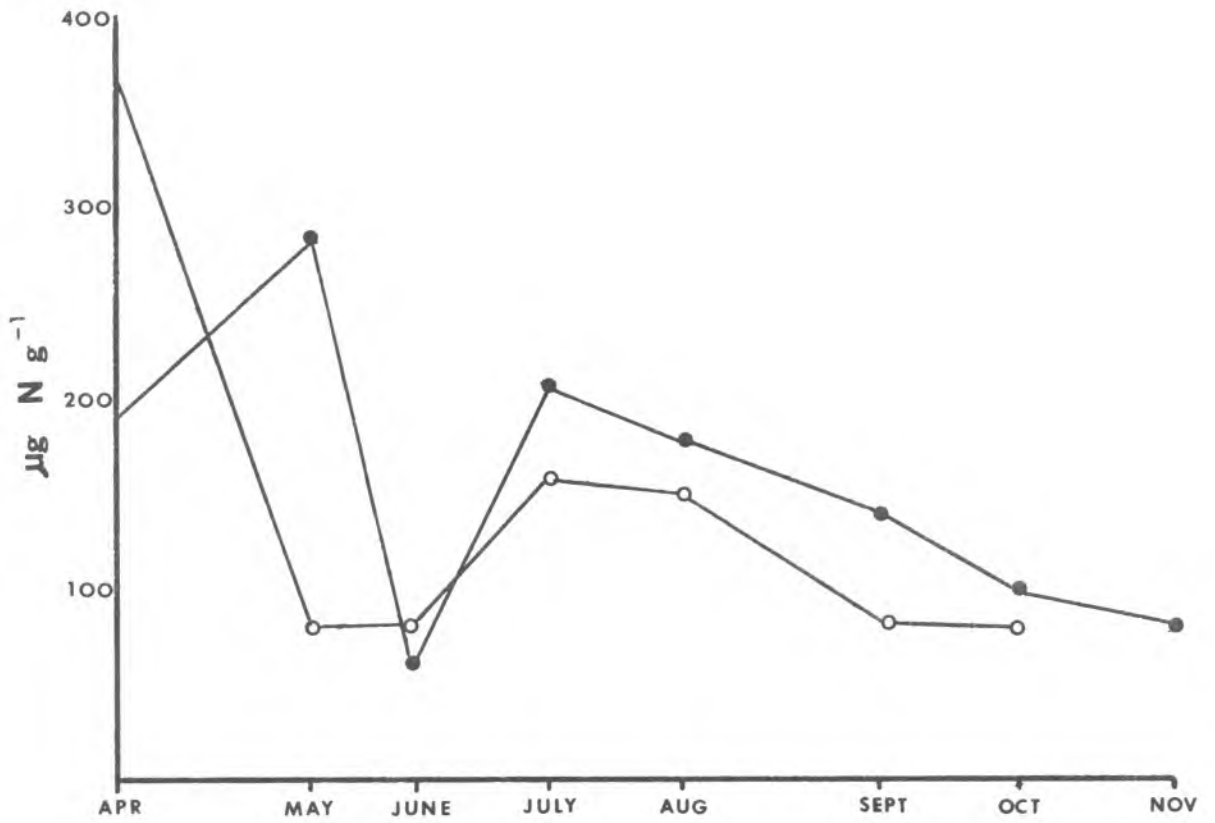


Fig. 17. Mean Kjeldahl nitrogen concentration of the sediments from Elodea sp. (●) and Potamogeton sp. and Nitella sp. (○) collection sites. The intervals between months on the x-axis are based on the number of days between samplings. Exact values and standard deviations are presented in Appendix 5.



D. Nitrogen, Phosphorus and Ash Content of Plants

The mean total nitrogen concentration of Elodea sp. and Nitella sp. gradually accumulated through the summer and fall and summer, respectively (Fig. 18). The mean total nitrogen concentration of Potamogeton sp. also increased through the summer and early fall, but declined in the late fall (Fig. 18).

The mean total phosphorus concentration of Elodea sp. was apparently highest in the winter. It was initially high in the spring, before declining through the summer and early fall. During late fall the concentration began to rise again (Fig. 19). The mean total phosphorus concentration of Potamogeton sp. increased through the entire growing season. This occurrence is abnormal, since a summer decline is typical. The phosphorus content of Nitella sp. was relatively stable during the plant's short existence, compared to Elodea sp. and Potamogeton sp.

The percent inorganic (ash) weight of dry weight for Elodea sp. declined during the early summer, which is typical for periods of positive net productivity. The total amount of inorganic constituents was not decreasing; alternately, the amount of organic matter, relative to inorganic matter, was increasing. In August, the percent inorganic weight rose sharply and subsequently declined through the rest of the season (Table 11).

The percent inorganic weight of dry weight for Potamogeton sp. was stable through the early summer (Table 11). This stability indicates that uptake of inorganic substances is approximately equal to utilization of inorganic substances.

Fig. 18. Mean total nitrogen in Elodea sp. (●), Potamogeton sp. (○), and Nitella sp. (x). The intervals between months on the x-axis are based on the number of days between samplings. Exact values and standard deviations are presented in Appendix 6.

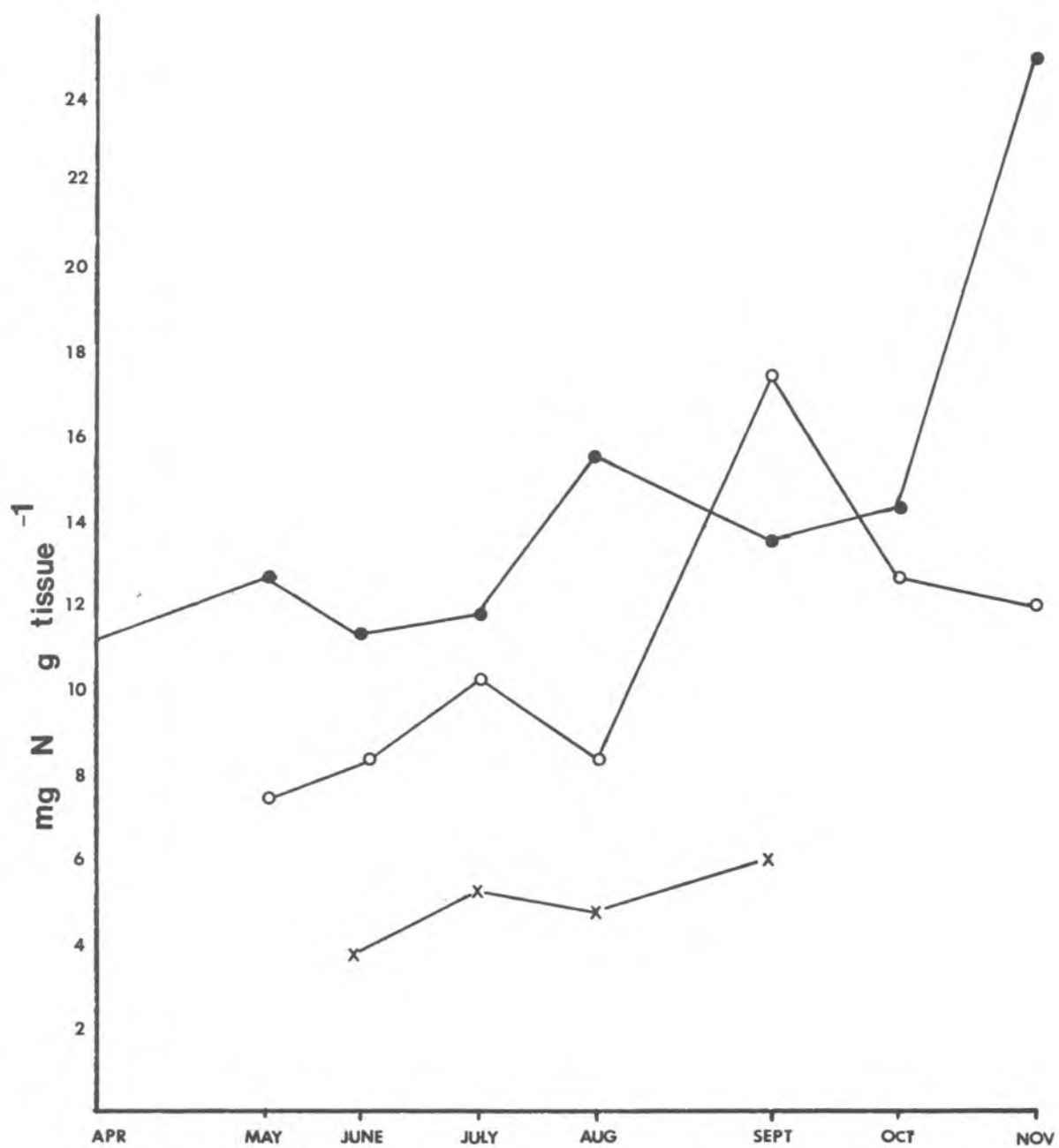


Fig. 19. Mean total phosphorus concentration of Elodea sp. (●), Potamogeton sp. (o), and Nitella sp. (x). The intervals between months on the x-axis are based on the number of days between samplings. Exact values and standard deviations are presented in Appendix 7.

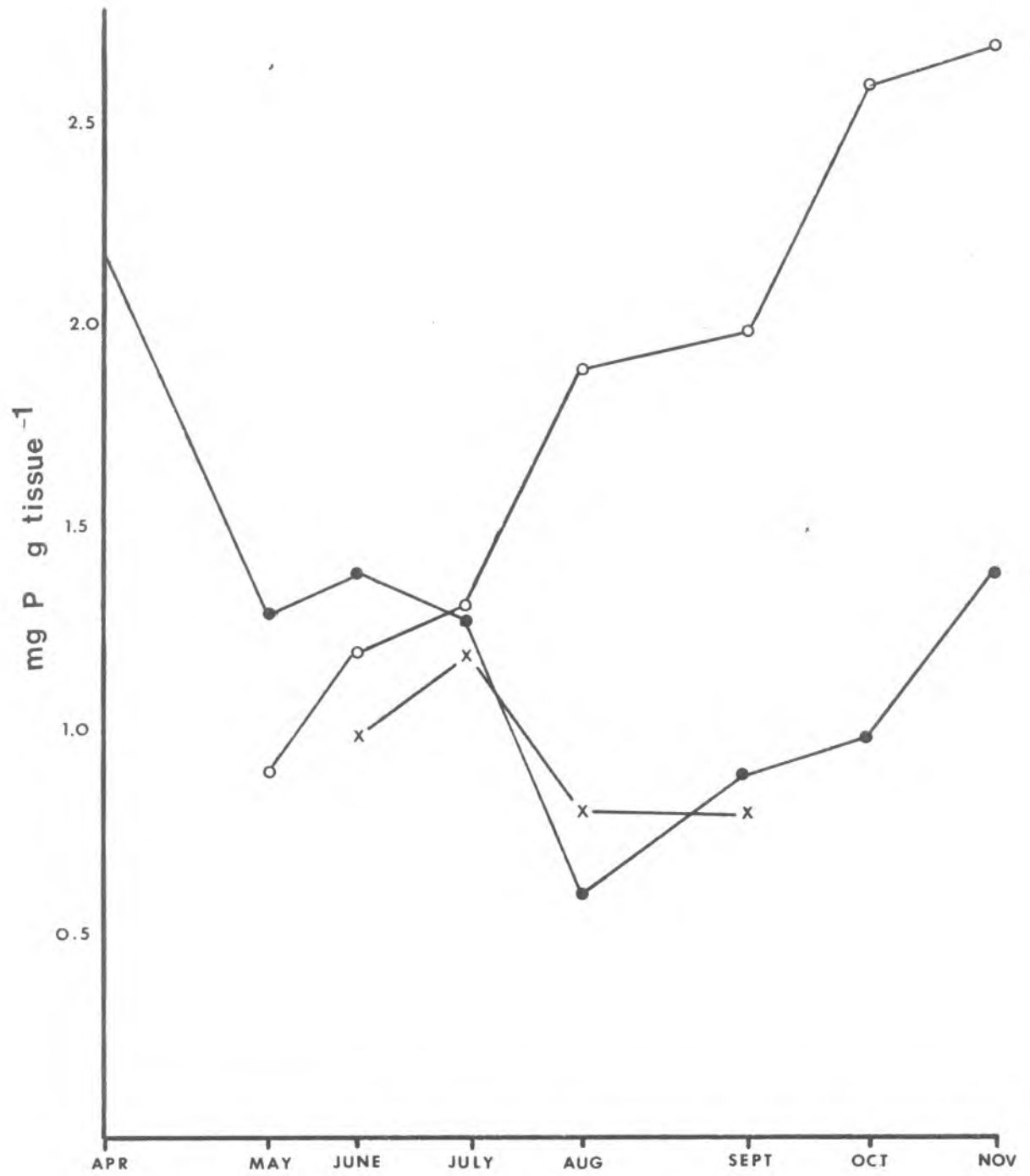


Table 11. Mean percent ash wt. of dry wt. (± 1 SD) of Elodea sp., Potamogeton sp., and Nitella sp. (n=4).

	<u>Elodea sp.</u>	<u>Potamogeton sp.</u>	<u>Nitella sp.</u>
April	20.3% $\pm$ 1.5		
May	22.3% $\pm$ 2.4	11.0% $\pm$ 1.5	
June	18.0% $\pm$ 4.6	10.3% $\pm$ 3.2	19.8% $\pm$ 5.3
July	10.8% $\pm$ 1.0	11.3% $\pm$ 1.5	25.8% $\pm$ 0.5
Aug.	37.5% $\pm$ 5.8	11.8% $\pm$ 0.5	31.0% $\pm$ 5.3
Sept.	35.3% $\pm$ 3.4	20.5% $\pm$ 2.1	32.3% $\pm$ 3.6
Oct.	34.5% $\pm$ 3.5	20.8% $\pm$ 5.6	
Nov.	21.3% $\pm$ 1.0	22.0% $\pm$ 2.4	

In September, the percent inorganic weight rose sharply; thus, suggesting a decline in utilization. The percent inorganic weight of dry weight of Nitella sp. gradually increased through the season (Table 11).

E. Correlation Coefficients

The correlation coefficients between a phosphorus or nitrogen concentration and the succeeding period of productivity yielded only two values significant at the 0.05 level. A significant positive correlation was present between the total dissolved phosphorus concentration of waters in Elodea sp. beds and the succeeding period of productivity ($r = 0.7$, $n = 16$). A significant negative correlation existed between the orthophosphate phosphorus concentration of water and the following period of productivity for Nitella sp. ($r = -0.94$, $n = 7$).

The correlation coefficients between a phosphorus or nitrogen concentration and the preceding period of productivity yielded only two significant negative correlations, *i.e.*, between the nitrate nitrogen concentration of water and the preceding period of productivity for Elodea sp. ($r = -0.63$, $n = 15$) and between the total dissolved phosphorus concentration of water and the preceding period of productivity for Nitella sp. ($r = -0.81$, $n = 7$).

No significant positive correlations were derived between the nitrogen and phosphorus concentration of plant tissues and productivity, between phosphorus and nitrogen content of waters and plant tissues, nor between the nitrogen and phos-

phorus concentration of sediments and plant tissues. A significant negative correlation was obtained between the orthophosphate phosphorus concentration in waters and the total phosphorus concentration in Nitella sp. ($r = -0.81$, $n = 7$).

VI. DISCUSSION

A. Seasonal Change in Biomass

The seasonal change in biomass of three species of macrophytes in Sam Rayburn Reservoir conformed closely to the characteristic sigmoid curve, as described by Westlake (1965b). Westlake states that the seasonal maximum biomass for plants of the northern hemisphere will probably occur in July or August. Whether there is actually a difference between the occurrence of the seasonal maximum biomass of similar latitudes in the northern and southern hemisphere, e.g., 40° S and 40° N, has yet to be substantiated.

Differences may exist between the occurrence of the seasonal maximum biomass of northern and southern latitudes in the northern hemisphere. Until now, such differences could not be determined because researchers have primarily limited their work on macrophytes to northern latitudes of the northern hemisphere; thus, no data have existed on which to base comparisons. In Sam Rayburn Reservoir, Elodea sp. and Potamogeton sp. reached their maximum biomass in July. The maximum biomass of Nitella sp. occurred in August.

The July and August occurrence of the maximum seasonal biomass values of the plants in Sam Rayburn Reservoir appear to substantiate Westlake's (1965b) opinion. However, as is pointed out in the following discussion, the maximum biomass

may not have occurred until 1 or 2 months later, had a draw-down in water level not occurred.

Nitella sp.'s late biomass is probably a result of the plant's seasonally late occurrence in the reservoir. The June occurrence of Nitella sp. may indicate that this plant is best suited for conditions which usually slow production of other plants, e.g., high temperatures and high light intensities. Although the vegetative portions of the plants did not appear until June, spores obviously had to be present in the reservoir before this time.

The greatest difference of Elodea sp. and Nitella sp. growth curves from the norm is the abrupt decline in tissues. Typically, the productivity gradually declines before the seasonal maximum biomass. All three taxa exhibited maximum growth rates prior to the seasonal maximum biomass. Each species abruptly shifted from its greatest positive net productivity to negative net productivity. This occurrence is not typical of macrophytes. Typically, most changes in productivity are gradual.

The decline of Potamogeton sp. was more gradual than for the other two taxa, yet was initially abrupt, too. However, after the initial switch from positive to negative net productivity, the decline of biomass was much more gradual than would be expected.

Most studies of macrophytes have been confined to lakes in which the water level is usually constant; thus, the effect of water level fluctuation on plant production has been poorly described and, apart from complete drying, is not understood.

Sam Rayburn Reservoir characteristically suffers a severe draw-down of approximately 3 - 4 m each summer due to the demands of hydroelectric generation and down stream requirements during this period of low precipitation.

The draw-down apparently had a severe effect on the macrophyte production during the study, especially during July and August. In July, Elodea sp.'s apical tissues were floating on the surface, due to the draw-down. At this time net productivity reversed. In August, Nitella sp.'s apical tissues were at the surface and net productivity subsequently reversed. At the surface, both species began to deteriorate.

Because Potamogeton sp.'s leaves normally float at or near the surface, it was least affected by the draw-down. This phenomenon is illustrated by the gradual decline of Potamogeton sp.'s biomass (Fig. 1).

I suggest that had the water level remained constant, positive net productivity of Elodea sp. and Nitella sp. would have continued for at least one to two months more. Thus, the maximum biomass would have occurred an equivalent amount of time later. This conclusion is based on the abruptness of the transformation from positive to negative net production.

If production had remained positive for two more months, the seasonal production of Elodea sp. and Nitella sp. would have increased by 200-300 and 100-200 g dry wt m⁻², respectively. These predictions are based on extrapolation of the curves of Fig. 10.

The exact mechanism, brought on by the draw-down, which inhibits photosynthesis or increases respiration and loss of

tissue is not clear. Hough and Wetzel (1972) demonstrated that photorespiration occurs in aquatic plants, but is limited in comparison to terrestrial plants. Hough and Wetzel (1973), however, suggest that photorespiration "...may be a significant factor in reduction of photosynthetic efficiency of aquatic macrophytes." They state that the rate of photorespiration is directly proportional to (1) light intensity (2) oxygen concentration, and (3) temperature.

Plants being brought closer to the surface, because of a draw-down, would experience an increase in each of the above three factors. The highest light intensities are near the surface. Oxygen concentration would be greatest near the surface as the diffusion gradient decreases with depth. Higher temperatures exist near the surface as the warming wavelengths of light are absorbed most rapidly. Thus, photorespiration is a potential reason for the abrupt negative productivity of Elodea sp. and Nitella sp., as both plants were being increasingly exposed to the factors stimulating photorespiration.

Photorespiration may not apply to Potamogeton sp. since it is probably well adapted for the higher temperatures, light intensities and oxygen concentrations because the leaves typically float at the surface. Alternately, Potamogeton sp. may normally undergo some photorespiration; thus, the effect of the draw-down in increasing photorespiration would be negligible.

Increased vulnerability of tissues to intense wave action at the surface poses as another possible explanation for the sharp drop in biomass. Elodea sp. and Nitella sp. are accustomed to little turbulence at the bottom, as compared to the

surface; therefore, no strong tissues exist in these plants which could withstand intense wave action brought on by boats or wind. Because the major Elodea sp. sampling sites were in bays where boat ramps and a marina were located, wave action due to boats may have been significant. However, the bays were somewhat free of wind effects.

Another possible reason for the early decline of Elodea sp. might have been the presence of dense concentrations of phytoplankton. Mulligan, et al., (1976) and Jupp and Spence (1977) credited high densities of phytoplankton with the decline of aquatic vascular plants, through the attenuation of light. Mulligan, et al., (1976) found this phenomenon especially true with continued enrichment of waters. In June, the total phosphorus concentration in waters of Elodea sp. collection sites in Sam Rayburn Reservoir rose sharply and remained high through the rest of the summer (Fig. 12). Immediately after the first high total phosphorus value, Elodea sp.'s net productivity became negative (Fig. 11). The sudden change in productivity may have been due to an increase in phytoplankton concentration, as a result of the high phosphorus load. Unfortunately, no chlorophyll analyses or phytoplankton counts were performed on the waters of the littoral zone to substantiate this hypothesis. Mulligan, et al., (1976) noted that Elodea canadensis could survive high densities of phytoplankton, but growth was less than the control.

No explanation adequately deals with the loss of tissue by Potamogeton sp. But as already pointed out, the decline of Potamogeton sp. tissues was much more gradual than the decline

of tissues of the other two species. This occurrence may indicate that Potamogeton sp. was less affected by the draw-down. However, the decline may have been a result of sampling. Variation in biomass among Potamogeton sp. sites was greater than Elodea sp. and Nitella sp. sites. Also, the statistics were not as reliable late in the season as early, because the number of sampling sites decreased through the season as beds dried up due directly to the draw-down. Coupling these two factors possibly indicates that the observed decline may be an artifact due to sampling, brought on by the draw-down.

The variation in biomass among Potamogeton sp. sites may have been due to some beds occurring in areas vulnerable to wave action, while other beds were protected in bays. No relationship was apparent between biomass values and the nitrogen or phosphorus concentrations in the water or sediment.

B. Comparisons Between the Seasonal Maximum Biomass of Plants in Sam Rayburn Reservoir and Plants of Other Localities

With the exception of Potamogeton sp., the seasonal maximum biomass values of the submerged plants from Sam Rayburn Reservoir are much greater than values reported for other localities (Table 12). The maximum biomass of Nitella sp. was over 1/3 higher than the highest previously reported biomass value. The maximum biomass of Elodea sp. was approximately 11 times greater than the maximum biomass of Elodea canadensis in Chautauqua Lake, New York.

The higher biomass values of Sam Rayburn plants are probably a product of the southern latitude. Brylinsky and Mann (1975), after investigating numerous factors, reported

Table 12: Seasonal Maximum Biomass Values from the literature and Sam Rayburn Reservoir.

Lake	Plant Species	Seasonal Maximum Biomass	*
Trout L., Wis.	Chara sp. & Nitella sp.	0.07 g m ⁻²	1
Weber L., Wis.	Chara sp. & Nitella sp.	16.80 g m ⁻²	2
L. Mendota, Wis.	Chara sp. & Nitella sp.	202.00 g m ⁻²	3
Lawrence L., Mich.	Chara sp.	110.00 g m ⁻²	4
River Yare, England	Potamogeton lucen	380.00 g m ⁻²	5
River Colne, England	Potamogeton pectinatus	120.00 g m ⁻²	6
Chautauqua L., N.Y.	Potamogeton crispus	260.90 g m ⁻²	7
Chautauqua L., N.Y.	Elodea canadensis	97.90 g m ⁻²	7
Sam Rayburn Reservoir	Nitella sp.	327.60 g m ⁻²	7
Sam Rayburn Reservoir	Potamogeton sp.	168.40 g m ⁻²	7
Sam Rayburn Reservoir	Elodea sp.	1013.60 g m ⁻²	7

*

- (1) Wilson, (1941).
- (2) Potzer and Engel, (1942).
- (3) Rickett, (1921).
- (4) Rich, et.al., (1971).
- (5) Owens and Edwards, (1962).
- (6) Westlake, (1961).
- (7) Best and Nicholson, (1974).

that latitude was the most important factor determining the production of phytoplankton. The same may be true for macrophytes. Unfortunately, other studies of submergents are lacking to confirm this conclusion, since most macrophyte studies have been restricted to the northern latitudes.

The latitudinal hypothesis is not supported by Potamogeton sp. The maximum biomass of Potamogeton sp. is comparable to data from northern localities, but is approximately one-half as great as the highest value from England (Table 12). However, the fact that the River Yare is "mildly polluted" (Sculthorpe, 1967), may account for the higher biomass values. The lower values for Potamogeton sp. in Sam Rayburn Reservoir may be due to intense wave action. Rough water is characteristic of Sam Rayburn Reservoir, particularly when the wind is from the northwest. The rough wave action may be sufficient to cause enough loss of tissue of this floating-leaved species to offset the advantage of a southern latitude.

C. The Production of Phytoplankton and Macrophytes in Sam Rayburn Reservoir Compared

The annual production of phytoplankton in Sam Rayburn Reservoir is estimated by Lind (in progress) as being approximately $60 \text{ g dry wt m}^{-2} \text{ surface yr}^{-1}$. Table 8 lists the annual production of macrophytes in Sam Rayburn Reservoir. The combined production of the three plant species was 80,528.16 (Table 9) $\text{kg dry wt lake}^{-1} \text{ year}^{-1}$. This value is approximately 0.289% of the phytoplankton production in the reservoir. Therefore, the production of macrophytes in Sam Rayburn Reservoir contributes little to the trophic status of the reservoir.

D. The Nutritional Dynamics of Elodea sp.

1. The seasonal trend in ash weight, as related to the productivity, nitrogen and phosphorus tissue concentration and the secretion of phosphorus.

The ash weight of Elodea sp. during the early portion of the growing season followed the expected decline. However, in August, a dramatic shift occurred as the percent ash weight jumped from 10.8% to 37.5%. This increase coincides closely with the time plants were exposed and deteriorating at the surface, due to the draw-down. Also, from July to August, there was a severe turn-about in productivity. The sudden rise in percent ash weight can be accounted for by both events.

Decomposition of organic matter in plant tissues caused by the plants being at the surface is a possible hypothesis for the increase in proportion of inorganic matter in tissues. In addition, should absorption of inorganic nutrients continue in tissues at the same rate during periods of negative net productivity, as occur during periods of positive net productivity, the percent inorganic content would rise. This excess uptake, relative to requirements, may occur during periods of negative productivity since macrophytes have been demonstrated to have luxuriant uptake (Wetzel, 1975). The reasoning is such that, positive net productivity results in constant usage of absorbed inorganic nutrients and negative net productivity allows inorganic nutrients to concentrate in tissues. This concentration would be reflected by an increase in percent ash weight. During a period of negative net productivity, nutrient usage still occurs (gross productivity), but not at as high a rate as positive net productivity.

The above hypothesis is supported by the fact that during the first two periods of negative net productivity (Fig. 11) the total nitrogen concentration in tissues rose (Fig. 18). Following these two negative net productivity periods, a time of slightly positive net productivity occurred and was accompanied by a slight drop in the concentration of nitrogen. The short period of positive net productivity was followed by another negative net productivity period and was again accompanied by an increase in the concentration of nitrogen. Thus, the trend was stable nitrogen concentration during the periods of positive net productivity and increased concentration during the periods of negative net productivity.

The total phosphorus concentration of the tissues showed an absolute decline through the spring and summer before rising again in the fall (Fig. 19), which is typical (Caines, 1963; Boyd, 1969; Nichols and Keeney, 1976). The initial decline was probably the result of higher usage, due to positive net productivity, rather than absorption. A tenable explanation exists for the continued decrease in total phosphorus during the period of negative net productivity and nitrogen accumulation. DeMarte and Hartman (1974) have observed a release of phosphorus to surrounding waters by Myriophyllum exalbescens. The release was increased by damage to the shoot. It is possible that the same mechanism exists in Elodea sp. The continued decrease in total phosphorus content may be due to phosphorus being lost to the waters as tissues deteriorated or were damaged by wave action.

Secretion of phosphorus is substantiated by the rise in total phosphorus of the waters within the bed between July and August (Fig. 12). The fact that total phosphorus values were higher in Elodea sp. beds than Potamogeton sp. and Nitella sp. beds further strengthens the hypothesis of phosphorus excretion by Elodea sp.

The phosphorus concentration within and outside the Elodea sp. beds indicated a slight diffusion gradient (Table 10). Orthophosphate phosphorus and total phosphorus show the strongest diffusion gradient. The August total phosphorus samples did not show a diffusion gradient. The existence of diffusion gradients adds further support to the phosphorus release hypothesis. Apparently, the secretion of phosphorus is not proportional to the productivity, as no significant positive correlations were derived between productivity and the succeeding month's concentration of phosphorus.

2. The relationship between internal and external concentrations of nutrients.

Contrary to the work of Gerloff and Krombholz (1966), no significant correlation between the nitrogen and phosphorus concentration of plant tissues and the water was observed. Gerloff and Krombholz showed in the laboratory that the nutrient concentration of plant tissues was indicative of the concentration of the same nutrient in the waters. Boyd and Hess (1970) found in the field that only 32% of the variation in tissue nutrient concentrations is explained by environmental levels of nutrients. Boyd (1970b) also reported that the ratio of nutrients in plants of Par Pond, S. C. were not

similar to the ratios of the same nutrients in the water.

Gerloff and Krombholz (1966) indicated that water and tissue nutrient concentrations are related only when the nutrient in question is limiting. Only one significant positive correlation between productivity of Elodea sp. and the total dissolved phosphorus concentration of the water was derived. This correlation indicates that phosphorus may possibly be limiting; thus, according to Gerloff and Krombholz, a positive correlation should have existed between the internal and external phosphorus concentrations, relative to the plant. Because nitrogen concentrations of the water and sediment were apparently not limiting in Elodea sp. of Sam Rayburn Reservoir, a high correlation between environmental and tissue concentrations was not expected.

It is not surprising that only one significant correlation between nutrient concentrations and productivity was derived. In a study similar to this, but on emergent vegetation, no significant correlations were found between nutrient concentration and productivity (Boyd and Vickers, 1971).

Factors other than nutrient regimes influence nutrient uptake (Boyd and Hess, 1970). Sutcliffe (1962) pointed out that the uptake and concentration of nutrients is dependent on many factors, e.g., different plant types and the proportion of various nutrients to one another in water. Because of these interrelationships, Gerloff and Krombholz (1966) could not duplicate conditions as they actually exist;

thus, their work is probably not a valid indication of the relationship existing between the concentration of nutrients in waters and plant tissues in the environment. My work illustrates this point, because of the lack of significant correlations between the internal and external nitrogen and phosphorus concentrations.

Bristow and Whitcomb (1971) demonstrated that as much as 75% of absorption of nutrients in Elodea canadensis is accomplished by the roots. Root absorption, as opposed to shoot absorption, is a strong alternative explanation for the lack of a significant correlation between nitrogen and phosphorus concentrations of tissues and water. However, no significant correlations were found between sediment nitrogen and phosphorus and tissue nitrogen and phosphorus, indicating non-limiting quantities.

Some researchers have reported relationships between environmental levels of nutrients and standing crops of plants (Pearsall, 1917, 1918, 1920, 1921; Misra, 1938). High environmental nutrient concentrations yielded high standing crops of plants. However, in this study no apparent relationship existed between the standing crop of Elodea sp. and either nitrogen or phosphorus concentrations in water or sediment.

E. The Nutritional Dynamics of Potamogeton sp.

1. The seasonal trend in ash weight as related to the productivity and nitrogen and phosphorus tissue concentration.

The trend in change of percent ash weight of Potamogeton sp. is very similar to that of Elodea sp. (Table 11). During

the early portion of the growing season (April to July), the percent ash weight was stable; however, in the following period, ash weights more than doubled. This increase follows one month behind the increase in percent ash weight of Elodea sp.

The increase in ash weight was possibly due to two events. The rise may have been an effect caused by the draw-down. If this hypothesis is true, the earlier suggestion that Potamogeton sp. was little affected by the draw-down is weakened. Alternatively, the rise in ash weight may have been a side effect of continued negative net production.

Through the growing season the nitrogen and phosphorus concentration of Potamogeton sp. increased. The rise in percent ash weight may be a reflection of the accumulation and concentration of inorganic nutrients, especially during the periods of negative net productivity.

The increase in nitrogen and phosphorus through the season indicates that neither nutrient is limiting. This hypothesis is supported by the fact that no significant correlations were yielded between productivity and the nitrogen or phosphorus concentration in the water or tissue.

2. The relationship between internal and external nutrient concentrations.

No apparent relationship existed between the environmental concentrations of nitrogen and phosphorus and the tissue concentrations of nitrogen and phosphorus, as illustrated by lack of significant correlations. As with Elodea sp., probably a great deal of nutrient absorption is by the roots of

Potamogeton sp. Yet, no significant correlations were derived between the nitrogen and phosphorus concentrations of sediments and tissues.

Potamogeton sp. biomass values among collection sites were not related to the environmental concentrations of nitrogen and phosphorus. This phenomenon is surprising because of the large variation in biomass values (Appendix 1) and the reports that standing crops are often controlled by environmental concentrations of nutrients (Pearsall, 1917; 1918, 1920, 1921; Misra, 1938). Perhaps, degrees in exposure of plants to wave action is more important than environmental concentrations of nutrients in controlling the magnitude of Potamogeton sp.'s production in Sam Rayburn Reservoir.

3. The secretion of nutrients.

No known studies have credited Potamogeton sp. with the ability to secrete nutrients. In this study, no evidence of secretion of nutrients by Potamogeton sp. was observed based on no significant correlations being found between productivity and the succeeding month's nitrogen and phosphorus concentration in the waters. Lower total phosphorus concentrations in waters surrounding the Potamogeton sp. beds, as compared to the waters of Elodea sp. beds, which is known to secrete phosphorus, is a further indication of this hypothesis (Figs. 12 and 13).

F. The Nutritional Dynamics of Nitella sp.

The seasonal trends in percent ash weight and nutrient concentration of tissues of Nitella sp. are not easily

explained (Figs. 18 and 19, and Table 11). The reason for the lack of a tenable explanation is probably due to the short duration of Nitella sp.'s existence (4 months).

Throughout the season, percent ash weight gradually increased. The nitrogen and phosphorus concentrations of tissues did not have a simultaneous increase. The increases in percent ash weight do not coincide with decomposition of tissues or periods of net productivity. Thus, the factors regulating the ratio of inorganic to organic weight of Nitella sp. are not similar to those factors controlling the percent inorganic weight of Elodea sp. and Potamogeton sp. This difference may be because Elodea sp. and Potamogeton sp. are angiosperms and Nitella sp. is an alga, and thus, a reflection of anatomical and physiological differences between vascular and nonvascular plants.

Many high negative and positive correlations were derived; however, only three negative correlations were significant at the 0.05 level. These were between orthophosphate phosphorus concentrations in water and the succeeding period of productivity, total dissolved phosphorus concentration in water and the preceding period of productivity, and the total phosphorus in tissues and orthophosphate phosphorus concentration in the waters. The high correlations are probably an artifact of having only a few samples because of the brief occurrence of Nitella sp. But, alternately, of the three species, Nitella sp. should show the highest correlation between nitrogen and phosphorus concentrations of the waters and productivity, and the nitrogen and phosphorus concentra-

tions in the tissues and waters. The close relationships of the above factors is due to the fact that Nitella sp. has no roots; thus, it depends on foliar uptake for nutrition. This relationship would only exist when environmental nutrient concentrations are below the concentrations required by the plant.

VII. CONCLUSIONS

A. The Production of Macrophytes of Sam Rayburn Reservoir

The seasonal production of macrophytes in Sam Rayburn Reservoir followed the typical sigmoid growth curve with the seasonal maximum biomass values occurring in July or August. However, the effect of a draw-down on the reservoir apparently caused an early seasonal maximum biomass for the plants. Consequently, positive net productivity was terminated early. Should the draw-down not have occurred, the seasonal maximum biomass values may have been one to two months later.

Even so, the seasonal maximum biomass values of Elodea sp. and Nitella sp. were greater than values from the literature for plants from northern latitudes. This increase was presumably due to the difference in latitude.

The annual production of macrophytes in Sam Rayburn Reservoir was $80,528.16 \text{ kg dry wt m}^{-2} \text{ yr}^{-1}$. This value was approximately 0.289% of the production of phytoplankton. Thus, the production of macrophytes contributes little to the trophic status of Sam Rayburn Reservoir.

Plant production was not limited by either environmental or internal concentrations of nitrogen or phosphorus. Although there was indication of phosphorus limitation in the Elodea

sp. stands, phosphorus was assumed not to be limiting. This assumption was based on the lack of significant correlations occurring between the external and internal levels of phosphorus, relative to the plant.

B. The Seasonal Trends in Ash Wt., Nitrogen
Concentration, and Phosphorus
Concentration in Plant
Tissues

The ash weights of Elodea sp. and Potamogeton sp. initially decreased as expected. However, during mid-summer the ash weights of both plants increased significantly. This increase was thought to be a result of negative net productivity, due to a draw-down on the reservoir, and the accumulation of nutrients. Nitella sp.'s ash weights exhibited an increase during the plant's short existence, but the rise could not be adequately explained.

The concentration of nitrogen and phosphorus in plant tissues through the season did not illustrate the typical spring and autumn high and summer minimum. These differences, were probably the result of several factors, e.g., negative net productivity, luxuriant nutrient uptake, and phosphorus secretion.

C. Internal and External Concentrations
of Nitrogen and Phosphorus

The internal concentrations of nitrogen and phosphorus were not found to be indicative of nitrogen and phosphorus concentrations in the water. Probably, no relationship was found because of the complex physiological mechanisms of the

plant which govern nutrient uptake, accumulation and utilization; plus, the assumed occurrence of root absorption of nitrogen and phosphorus.

The concentration of phosphorus in waters appeared to have been affected by secretion of phosphorus by Elodea sp. This hypothesis was substantiated by the existence of diffusion gradients between the interior and exterior of the Elodea sp. beds. Further support was given by the fact that during the summer the total phosphorus concentration in the waters rose sharply as tissue phosphorus decreased sharply.

Appendix 1: Mean monthly biomass (± 1 SD, g dry wt. m^{-2}) of Elodea sp., Potamogeton sp., and Nitella sp.

	<u>Elodea</u> sp.	<u>Potamogeton</u> sp.	<u>Nitella</u> sp.
April	617.6 $\pm$ 124.9	—	—
May	699.2 $\pm$ 128.4	15.2 $\pm$ 5.2	—
June	720.4 $\pm$ 75.6	57.6 $\pm$ 24.0	73.2 $\pm$ 32.8
July	1013.6 $\pm$ 183.0	168.4 $\pm$ 95.8	197.2 $\pm$ 49.1
Aug.	870.6 $\pm$ 79.8	138.0 $\pm$ 48.0	327.6 $\pm$ 44.4
Sept.	416.4 $\pm$ 130.1	131.1 $\pm$ 29.2	143.6 $\pm$ 48.8
Oct.	459.6 $\pm$ 163.2	109.3 $\pm$ 25.7	—
Nov.	448.0 $\pm$ 131.9	64.4 $\pm$ 5.7	—

Appendix 2: The mean productivity (g dry wt. day⁻¹ m⁻²) of Elodea sp., Potamogeton sp., and Nitella sp.

	<u>Elodea sp.</u>	<u>Potamogeton sp.</u>	<u>Nitella sp.</u>
Apr. - May	2.0	—	—
May - June	1.0	2.0	—
June - July	10.11	3.8	4.3
July - Aug.	-5.3	-1.1	4.8
Aug. - Sept.	-11.1	-0.2	-4.5
Sept. - Oct.	1.5	-0.8	—
Oct. - Nov.	-0.4	-1.5	—

Appendix 3: Mean phosphorus concentration (± 1 SD, $\mu\text{g l}^{-1}$) of the waters from Elodea sp., Potamogeton sp., and Nitella sp. collection sites.

	<u>Elodea</u> sp. sites		
	<u>PO₄</u>	<u>Total Dissolved Phosphorus</u>	<u>Total Phosphorus</u>
April	—	—	—
May	*10.5	*18.6	*31.0
June	24.9 $\pm$ 19.5	34.8 $\pm$ 19.0	107.9 $\pm$ 18.2
July	7.2 $\pm$ 2.8	14.3 $\pm$ 4.7	98.3 $\pm$ 14.1
Aug.	13.9 $\pm$ 7.1	10.6 $\pm$ 0.0	112.4 $\pm$ 100.8
Sept.	11.2 $\pm$ 1.8	15.7 $\pm$ 0.0	104.8 $\pm$ 68.4
Oct.	14.0 $\pm$ 0.8	11.1 $\pm$ 0.7	36.0 $\pm$ 21.6
Nov.	3.0 $\pm$ 1.8	—	—

	<u>Potamogeton</u> sp. and <u>Nitella</u> sp. sites		
	<u>PO₄</u>	<u>Total Dissolved Phosphorus</u>	<u>Total Phosphorus</u>
April	—	—	—
May	*24.9	*18.6	*51.0
June	14.1 $\pm$ 11.9	20.9 $\pm$ 12.5	89.3 $\pm$ 44.6
July	8.3 $\pm$ 8.2	15.7 $\pm$ 9.6	37.0 $\pm$ 18.0
Aug.	18.5 $\pm$ 13.6	14.7 $\pm$ 5.7	60.0 $\pm$ 22.3
Sept.	16.6 $\pm$ 12.4	25.2 $\pm$ 12.3	59.6 $\pm$ 10.3
Oct.	*6.7	*10.6	*71.7
Nov.	*2.4	—	—

* - based on one determination.

Appendix 4: Mean nitrogen concentration (± 1 SD, $\mu\text{g l}^{-1}$) of the waters from Elodea sp. and Potamogeton sp. and Nitella sp. collection sites.

<u>Elodea sp. sites</u>			
	<u>Organic Nitrogen</u>	<u>NH₃</u>	<u>NO₃</u>
April	—	—	—
May	*238.0	*0.0	*66.2
June	198.5 $\pm$ 2.2	21.5 $\pm$ 6.3	50.1 $\pm$ 26.8
July	189.6 $\pm$ 88.6	41.5 $\pm$ 0.0	36.1 $\pm$ 5.4
Aug.	*275.0	*41.5	*86.6
Sept.	174.3 $\pm$ 57.5	122.9 $\pm$ 35.9	12.3 $\pm$ 2.1
Oct.	201.8 $\pm$ 129.8	*22.5	7.9 $\pm$ 4.1
Nov.	102.4 $\pm$ 15.4	19.3 $\pm$ 3.8	7.9 $\pm$ 4.1

<u>Potamogeton sp. and Nitella sp. sites</u>			
	<u>Organic Nitrogen</u>	<u>NH₃</u>	<u>NO₃</u>
April	—	—	—
May	*237.0	*15.0	*80.0
June	163.7 $\pm$ 72.9	32.1 $\pm$ 26.5	51.8 $\pm$ 7.2
July	198.4 $\pm$ 48.0	45.7 $\pm$ 23.5	40.6 $\pm$ 31.3
Aug.	292.6 $\pm$ 40.5	113.4 $\pm$ 72.7	37.1 $\pm$ 4.0
Sept.	161.2 $\pm$ 26.7	0.0	7.9 $\pm$ 5.0
Oct.	*108.0	*36.7	*0.0
Nov.	*137.7	* 0.0	*0.0

* - based on one determination.

Appendix 5: Mean (± 1 SD) Kjeldahl nitrogen and mean total phosphorus concentration ($\mu\text{g g}^{-1}$) of the sediment beneath Elodea sp. and Potamogeton sp. and Nitella sp. collection sites.

Elodea sp. sites

	<u>Phosphorus</u>	<u>Nitrogen</u>
April	*10.9	*199.0
May	*22.3	285.0 $\pm$ 77.8
June	15.9 $\pm$ 4.0	*60.0
July	14.5 $\pm$ 4.5	209.5 $\pm$ 28.9
Aug.	24.1 $\pm$ 10.2	165.0 $\pm$ 7.1
Sept.	14.5 $\pm$ 0.8	140.0 $\pm$ 42.4
Oct.	12.9 $\pm$ 12.8	100.0 $\pm$ 14.1
Nov.	19.1 $\pm$ 9.1	*40.0

Potamogeton sp. and Nitella sp. sites

	<u>Phosphorus</u>	<u>Nitrogen</u>
April	—	—
May	*16.6	*370.0
June	16.8 $\pm$ 7.7	80.0 $\pm$ 14.1
July	14.3 $\pm$ 2.3	80.0 $\pm$ 56.5
Aug.	24.8 $\pm$ 9.3	*160.0
Sept.	16.2 $\pm$ 4.1	150.0 $\pm$ 56.6
Oct.	17.4 $\pm$ 5.9	83.0 $\pm$ 25.2
Nov.	*13.3	* 80.0

* - based on one determination.

Appendix 6: Mean (± 1 SD) total nitrogen (mg g tissue⁻¹) in Elodea sp., Potamogeton sp., and Nitella sp. tissues.

	<u>Elodea</u> sp.	<u>Potamogeton</u> sp.	<u>Nitella</u> sp.
April	11.2 $\pm$ 2.2	—	—
May	12.6 $\pm$ 1.6	7.5 $\pm$ 1.0	—
June	11.3 $\pm$ 1.8	8.3 $\pm$ 0.6	3.8 $\pm$ 0.7
July	11.8 $\pm$ 1.2	10.2 $\pm$ 1.5	5.1 $\pm$ 0.1
Aug.	15.6 $\pm$ 1.3	8.4 $\pm$ 0.0	4.9 $\pm$ 0.6
Sept.	13.6 $\pm$ 2.5	17.5 $\pm$ 3.4	6.0 $\pm$ 0.1
Oct.	14.3 $\pm$ 1.8	12.8 $\pm$ 3.5	—
Nov.	25.0 $\pm$ 2.4	12.0 $\pm$ 0.3	—

Appendix 7: Mean ($\pm$ 1 SD) total phosphorus content (mg g tissue⁻¹) of Elodea sp., Potamogeton sp., and Nitella sp. tissues.

	<u>Elodea</u> sp.	<u>Potamogeton</u> sp.	<u>Nitella</u> sp.
April	2.2 $\pm$ 0.12	—	—
May	1.3 $\pm$ 0.09	0.9 $\pm$ 0.17	—
June	1.4 $\pm$ 0.04	1.2 $\pm$ 0.00	1.0 $\pm$ 0.10
July	1.3 $\pm$ 0.10	1.3 $\pm$ 0.15	1.2 $\pm$ 0.10
Aug.	0.6 $\pm$ 0.24	1.9 $\pm$ 0.08	0.8 $\pm$ 0.00
Sept.	0.9 $\pm$ 0.20	2.0 $\pm$ 0.08	0.8 $\pm$ 0.02
Oct.	1.0 $\pm$ 0.50	2.6 $\pm$ 0.46	—
Nov.	1.4 $\pm$ 0.04	2.7 $\pm$ 0.12	—

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