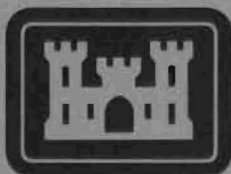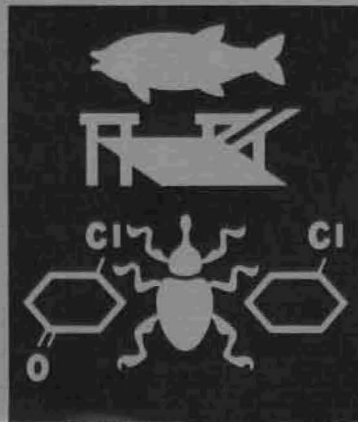Not copied

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TECHNICAL REPORT A-82-3

SEDIMENT-SUBMERSED MACROPHYTE RELATIONSHIPS IN FRESHWATER SYSTEMS

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    The capabilities of four species of submersed freshwater macrophytes in mobilizing nitrogen (N), phosphorus (P), and potassium (K) from three different sediments were comparatively examined in relation to their requirements for these nutrients during a 10-week period of growth under controlled environmental conditions. With all species, N and P were readily mobilized from each of the sediments and concentrated in plant shoots at levels well above those

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20. ABSTRACT (Continued).

required for growth. However, the mobilization of K from all sediments was much less effective and may have limited the growth of the species considered. Sediments represent a large and important source of N and P for rooted aquatic macrophytes, but K is probably supplied to these plants primarily from the water.

Only small quantities, or none at all, of N and P were excreted from the species considered during active growth. However, considerable quantities of these nutrients can be released to the water due to plant senescence and associated decay processes. Since a large fraction of the total nutrients, in particular N and P, released during decay may derive from the sediment, this mechanism represents an important mode of sediment-nutrient recycling in aquatic systems.

In a subsequent related investigation, K uptake by *Hydrilla verticillata* Royle from sediment versus overlying water was evaluated in relation to the K demands incurred by this species during an 8-week period of growth. The investigation was conducted on a heterogeneous assemblage of sediments and in two solutions differing fundamentally in the presence (2.3 mg ℓ^{-1}) and absence of K.

Both biomass production and shoot morphology in *Hydrilla* varied significantly between solutions and among sediments. In contrast to N and P, which were readily mobilized from most sediments, K was mobilized from all sediments to only a minor extent by this species. Mobilization of K was proportional to interstitial water K concentrations; yet on at least four of the six sediments examined, K supplied from sediments was insufficient to support the maximal growth of *Hydrilla*. The open water rather than the sediment appears to be the primary source of K supply to this species and perhaps to most other submersed freshwater macrophytes.

Where K was supplied in solution, sediment-related differences in the growth of *Hydrilla* negatively correlated with sediment organic matter content over the range of 1.6 to 56.2 percent dry sediment mass. It is tentatively suggested that the organic composition of sediments may influence the species composition of aquatic macrophyte communities.

PREFACE

The investigations reported herein were supported by the Aquatic Plant Control Research Program (APCRP) and the Environmental Water Quality and Operational Studies (EWQOS) Program, both sponsored by the Office, Chief of Engineers, and managed by the U. S. Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss.

Manager of the APCRP was Mr. J. Lewis Decell. Manager of the EWQOS Program was Dr. Jerome L. Mahloch. General supervision was provided by Drs. Rex L. Eley and Robert M. Engler, Division and Group Chiefs, respectively, in the Ecosystem Research and Simulation Division of the Environmental Laboratory (EL). Investigators were Dr. John W. Barko, Ms. Dwilette G. Hardin, Ms. M. Susan Matthews, and Mr. R. Michael Smart. Dr. Barko wrote this report.

The authors wish to acknowledge the constructive review comments provided anonymously by members of the Editorial Board of Aquatic Botany, a scientific journal in which manuscripts forming the basis for this report were published.

Assistance in collecting sediments was provided by Dr. John Anderson, Omaha District, CE; Mr. Angus Gholson and Mr. Joseph Kight, Lake Seminole; Mr. Loren Mason and his staff at Kerr Reservoir; and Dr. Dean Martin and his students from the University of South Florida working on Lake Starvation. Discussions with Dr. Martin and Mr. Kight provided information on Lakes Starvation and Seminole, respectively. Mr. Derrick J. Bates, EL, is acknowledged for his statistical assistance and for his review of some sections of this report. Excellent support was provided by the Analytical Laboratory Group and the Word Processing Section of the EL.

Chief of the EL during the conduct of these investigations and preparation of this report was Dr. John Harrison. Commanders and Directors of the WES were COL Nelson P. Conover, CE, and COL Tilford C. Creel, CE. Technical Director was Mr. F. R. Brown.

1

This report should be cited as follows:

CONTENTS

SEDIMENT--SUBMERSED MACROPHYTE RELATIONSHIPS
IN FRESHWATER SYSTEMS

PART I: INTRODUCTION

1. Despite the reduced structure and extent of the root system of
most submersed macrophytes when compared with terrestrial plants, roots
of the former may possess many (if not all) of the functional charac-
teristics of the latter (Tomlinson 1969; Bristow 1975). Experiments
with submersed macrophytes have demonstrated the uptake of a variety of
nutrients by roots and the subsequent translocation of these nutrients
to shoots. In this regard, phosphorus (P) has been examined most exten-
sively, leading to the generally accepted concensus that submersed macro-
phytes can obtain their P largely from the sediment (Bole and Allan 1978;
Barko and Smart 1979a, 1980, 1981; Carignan and Kalff 1979, 1980). Much
of the recent information available on specific processes of uptake,
translocation, and excretion of P by submersed macrophytes is critically
examined in Welsh and Denny (1979). The understanding of the mobiliza-
tion (i.e., uptake by roots and transport to shoots) of other nutrients
by submersed macrophytes is far less complete. A relatively small num-
ber of studies have indicated that nitrogen (N) (Toetz 1974; Nichols and
Keeney 1976a,b; Best and Mantai 1978), iron (Fe) (DeMarte and Hartman
1974; Gentner 1977; Basiouny, Haller, and Garrard 1977), and calcium (Ca)
(DeMarte and Hartman 1974) can be mobilized to a variable extent by sub-
mersed macrophytes. Additionally, carbon uptake from sediments by roots
of submersed species possessing an extensive lacunar system has been
demonstrated to be significant in comparison with its uptake by shoots
(Sand-Jensen and Søndergaard 1979; Søndergaard and Sand-Jensen 1979).

2. The extent to which nutrients mobilized from sediments re-
place, complement, or represent an addition to nutrients obtained from
the water by submersed macrophytes is unclear. The ability to better
understand the influence of submersed macrophytes on lacustrine nutrient
cycles will continue to depend in large part on the resolution of this

4

quandary. Moreover, the importance of nutrients compared with other factors affecting the growth of submersed macrophytes cannot be adequately assessed without better information on specific nutrient source-sink relations involving sediment, plant, and water.

3. An important aspect of much of the work on the nutrition of submersed macrophytes is that it was stimulated by early experimental accounts and observations of sediment-related variations in the growth and distribution of freshwater macrophytes (e.g., Misra 1938; Moyle 1945; Pearsall 1920; Pond 1905). More recently the influence of sediments on the growth of submersed macrophytes has been reemphasized in the studies of Aiken and Picard (1980), Anderson (1978), Barko and Smart (1980), and Denny (1972). However, the specific causes of macrophyte growth regulation by sediments remain unknown and no testable hypotheses have heretofore been suggested.

4. This report considers the results of two separate, yet related, investigations. In the first investigation, the abilities of four different submersed macrophyte species to mobilize N, P, and K from a variety of sediments were examined in relation to their respective requirements for these nutrients. Additionally, in the same investigation, losses of N and P from macrophyte shoots into the surrounding water during growth were determined to assess the signficance of excretion in comparison with potential losses of these nutrients due to decay-related processes. The species examined, being representative of three distinctly different taxonomic groups, included *Bacopa caroliniana* (Walt.) Robins, *Myriophyllum braziliense* Camb., *Potamogeton illinoensis* Morong, and *Proserpinaca palustris* L. Among these species, *Bacopa*, *Myriophyllum*, and *Proserpinaca* are heterophyllous and capable of emergence from the water (Sculthorpe 1967). However, *Potamogeton* produces a single leaf form and is not strictly adaptable to aerial existence.

5. In the second investigation, the availability of K to *Hydrilla verticillata* Royle from sediment versus overlying solution was examined to evaluate the possibility that the open water rather than the sediment may be the principal source of K supply to submersed, freshwater macrophytes (Barko and Smart 1981). Additionally, the influence of a

5

heterogeneous assemblage of sediments on the growth of this species was evaluated with emphasis given to differences in sediment composition. The sediment-based N and P nutrition of *Hydrilla* also was considered in relation to growth as affected by the experimental conditions of this second investigation.

PART II: MATERIALS AND METHODS

6. The investigations were conducted in a controlled environment
facility of the U. S. Army Engineer Waterways Experiment Station (WES)
Environmental Laboratory (EL), Vicksburg, Mississippi (U.S.A.). Tempera-
ture was maintained at 24°C, and light was provided at ca. 350 μeinsteins
$\cdot m^{-2} \cdot sec^{-1}$ during a 14-hr photoperiod each day. Plants were grown on
a variety of sediments contained in the bases of clear lucite columns
(20-ℓ volume and 150 cm tall). A detailed description of the environ-
mental chamber, the plant growth columns, and ancillary apparatus is
provided in Barko and Smart (1980).

7. Surficial sediments were manually dredged from lakes located
throughout the United States (Table 1). Lakes and sites within lakes
were selected for apparent or reported variations in their abilities to
support the growth of submersed macrophytes. Each sediment was thor-
oughly mixed in the laboratory to ensure homogeneity before being

Table 1

Names and Locations of Reservoirs and Natural Lakes

from Which Sediments were Obtained

Lake*	Designation**	Location
Branched Oak	Bro	Eastern Nebraska
Grassy Pond	GP	Southern Georgia
Kerr (Site 1)	Kerr-1	Eastern Oklahoma
Kerr (Site 2)	Kerr-2	Eastern Oklahoma
Keystone	Key	Central Oklahoma
Pawnee	Pawn	Eastern Nebraska
Seminole (Site 1)	Sem-1	Northern Florida
Seminole (Site 2)	Sem-2	Northern Florida
Starvation	Starv	Central Florida

  * Branched Oak, Kerr, Keystone, Pawnee, and Seminole are relatively
     large Corps of Engineers reservoirs. Grassy Pond is a small
     artificial lake. Starvation is a small natural lake.
 ** Designations are abbreviated lake names that are used extensively
     in the text.

placed into 30-cm-tall sediment containers (removable components of the plant growth columns). Sediments were allowed to settle for several weeks with necessary adjustments made in volume prior to planting. Sub-samples of each sediment were similarly treated prior to determining physical and chemical characteristics. Sediment texture was determined by the procedure of Day (1956). Organic matter was estimated from loss of oven-dry mass (100°C) after a 4-hr period of combustion in a muffle furnace at 550°C. Sediment interstitial water samples for nutrient determinations were obtained by high-speed centrifugation at 4°C, followed by immediate millipore filtration (0.45 μ) in a nitrogen atmosphere to avoid the formation of precipitates. Sediment total Kjeldahl nitrogen (TKN) was determined by the method of Bremner (1965). Other nutrients in the total sediment were determined following digestion in red fuming nitric acid.

8. The solution used in the first investigation was formulated by additions of reagent-grade $NaHCO_3$, $CaCl_2$, and HCl to glass-distilled water. Alkalinity, conductivity, and pH of the solution were ca. 0.9 meq·ℓ^{-1}, 280 μmhos·cm^{-1} (20°C), and 7.5, respectively. Two solutions, differing fundamentally in the presence and absence of K (designated as K solution and K-free solution), were used in the second investigation. Both solutions were formulated by additions of reagent-grade chemicals to glass-distilled water to approximate average concentrations of most major nutrients in river water (Riley and Chester 1971) and 0.1 strength concentrations of all essential trace nutrients speci-fied in Bold's Basal Medium (Nichols and Bold 1965). The K solution was formulated by adding 2.3 mg K·ℓ^{-1} as KCl to the K-free solution. Alka-linity and pH of the K and K-free solutions were nearly identical at ca. 0.8 meq·ℓ^{-1} and 7.3, respectively. Conductivity of the K solution (140 μmhos·cm^{-1} at 20°C) was slightly greater than that of the K-free solution (130 μmhos·cm^{-1} at 20°C). Nitrogen and phosphorus were omitted from all solutions used in these investigations in order to determine the mobilization of these two nutrients from sediments.

9. In the first investigation, apical shoots (ca. 10 cm in length) of all species were clipped from greenhouse-cultured stock and planted

8

singly to a sediment depth of ca. 5 cm through each of four openings in opaque lucite lids designed to minimize the extrusion of sediment and interstitial water from the containers. Initial biomass and plant nutrient concentrations are given in Table 2. After planting, the

Table 2

Initial Plant Biomass (g dry weight) and Nutrient Concentrations $(mg \cdot g^{-1})$.* Means and Standard Errors are Based on Three Replications

Species	Biomass	Nutrients		
		N	P	K
Bacopa	0.13	20.3 + 0.7	4.3 + 0.4	30.0 + 1.2
Myriophyllum	0.38	7.7 + 0.0	1.1 + 0.1	6.4 + 0.6
Potamogeton	0.19	8.1 + 1.7	1.9 + 0.9	18.4 + 1.7
Proserpinaca	0.21	21.2 + 1.6	3.4 + 0.5	17.8 + 1.1

* Biomass and nutrient concentrations were determined at time of planting.

openings around the shoots were sealed with eicosane (Eastman Kodak Co.). The sediment containers were inserted into the experimental columns, and 5 ℓ of solutions was immediately added to completely submerse the plant shoots. Four replicate columns per species were prepared using each of the three sediments. Additionally, two unplanted columns for each sediment were prepared to serve as controls.

10. During the conduct of this investigation, solutions were sampled every 2 weeks for determinations of N and P losses from the living plants. Samples of 250 ml were digested for total P analysis using the method (modified for differences in sample volume) of Jeffries, Dicken, and Jones (1979). Phosphorus analyses were performed on the digested samples using Technicon Autoanalyzer procedures enabling an $8-\mu g \cdot \ell^{-1}$ lower limit of P detection. Analyses of TKN in separate solution samples were performed directly on Technicon Autoanalyzers enabling a $100-\mu g \cdot \ell^{-1}$ lower limit of N detection.

11. Losses of N and P from the plants were corrected for the

9

possible introduction of these nutrients into solution due to sediment (and interstitial water) leakage around seals and other possible sources of contamination by subtracting nutrients contributed to the control columns. Cumulative losses of N and P were calculated from biweekly concentration data and known solution volumes. Solution volumes were incrementally increased to keep pace with the elongation of plants in the columns. Once the maximum volume of the columns was achieved (i.e. plants had grown to the top), 33 percent of the solution was replaced after each sampling.

12. In the second investigation, four apical tips of *Hydrilla* (ca. 10 cm in length) obtained from Florida were planted to a sediment depth of ca. 5 cm. Initial plant biomass, representing four apical tips combined, was 0.24 ± 0.05 (S.E.) g dry mass per sediment container. Sediment surfaces were overlain with ca. 2 cm of washed silica sand to minimize physical and chemical exchanges between sediments and the overlying solution. Immediately after planting, sediment containers were inserted into the plant growth columns and 5 ℓ of solution was added. Solution volumes were incrementally increased during the study to keep pace with the growth of *Hydrilla*. Each week at least one third of the solution volume in all columns was replaced in order to maintain defined water chemistry conditions.

13. During both investigations, filtered and humidified air obtained from an outside source was continuously delivered to the columns through plastic dispersers positioned at the base of the plants. Aeration provided gentle mixing of the solutions and gaseous equilibrium with outside air. Columns were inspected daily for plant damage. Fragments were retrieved, dried, and later combined with harvested shoot biomass at the end of the study. The purpose in removing these materials was to minimize the release of nutrients into the columns due to tissue decay.

14. Shoot length in all species was estimated every week during the investigations as well as at their completion. Changes in the rate of shoot elongation were considered as an index of growth rate. Reduced growth rates dictated the termination of the first investigation after

10

10 weeks and the second investigation after 8 weeks. Shoot number and branch number were determined only for *Hydrilla*. Original shoots and those initiated either beneath the sediments or within 5 cm of the sediment surface were included in the shoot number count. Subdivisions of these shoots were counted as branches. In both investigations, total plant biomass was harvested separately as shoots and roots. No attempt was made to remove shoot epiphytes, which were present in only minor quantities. Roots were thoroughly washed in distilled water over a 1-mm mesh plastic sieve. All biomass was dried at 80°C to a constant mass and ground in a Wiley Mill prior to digestion according to the procedure of Allen et al. (1974).

15. Nutrient analyses were performed by the WES Environmental Laboratory Analytical Group using Technicon Autoanalyzers for N and P determinations and a combination of flame photometry and DC Argon Plasma Emission apparatus for other elements. Orchard leaves (reference No. 1571) obtained from the National Bureau of Standards (NBS) were included in all plant tissue sample sets. Of the tissue nutrients of concern in this investigation, only K deviated notably (ca. 8 percent too low on the average) from the value certified by the NBS. However, this deviation from the reference value did not exceed coefficients of variation associated with experimental sample means. All experimental data considered in this report were statistically analyzed using the analysis of variance (ANOVA) and post-ANOVA capabilities of the Statistical Analysis System (Raleigh, N. C.). Statements of significance made in the report refer to the 5-percent level or less of statistical confidence.

PART III: RESULTS

First Investigation

16. The three sediments examined here (Bro, Key, and Pawn) were texturally similar, primarily consisting of fine-grained particles. Average textural fractions and associated ranges among sediments (uncorrected for organic matter) were: 6 (5-7) percent sand, 53 (48-57) percent silt, and 41 (38-45) percent clay on a dry weight basis. The organic content of each of these three sediments was 8 percent of the dry weight.

17. With few exceptions, nutrient concentrations were lower in the total sediment and in the interstitial water of Key compared to their respective concentrations in sediments of the other two reservoirs (Table 3). For the most part, the sediments from Bro and Pawn reservoirs were nutritionally similar, reflecting their close proximity

Table 3

Sediment Nutrient Characterization for Three Reservoir Sediments:

Nitrogen, Phosphorus, and Potassium in the Total Sediment

$(mg \cdot g^{-1}$ dry wt) and in the Interstitial Water $(mg \cdot \ell^{-1})$.

Means and Standard Errors are Based

on Three Replications

Nutrient	Sediment		
	Branched Oak	Keystone	Pawnee
Nitrogen			
Sediment TKN*	1.46 + 0.26	0.76 + 0.35	2.32 + 0.27
Interstitial NH_4-N	13.20 + 0.12	2.73 + 0.11	13.37 + 0.33
Phosphorus			
Sediment total P	0.60 + 0.02	0.50 + 0.04	0.67 + 0.02
Interstitial PO_4-P	0.33 + 0.02	0.16 + 0.01	0.69 + 0.03
Potassium			
Sediment total K	8.25 + 0.46	10.20 + 0.81	8.62 + 0.36
Interstitial total K	9.25 + 0.09	4.62 + 0.14	11.30 + 0.00

* Total Kjeldahl nitrogen.

12

in eastern Nebraska and their similar age (ca. 15 years). According to Hergenrader and Hammer (1973), both of these reservoirs exhibit characteristics associated with highly advanced stages of eutrophication. Their watersheds are small, but include fertile agricultural lands (Schwartzkopf and Hergenrader 1978). Keystone Reservoir has a relatively extensive watershed that contributes high concentrations of salts and other nutrients (Eley 1970).

18. Differences in nutrient concentrations among sediments in Table 3 were greater in the interstitial water fraction than in the total sediment. Whereas N and P in the interstitial water and in the total sediment from all reservoirs were positively related to one another, K in the interstitital water of Key was significantly lower than in other sediments despite its high total sediment concentration in the same sediment.

19. Consistent with their greater nutritional status, Bro and Pawn sediments provided significantly greater growth (i.e. accrual of total biomass) of all species in comparison with plant growth on Keystone sediment (Table 4). Growth of both *Bacopa* and *Potamogeton* was similar and exceeded the growth of *Myriophyllum* and *Proserpinaca* on all sediments.

20. Root to shoot biomass ratios in the three heterophyllous species exceeded ratios in *Potamogeton* on all sediments (Table 4). As evidenced in their high root to shoot ratios, the heterophyllous species examined here can be considered as intermediate in form between strictly submersed and emergent macrophytes. Among the heterophyllous species, ratios of root to shoot biomass on Bro and Pawn sediments, where plant growth was greatest, exceeded the ratios on Key sediment (Table 3). This pattern counters that observed in strictly submersed species (Denny 1972; Barko and Smart 1980) including *Potamogeton* (Table 3), in which growth and ratios of root to shoot biomass appear to be negatively related.

21. Values of N and P within species in Table 5 were similar among sediments. However, concentrations of K in all species grown on Keystone sediment were significantly lower than respective concentrations on

13

Table 4

Biomass (g dry wt) and Root to Shoot Biomass Ratios (R:S in %).*

Means and Standard Errors are Based on Four Replications

Species	Biomass	Sediment		
		Branched Oak	Keystone	Pawnee
Bacopa	Shoot	3.2 ± 0.1	1.5 ± 0.1	2.7 ± 0.1
	Total	4.6 ± 0.2	1.9 ± 0.1	4.1 ± 0.1
	R:S	41.1 ± 2.1	25.5 ± 4.4	49.3 ± 0.8
Myriophyllum	Shoot	1.5 ± 0.0	1.0 ± 0.2	1.7 ± 0.2
	Total	1.9 ± 0.1	1.1 ± 0.2	2.2 ± 0.2
	R:S	23.8 ± 2.4	18.4 ± 3.1	26.9 ± 2.6
Potamogeton	Shoot	4.3 ± 0.1	1.8 ± 0.2	4.1 ± 0.4
	Total	4.4 ± 0.1	1.9 ± 0.2	4.3 ± 0.4
	R:S	3.2 ± 0.4	9.7 ± 1.9	4.5 ± 0.9
Proserpinaca	Shoot	1.1 ± 0.0	0.7 ± 0.0	1.1 ± 0.0
	Total	1.2 ± 0.0	0.8 ± 0.0	1.3 ± 0.1
	R:S	16.5 ± 1.3	10.4 ± 1.2	17.3 ± 0.4

* Biomass and root to shoot ratios were determined after 10 weeks growth.

Branched Oak and Pawnee sediments. Nutrient concentrations in Table 5 differed significantly among species, with nutrients being generally more concentrated in the heterophyllous species than in *Potamogeton*.

22. In all species, concentrations of N and P in shoots at the end of the study (Table 5) exceeded or were statistically equivalent to preplanting concentrations (Table 2). Concentrations of N and P were well above the respective "critical" concentrations of these nutrients estimated to be minimal requirements for the growth of submersed macrophytes (Gerloff and Krombholz 1966). Plant growth was probably not limited by N or P in this study. In contrast, concentrations of K in these species significantly decreased (with few exceptions) during growth, particularly on Keystone sediment. Shoot concentrations of K were exceptionally low in comparison with the average value of 25.9 mg·g^{-1} dry weight calculated from extensive data for submersed macrophytes by Hutchinson (1975). Critical concentrations of K are not specifically known for the species considered herein. However, most values of K

14

Table 5

Nutrient Concentrations (mg·g^{-1} dry wt) in Plant Shoots.* Means and Standard Errors are Based on Four Replications

| | | Sediment | | |
Species	Nutrient	Branched Oak	Keystone	Pawnee
Bacopa	N	27.5 ± 0.2	24.7 ± 0.2	26.4 ± 0.1
	P	3.8 ± 0.2	3.8 ± 0.1	4.3 ± 0.1
	K	9.7 ± 0.2	5.8 ± 0.2	9.1 ± 0.5
Myriophyllum	N	32.5 ± 1.0	36.0 ± 2.0	32.6 ± 2.8
	P	4.8 ± 0.2	3.4 ± 0.4	4.3 ± 0.3
	K	5.0 ± 0.6	1.5 ± 0.1	4.0 ± 0.2
Potamogeton	N	16.3 ± 1.0	18.4 ± 0.5	16.6 ± 0.6
	P	2.1 ± 0.1	2.2 ± 0.1	2.4 ± 0.1
	K	4.2 ± 0.9	3.0 ± 0.4	4.0 ± 0.4
Proserpinaca	N	22.1 ± 1.0	23.1 ± 0.8	19.3 ± 0.8
	P	3.3 ± 0.3	3.3 ± 0.3	3.2 ± 0.2
	K	8.0 ± 0.2	5.8 ± 0.1	6.1 ± 0.3

* Nutrient concentrations were determined after 10 weeks growth.

concentration in Table 5 fell within the range of 3.5 to 8.0 mg·g^{-1} dry weight, respectively reported as critical K concentrations for *Myriophyllum spicatum* and *Elodea occidentalis* (Pursh) St. John (Gerloff 1975). Thus, it is possible that plant growth was limited by K in this investigation, particularly on Key sediment.

23. Nutrient contents presented in Table 6 are multiplicative products of shoot biomass (Table 4) and shoot nutrient concentrations (Table 5). Content is more closely related to concentration (r = 0.76) than to biomass (r = 0.40), when data are correlatively analyzed across species, nutrients, and sediments. However, both concentration and growth (i.e. biomass) contribute significantly to nutrient content, and differences in nutrient contents among individual species are very closely allied with differences in their biomass.

24. Nutrient contents in Table 6 represent nutrients mobilized from the sediments as well as generally minor contributions from the initial plantings. As is apparent in Table 7, N and P were mobilized from

Table 6

Nutrient Concents (mg per column) of Plant Shoots.* Means and

Standard Errors are Products of Shoot Mass and Nutrient

Concentration Based on Four Replications

| Species | Nutrient | Sediment | | |
		Branched Oak	Keystone	Pawnee
Bacopa	N	88.0 + 3.3	37.1 + 1.7	71.3 + 1.5
	P	12.2 + 0.8	5.7 + 0.3	11.6 + 0.2
	K	31.0 + 0.7	8.7 + 0.7	24.6 + 1.6
Myriophyllum	N	48.8 + 3.6	36.0 + 6.7	55.4 + 2.0
	P	7.2 + 0.6	3.4 + 0.7	7.3 + 0.5
	K	7.5 + 1.3	1.5 + 0.4	6.8 + 1.0
Potamogeton	N	70.1 + 3.1	33.1 + 3.2	68.1 + 7.6
	P	9.0 + 0.7	4.0 + 0.4	10.0 + 0.9
	K	18.1 + 0.2	5.4 + 1.0	16.4 + 2.1
Proserpinaca	N	24.3 + 0.5	16.2 + 0.8	21.2 + 0.8
	P	3.6 + 0.2	2.3 + 0.3	3.5 + 0.2
	K	8.8 + 0.4	4.1 + 0.1	6.7 + 0.3

* Nutrient contents were determined after 10 weeks growth.

all sediments much more effectively than K. Although appreciable
amounts of K were mobilized by all species from Bro and Pawn sedi-
ments, the ability of these species to mobilize K from Key sediment was
relatively poor. With the exception of *Proserpinaca*, the different
species demonstrated approximately equivalent capabilities in mobilizing
sediment nutrients (Table 7). The apparently lesser ability of
Proserpinaca in this regard may be a consequence of its initially high
tissue-nutrient concentrations (Table 1) combined with a low rate of
growth in this study.

25. Losses of N and P from the plants during growth were quite
variable (Table 8). In *Bacopa* and *Proserpinaca*, the magnitudes of these
losses were not appreciably influenced by decay processes. However,
Myriophyllum and *Potamogeton* underwent some leaching and autolysis as
they commenced senescence during the latter part of the study. In all
species, losses of N exceeded losses of P in relation to shoot contents

16

Table 7

Relative Mobilization of Nutrients from Sediments. Mobilization

Values (%) Represent (Final - Initial)/Final

Nutrient Contents*

Species	Nutrient	Sediment		
		Branched Oak	Keystone	Pawnee
Bacopa	N	97	93	96
	P	95	89	95
	K	87	54	84
Myriophyllum	N	94	92	95
	P	94	88	95
	K	67	0	63
Potamogeton	N	98	95	98
	P	94	88	95
	K	81	37	79
Proserpinaca	N	81	72	79
	P	81	70	80
	K	58	10	45

* Contents were calculated from shoot biomass and nutrient
   concentration data.

of the same. Because of an analytical problem, P losses were accumulated
over a period 2 weeks shorter than N, and thus were somewhat underesti-
mated. To what extent N determined in the columns may have been af-
fected by processes of denitrification or N fixation is unknown.
Clearly, these processes could have obfuscated the N data in Table 7.
In general, losses of N and P were greater on Bro and Pawn than on Key
sediment, perhaps reflecting a more extensive shoot surface area asso-
ciated with the greater shoot biomass of all species on the former
sediments.

Second Investigation

26. Sediments included in this investigation differed substan-
tially in textural and organic matter composition (Table 9). Sedi-
ments GP, Kerr-2, and Starv were predominately coarse textured, and

Table 8

Cumulative Losses* of Nitrogen and Phosphorus (%) from Shoots
in Relation to their Respective Nutrient Contents.** Means
and Standard Errors are Based on Four Replications

| | | Sediment | | |
Species	Nutrient	Branched Oak	Keystone	Pawnee
Bacopa	N	1.4 + 0.4	0.0 + 0.0	1.9 + 1.3
	P	0.0 + 0.0	0.0 + 0.0	0.0 + 0.0
Myriophyllum	N	10.6 + 3.5	19.6 + 9.8	18.1 + 5.3
	P	0.7 + 0.2	4.6 + 0.6	0.8 + 0.3
Potamogeton	N	11.3 + 1.5	8.0 + 2.7	7.5 + 1.2
	P	0.4 + 0.0	1.8 + 0.9	0.3 + 0.0
Proserpinaca	N	12.8 + 6.3	0.0 + 0.0	8.4 + 4.2
	P	0.0 + 0.0	0.0 + 0.0	0.0 + 0.0

 * Cumulative losses of N and P were determined over a 10- and 8-week
   period of growth, respectively.
** Contents were calculated from shoot biomass and nutrient concen-
   tration data.

possessed high percentages of sand. Sediments Kerr-1, Sem-1, and Sem-2
were predominately fine textured, but demonstrated a wide range in their
proportions of silt and clay. Among all sediments, Kerr-2 and Sem-2
represented extremes in organic matter content--low in the former and ex-
ceptionally high in the latter. Starv sediment also possessed a very
high organic content with a major portion of its organic matter con-
sisting of coarse particulate materials. This contrasted with the fine
particulate nature of the organic matter in Sem-2 sediment.

27. Interstitial water concentrations of Ca, Mg, and K (Table 10)
were significantly intercorrelated and reflected differences in the over-
all ionic strength of source waters. Total sediment concentrations of
these nutrients (Table 11) suggested substantial geochemical differences
in the watersheds associated with the lakes and sites from which the sedi-
ments were obtained. Of particular concern in this investigation, K con-
centrations in total sediments and in their interstitial waters spanned
nearly a tenfold range, but were generally lower than those reported for

Table 9

Sediment Texture and Content of Organic Matter. Means and

Standard Errors are Given in Percent Dry Sediment Mass

| Sediment | Texture* | | | Organic Matter |
	Sand	Silt	Clay	
GP	73.7 + 0.0	15.7 + 0.7	10.7 + 0.7	10.1 + 0.2
Kerr-1	31.2 + 0.0	60.0 + 0.0	8.8 + 0.0	1.6 + 0.0
Kerr-2	83.7 + 0.0	11.9 + 0.6	4.4 + 0.6	0.2 + 0.0
Sem-1	41.2 + 0.0	41.3 + 0.0	17.5 + 0.0	13.4 + 0.2
Sem-2	25.0 + 0.0	42.5 + 2.5	32.5 + 2.5	56.2 + 0.7
Starv	86.2 + 0.0	7.5 + 0.0	6.3 + 0.0	29.0 + 1.1

* Texture was determined by size and includes organic as well as
  inorganic matter. Means and standard errors are based on duplicate
  determinations.

Table 10

Nutrient Concentrations in Sediment Interstitial Water. Means and

Standard Errors are Based on Triplicate Determinations

And Presented in Milligrams per Litre

Sediment*	NH4-N	PO4-P	K	Ca	Mg
GP	5.2 + 0.1	0.35 + 0.03	2.2 + 0.1	3.6 + 0.3	1.2 + 0.1
Kerr-1	5.0 + 0.1	0.03 + 0.01	10.3 + 0.9	128.0 + 1.0	32.8 + 0.4
Sem-1	3.6 + 0.4	0.05 + 0.02	0.9 + 0.0	21.5 + 0.1	1.4 + 0.1
Sem-2	1.4 + 0.3	0.05 + 0.01	1.3 + 0.1	11.6 + 0.7	0.8 + 0.1
Starv	9.5 + 0.1	0.29 + 0.07	3.9 + 0.1	15.0 + 0.4	1.4 + 0.0

* Interstitial water data were obtained following millipore filtration
  (0.45-μ porosity). Data were unobtainable from Kerr-2 sediment
  because of its negligible water content.

Table 11

Sediment Nutrient Concentrations.* Means and Standard Errors are
Based on Triplicate Determinations and Presented in
Milligrams per Gram, Dry Sediment Mass

Sediment	TKN	P	K	Ca	Mg
GP	4.8 ± 0.2	1.00 ± 0.02	0.51 ± 0.08	1.3 ± 0.0	0.39 ± 0.01
Kerr-1	0.5 ± 0.0	0.24 ± 0.01	2.86 ± 0.10	8.8 ± 0.4	3.52 ± 0.15
Kerr-2	0.1 ± 0.0	0.09 ± 0.01	0.71 ± 0.01	2.8 ± 0.1	0.54 ± 0.01
Sem-1	5.2 ± 0.3	0.35 ± 0.00	0.93 ± 0.02	2.7 ± 0.1	0.72 ± 0.01
Sem-2	12.3 ± 1.2	0.54 ± 0.01	0.67 ± 0.01	7.2 ± 0.1	0.69 ± 0.02
Starv	5.6 ± 1.1	0.31 ± 0.00	0.31 ± 0.07	2.8 ± 0.4	0.12 ± 0.00

* Nutrient concentrations were determined following strong acidic
   digestion of sediments.

sediments obtained from the agriculturally enriched reservoirs consid-
ered in the first investigation. Interstitial water NH4-N and PO4-P
concentrations in Table 10 generally fell within, but toward the lower
end of, the ranges reported for sediments obtained from eutrophic areas
of the Great Lakes (Barko and Smart 1979b). The high TKN concentra-
tions in Starv and Sem-2 sediments (Table 11) reflected their respectively
high organic contents.

28. Weekly determinations of shoot length, which at the end of
this investigation was positively correlated with shoot biomass (R^2
= 0.76**), provided a simple means for following *Hydrilla* growth during
the study (Figure 1). It is apparent that both sediment and solution
promoted significant differences in the growth of *Hydrilla*. Differences
in shoot length between solutions were established very early on those
sediments with low interstitial water K concentrations (Sem-1 and GP).
However, on Kerr-1 sediment, with the highest concentration of inter-
stitial water K, shoot length did not differ significantly between solu-
tions until the later portion of the study period. Differences in shoot
length between solutions on Kerr-2, Starv, and Sem-2 were either minor
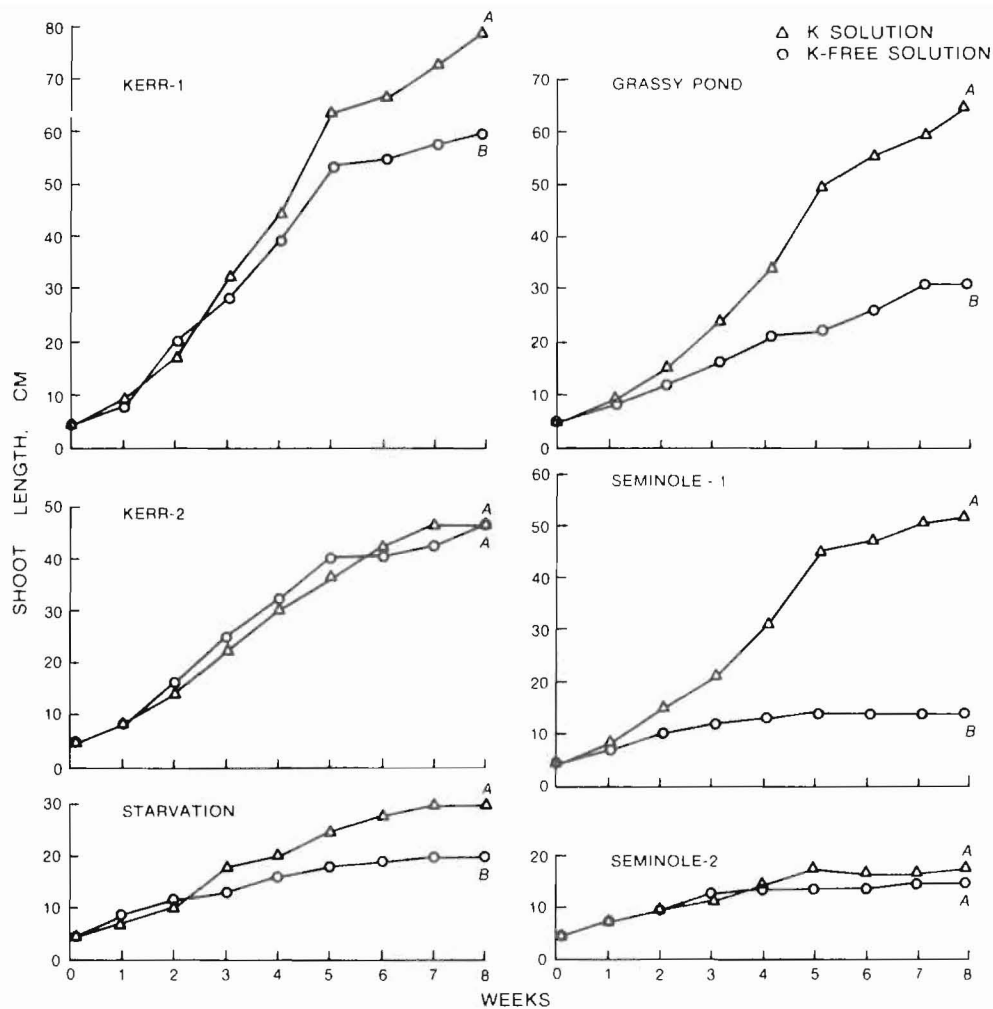or nonexistent throughout the study period, suggesting the influence of

20

Figure 1. Growth of *Hydrilla* as shoot length (cm) on
six different sediments in K solution vs. K-free so-
lution. Line graphs characterized by different let-
ters indicate a significant difference in growth at
8 weeks between solutions within a particular
sediment

factors other than K in determining growth on these sediments.

29. The growth of *Hydrilla* (as total biomass accrual) was signif-
icantly greater in the K solution than in the K-free solution on four of
the six sediments examined (Figure 2). Total biomass of *Hydrilla* across
all sediments in the K-free solution is positively correlated with in-
terstitial water K concentration ($R^2 = 0.97**$). Positive correlations
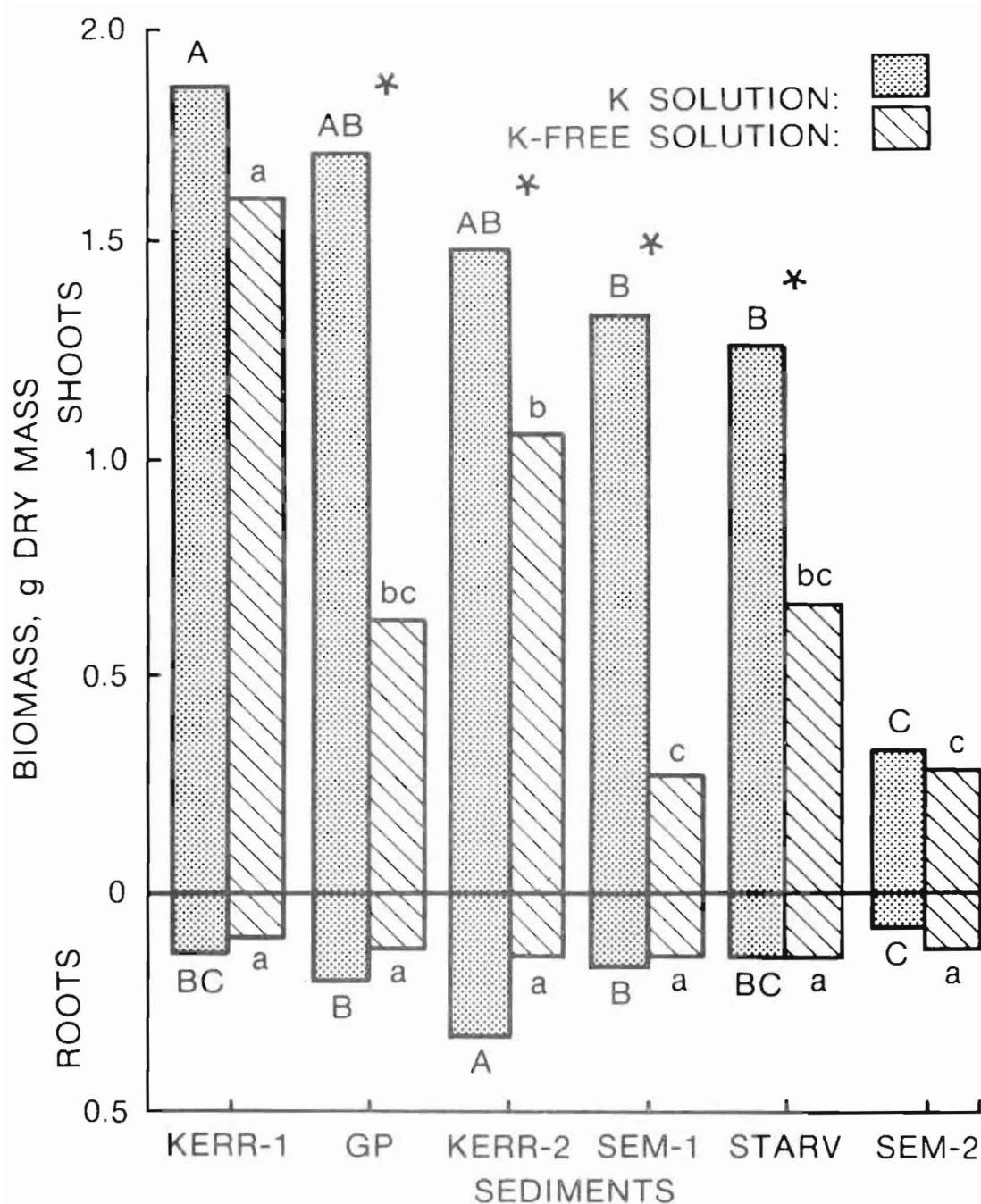of biomass with interstitial water Ca and Mg are also significant

21

Figure 2. Growth of *Hydrilla* as biomass (g dry mass) of shoots plus roots = total biomass. Asterisks indicate significant effects of K solution vs. K-free solution on growth. Within each solution, biomass values sharing the same letter across sediments do not differ significantly from each other

because of their intercorrelation with K (noted earlier). Kerr-1 sediment, with a substantially greater interstitial water K concentration than all other sediments, supported maximum biomass production in the K-free solution. In contrast, Sem-1 and Sem-2 sediments, with the lowest interstitial water K concentrations, provided only minimal biomass production in the K-free solution. In a related regard, it is interesting that additions of K to the overlying water (i.e. in the K solution) promoted an increase in biomass on Sem-1 but not on Sem-2. Biomass production in both solutions on Sem-2, with the greatest organic matter concentration, was exceptionally reduced in comparison with biomass production on the other sediments. Furthermore, the total biomass of *Hydrilla* on all sediments in the K solution negatively correlates with sediment organic matter concentration ($R^2 = 0.93**$).

30. Substantial variations in external shoot morphology (shoot length and the number of branches per shoot) in *Hydrilla* (Figure 3) closely parallel variations in shoot biomass as affected by differences among sediments and between solutions (Figure 2). However, it is notable that these morphological characteristics of growth were reduced to a greater extent than biomass on those sediments (Starv and Sem-2) providing the poorest overall growth of *Hydrilla* in this investigation. Differences in shoot morphology correlatively account for 90 percent of the variation in shoot biomass between solutions when both shoot length and the number of branches per shoot are included as independent variables in a multiple regression model. Shoot number (not presented) was unrelated to shoot biomass.

31. Among N, P, and K, the three essential nutrients omitted from the K-free solution, K was mobilized from sediments least effectively (Figure 4). Concentrations of K in the shoots of *Hydrilla* grown in the K-free solution decreased substantially on all sediments during the study. Whole-plant K content under the same conditions varied only slightly, but varied in direct relation to interstitial water K concentration ($R^2 = 0.92**$). Shoot K concentrations among sediments in the K-free solution are remarkably uniform and average 8 mg·g^{-1} dry mass. This value precisely corresponds with the shoot K concentration suggested by
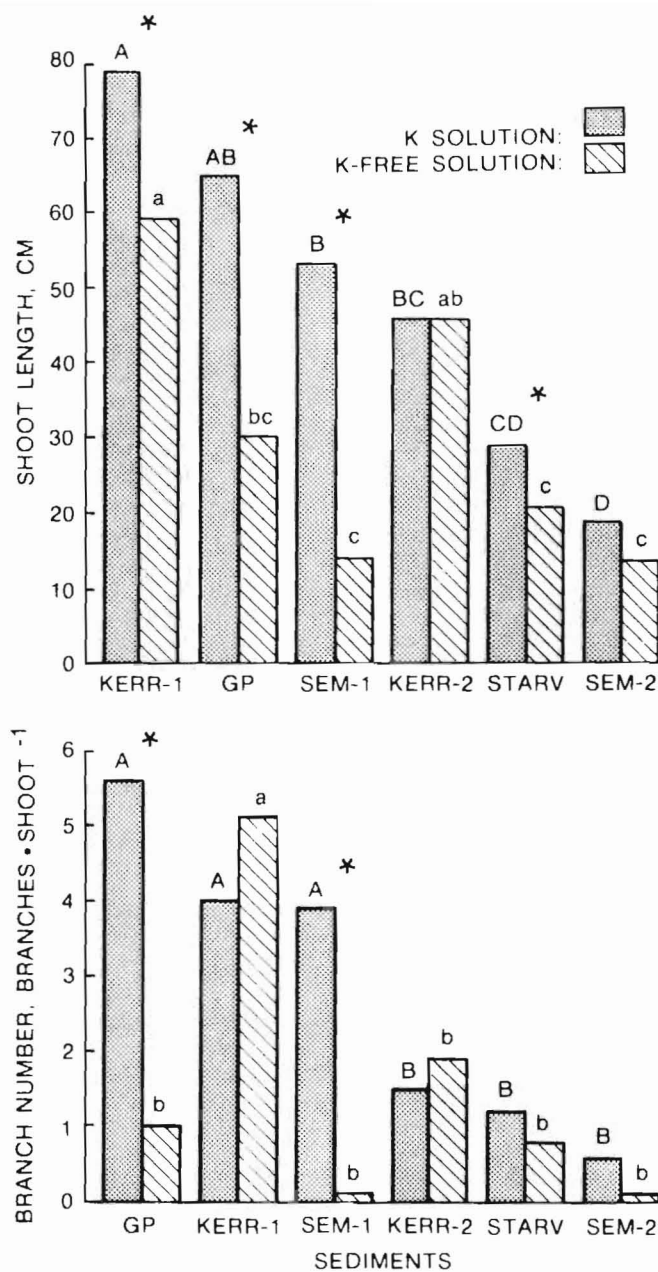
23

Figure 3. Morphological characteristics of the growth of *Hydrilla*, shoot length (cm) and branch number per shoot. Asterisks indicate significant effects of K solution vs. K-free solution on growth. Within each solution, morphological response variables sharing the same letter across sediments do not differ significantly from each other
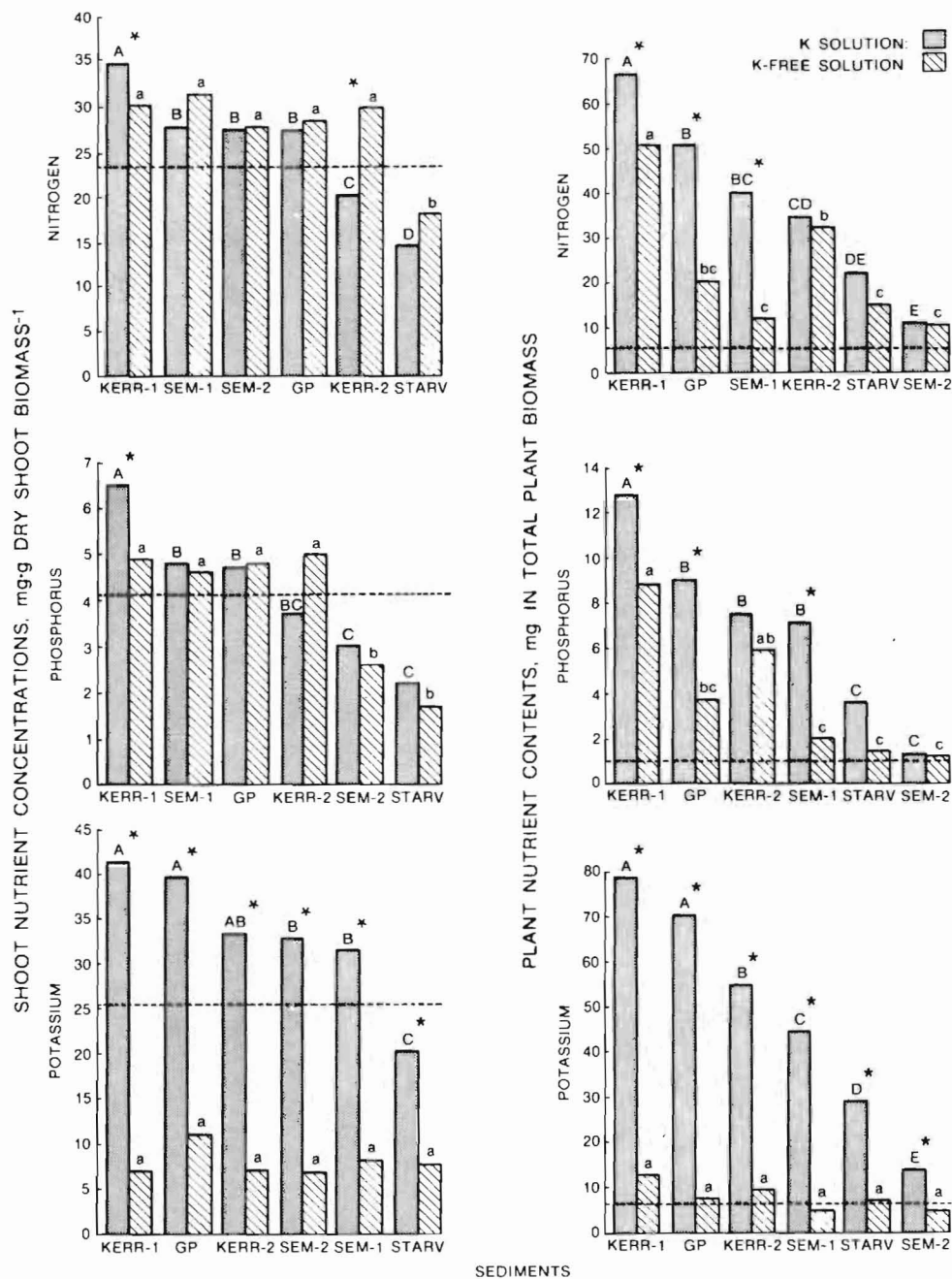
24

Figure 4. Shoot nutrient concentrations ($mg \cdot g^{-1}$ dry mass) and nutrient contents (mg) in total plant biomass. Broken horizontal lines indicate initial (i.e. preplanting) concentrations. Asterisks indicate significant effects of K solution vs. K-free solution on nutrition. Within each solution, nutritional response variables sharing the same letter across sediments do not differ significantly from each other

25

Gerloff (1975) as critical (i.e. growth limiting) to *Elodea occidentalis* (Pursh) St. John, a species taxonomically and morphologically related to *Hydrilla*. On all sediments with the exception of Starv, N and P concentrations in the shoots of *Hydrilla* exceeded the respective critical values suggested by Gerloff for *E. occidentalis*.

32. Absorption of K from the K solution, mobilization of K from sediments in the K-free solution, and mobilization of N and P from sediments in both solutions were generally greatest on sediments providing maximum plant growth (Kerr-1 and GP) and least on sediments providing minimum plant growth (Starv and Sem-2). Accordingly, the final tissue contents of these nutrients in *Hydrilla* (Figure 4) are closely related to biomass production (Figure 2).

33. Variations in root nutrient concentrations among sediments and within solutions (not presented) generally conform to those demonstrated in Figure 4 for shoots. Concentrations of N, P, and K in shoots and roots, averaged across sediments, are contrasted by solution in Table 12. Only shoot K concentration shows an appreciable solution effect. On the average, this variable is fourfold greater in the K solution than in the K-free solution. In both solutions, N concentrations are somewhat greater in shoots than in roots, while P concentrations demonstrate the opposite trend. The large differences between shoot and root K concentrations suggest a translocation gradient from shoots to roots in the K solution and from roots to shoots in the K-free solution, reflecting related differences in sources of K supply.

Table 12

Concentrations of N, P, and K in Shoots and Roots of *Hydrilla*

Verticillata in Relation to K Supply in Solution. Values

are Averages Expressed as Milligrams per Gram Dry Mass

With Coefficients of Variation Given in Percent*

Nutrient	Solution**	Shoots	Roots
N	+	25.2(12)	19.0(18)
	0	27.6(8)	22.3(9)
P	+	4.2(27)	5.0(17)
	0	3.9(12)	5.4(17)
K	+	33.2(18)	21.5(19)
	0	8.0(28)	17.7(19)

---

* Average values are derived from tissue nutrient concentrations
   determined for *Hydrilla* grown on six sediments (N = 18). Coeffi-
   cients of variation are based on a pooled error term from the
   ANOVA.
** Solutions differed in presence, 2.3 $mg \cdot \ell^{-1}$ (+), and absence (0)
   of K.

PART IV: DISCUSSION

Sediment Nutrient Mobilization

34. Root to shoot biomass ratios in the species considered herein
span a broad range, but have little influence on nutrient mobilization
from the different sediments. As emphasized in Barko and Smart (1980),
the uptake of nutrients by roots is much more likely to be dependent
upon root surface area, internal anatomy, physiological transport mech-
anisms, and many sediment-related factors, than upon root biomass. The
apparently high degree of dependence of species such as *Hydrilla*
verticillata Royle on its relatively minor root system (Denny 1972) may
typify the functional importance of roots in most (if not all) rooted
macrophytes. Because of the normally greater abundance of nutrients in
sediments compared to the water of most aquatic systems, sediments pro-
vide a potentially large source of nutrient supply to rooted plants.

35. The submersed macrophytes examined herein are clearly able to
satisfy their N and P requirements by mobilizing these nutrients direct-
ly from sediments. Similar capabilities have been identified in *Egeria*
densa, *H. verticillata*, and *Myriophyllum spicatum* (Barko and Smart 1981).
The ability of *M. spicatum* to mobilize N and P from sediments has been
demonstrated to be an important factor in its high growth rate in sys-
tems where these nutrients are present in low abundance in the water
(Best and Mantai 1978). Similarly, Patriquin (1972) demonstrated the
ability of *Thalassia testudinum*, Konig, a submersed marine angiosperm,
to maintain high rates of production by mobilizing N and P from the
sediment in notably nutrient-poor tropical waters. The ability of
rooted macrophytes to utilize sediment nutrients may partially account
for their greater productivity in comparison with planktonic algae in
many lacustrine systems (Wetzel 1975). This may be particularly rele-
vant in oligotrophic systems characterized by high macrophyte produc-
tivity (e.g. Lawrence Lake, Michigan, Rich, Wetzel, and Thuy (1971)),
where the productivity of epiphytes may be enhanced by macrophyte-
nutrient mobilization as well.

36. As reported herein, variations in N and P mobilization
strongly reflect differences in plant growth (as biomass accrual) be-
cause rates of nutrient absorption by higher plants are apparently de-
termined by the demand for nutrients created by growth (Clarkson and
Hanson 1980). Averaged across sediments, the ratio of N to P concentra-
tion in shoots of the macrophyte species considered here was ca. 7 to 1
on a mass basis, which is considered typical for plant tissues of
aquatic algae and macrophytes (Barko and Smart 1979b; Vallentyne 1974
as cited in Wetzel 1975). Thus, these two nutrients appear to be
mobilized from sediments in a balanced fashion relative to macrophyte
tissue requirements.

37. Considering the very limited mobilization of K from all sedi-
ments along with the concomitantly (and critically) low shoot K concen-
trations in *Hydrilla*, it is concluded that the growth of this species on
at least four of the six sediments in the second investigation was lim-
ited by K in the K-free solution. Potassium was mobilized from sedi-
ments very ineffectively by all species in the first investigation as
well. The sediment interstitial water does represent a source of K sup-
ply to rooted macrophytes. However, K mobilization from sediments by
Hydrilla accounted for reductions in interstitial water K content (i.e.
concentration × interstitial water volume) amounting to less than 50 per-
cent of that provided initially by the sediments. In contrast, P has
been demonstrated to be mobilized from sediments by submersed macro-
phytes in quantities 1000-fold greater than the phosphate-P content of
sediment interstitial water (Barko and Smart 1980), suggesting a far
greater ability of rooted macrophytes to access P in comparison with K
from the total sediment. Extending this comparison, it is postulated
that nutrient uptake systems in submersed freshwater macrophytes may be
rather specialized, with variable affinities for particular nutrients
from different sources, perhaps dependent upon long-term exposure to
geochemical differences in the abundance and/or availability of nutri-
ents in sediment versus the open water.

38. Ammonium and potassium ions have the same charge and nearly
identical atomic radii. In soils, they compete for cation exchange sites

29

(Tisdale and Nelson 1966). In this connection, they may also compete for exchange sites on root surfaces. Thus, the greater mobilization of N compared to K in this study suggests the possibly greater availability of N in sediments. Considering the similar concentrations of ammonium and potassium ions in the interstitial water of the sediments studied, apparent differences in the availability of sediment N and K may reflect some selectivity in ion uptake by plant roots. Such selectivity would be of obvious benefit to root submersed macrophytes since it could enable adjustments in modes of nutrient uptake in accordance with differences in the capacity of the water and sediment to supply essential nutrients.

39.   Few data are available to allow direct comparisons of sediment interstitial water and overlying water K concentrations in lacustrine systems; however, the data of Barsdate and Prentki (1973) and of Weiler (1973) indicate a good correspondence between the two with K in the sediment interstitial water being somewhat more concentrated than K in the overlying water. The range in K concentration (1 to 10 $mg \cdot \ell^{-1}$) in the interstitial water of sediments used experimentally in this and related investigations undertaken in our laboratory is very similar to that reported for the open water of a wide variety of lakes (Golterman 1975; Hutchinson 1957; Patterson and Brown 1979). Thus, the K concentration of sediment interstitial water can essentially be considered as an extension of the open water where K is normally abundant in available forms (Wetzel 1975). Considering the much greater volume of open water compared to interstitial water in contact with absorptive surfaces of submersed macrophytes, the sediment probably provides only a minor fraction of the tissue K content of these plants in lacustrine systems. The foregoing information strongly suggests that the open water rather than the sediment is the principal source of K supply to rooted submersed freshwater macrophytes. This possibility is supported by the results of Mickle and Wetzel (1978) indicating a greater than 30-percent reduction in K concentration of water passing through a *Myriophyllum*-epiphyte complex in a simulated littoral system.

40.   It is very necessary to emphasize that the low shoot K levels

reported herein resulted from the complete absence of K from the experimental solutions--a condition that does not occur in natural aquatic systems. The importance of K as a growth-limiting nutrient has been demonstrated for *M. spicatum* in Lake Wingra, Wisconsin (Gerloff 1975), but could not be corroborated in a later, more extensive investigation conducted by Carpenter and Adams (1977). The possible role of K as a factor influencing the growth of submersed macrophytes requires further study.

Macrophyte Nutrient Losses

41. Losses of nutrients from aquatic macrophytes can occur through excretion, leaching, autolysis, and microbial decomposition. Only small quantities (or none at all) of N and P were lost due to excretion during active growth from the species investigated herein. Nutrient losses from macrophytes are viewed as primarily occuring during senescense and decay, involving the processes of leaching, autolysis, and decomposition. In several recent studies that included a variety of submersed macrophyte species, phosphorus excretion was demonstrated to be minor (Peverly and Brittain 1978; Smith 1978; Welsh and Denny 1979; Barko and Smart 1980; and this study). However, leaching and autolysis did result in rapid and quantitatively significant fluxes of N, P, and K from decaying macrophyte tissues (Howard-Williams and Howard-Williams 1978; Howard-Williams and Davies 1979). In general, plant decay can be considered to be more rapid in aquatic systems than on land. For example, complete in situ decomposition of *M. spicatum* occurred in about 50 days in a study conducted by Kistritz (1978). In two species of *Potamogeton*, Sudo et al. (1978) reported a 50- to 75-percent loss of N and P during 50 days of decay. In another study, 100-percent losses of N, P, and carbon (C) from three species of *Potamogeton* reportedly occurred within 50 to 64 days (Hill 1979).

42. Decay-related losses of nutrients from submersed macrophytes can substantially contribute to the internal nutrient loading of aquatic systems (Barko and Smart 1979b; Landers 1979; Lie 1979; Prentki et al.

1979; Welch et al. 1979; Carpenter 1980a). In Lake Wingra, Wisconsin, decomposition of *M. spicatum* alone accounted for about half of the observed flux of dissolved total P and dissolved organic matter from the littoral zone to the pelagial zone (Carpenter 1980a). In the same system, Prentki et al. (1979) independently estimated that the littoral zone exports to the pelagial zone quantities of total P and total C equivalent to 59 and 140 percent of total allochthonous inputs of these nutrients, respectively. These authors indicate that such inputs are primarily products of macrophyte autolysis and decay.

43. The turnover (i.e. senescence and decay) of biomass produced by most submersed macrophytes is appreciable, and is a continuous process in many aquatic systems (Westlake 1975). It is apparent that a large fraction of the total nutrients (particularly N and P) released from macrophytes during decay may derive from the sediment. This mechanism represents an important mode of sediment nutrient recycling in aquatic systems.

Sediment Effects on Macrophyte Growth

44. In the K solution, sediment-related variations in the growth of *Hydrilla* were probably not caused by nutritional deficiencies since all essential nutrients were provided by sediment and solution combined. The negative correlation between the growth of this species and sediment organic matter content suggests that there may be some functional relationship between the two. In this regard it may be instructive to provide historical information on the organic loadings of Sem-2 and Starv sediments, which provided the poorest growth of *Hydrilla* in this study.

45. During the summer of 1979, a series of beaver dams located in the headwaters of Sem-2, an isolated section of Lake Seminole, were destroyed with the consequent inflowing of water that was reportedly high in tannins as evidenced by its "swamp water" appearance (Kight 1980). Presumably, the inflowing water contained large quantities of fine particulate organic matter, which accumulates in dammed streams (Bilby and Likens 1980). The organic content of the surficial sediment in this

area apparently increased from previously much lower levels (unpublished data provided by U. S. Army Corps of Engineers District, Mobile) to ca. 56 percent as reported herein. Prior to this disturbance, the Sem-2 area of Lake Seminole was occupied by an extremely productive macrophyte community dominated by *Hydrilla*. Since the disturbance, this area has been virtually devoid of *Hydrilla* in particular and other submersed vegetation in general. Restricted growth of *Hydrilla* has been reported in Lake Starvation, where the sediment is composed of large quantities of bald cypress (*Taxodium distichum* (L.) Richard) debris. An organic extract (2,000 to 10,000 molecular weight fraction) obtained from this sediment has been demonstrated to inhibit the growth of *Hydrilla* (Dooris and Martin 1980), although other macrophytes growing in the lake appear to be relatively unaffected. These data and observations highlight the results of the present study indicating that the high organic content of Sem-2 and Starv sediments may restrict the growth of *Hydrilla*. In other laboratory experimentation (Barko, unpublished data), the growth of *M. spicatum*--a species in many ways ecologically analogous to *Hydrilla* (Barko and Smart 1981)--has also been observed to be poor on Sem-2 and Starv sediments. Thus, the possible growth-restricting characteristics of these two sediments do not appear to affect *Hydrilla* alone.

46. The negative relationship noted here between sediment organic matter content and the growth of *Hydrilla* recalls similar observations made by Misra (1938) and Pearsall (1920) for several macrophyte species in English lakes. In Misra's investigation, for example, the growth of *Potamogeton perfoliatus* L. on a sediment possessing an organic content of 24 percent was substantially reduced in comparison with its growth on two other sediments with organic contents of 13 percent. Differences in the growth of *P. perfoliatus* on these sediments compared well with variations in the actual distribution of this species on the same sediments in Lake Windemere. Both Misra and Pearsall suggest that *P. perfoliatus* is an early to intermediate colonizer, which is replaced by floating-leaved and emergent macrophytes in English lakes as sediment organic matter increases. Similarly, in considering the vegetational changes occurring in a moorland fish pond over a 21-year period,

33

Macan (1977) ascribes variations in the distribution of particular macrophytes and in the species composition of the overall macrophyte community to the amount of plant remains added to the sediment in relation to rates of organic matter decomposition.

47. The primary point here is that macrophyte community composition may vary with sediment organic content. Yet, the question remains-- is the relatively poor growth of *Hydrilla* on the organic sediments highlighted in the present investigation merely an anomaly, or is it perhaps indicative of a pattern applicable to particular types of macrophytes in lacustrine systems over an extended geological period? After relatively short occurrences of explosive growth, an equally rapid decline has been reported for highly adventive species such as *M. spicatum* in Lake Wingra (Carpenter 1980b) and in the upper Chesapeake Bay (Bayley et al. 1978) and for *Elodea canadensis* Michx in Europe (Sculthorpe 1967). Macrophytes modify the sediment environment by promoting increased sedimentation through both their passive reception of allochthonous materials and their direct contributions of autochthonous primary production to the sediment (Carpenter in press; Patterson and Brown 1979; Wetzel 1979). It is intriguing to speculate that the development of unfavorable changes in the sediment, associated with the presence of highly productive macrophyte species, might eventually contribute to the decline of such species. In view of an increasing awareness of the importance of the littoral zone in the overall metabolism of lacustrine systems (Wetzel 1975, 1979), and an escalating emphasis on the development of appropriate "aquatic weed" management programs (Mitchell 1979), a better understanding of environmental controls on the growth of aquatic macrophytes is needed. In this regard, the influence of sediment composition on the growth and distribution of rooted aquatic macrophytes deserves increased investigative attention.

PART V: CONCLUSIONS AND RECOMMENDATIONS

48. Recent literature suggests that a variety of nutrients in the shoots of rooted macrophytes are more attributable to root uptake from sediments than to foliar absorption from the water. While nitrogen and phosphorus in macrophytes derive principally from sediments, the primary source of supply (sediment vs. overlying water) of other nutrients to macrophytes has not yet been unequivocally established. Potassium is an example of one nutrient that appears to be supplied to submersed macrophytes primarily from the water. Sediment and overlying water are likely to interact in satisfying macrophyte tissue nutrient requirements. In this connection, there is some basis for suggesting that site selectivity in nutrient uptake by rooted macrophytes may compensate for differences in the capacity of the sediment and open water to supply essential nutrients.

49. Aside from these considerations of nutrient supply sources, it is important to assert that the growth of rooted submersed macrophytes does not appear to be limited by nutrition, particularly in moderately eutrophic aquatic systems. The excessive accumulation of nutrients--especially nitrogen and phosphorus relative to macrophyte tissue requirements--seems to be common in many aquatic systems. Considerable quantities of nutrients are released from submersed macrophytes due to tissue decay during plant senescence. In most aquatic systems, macrophyte decay is a continuous process. Thus, nutrients mobilized from sediments by rooted macrophytes are potentially resupplied continuously to the open water, where nutrient-limited algal productivity may be stimulated. This mechanism represents an important mode of sediment-nutrient recycling in aquatic systems.

50. Sediment factors, perhaps including organic matter composition, can substantially influence macrophyte growth rates. There are some indications in the literature that different macrophyte species may be differentially sensitive to sediment organic matter. This possibility deserves increased investigative attention because it could account in part for changes in the species composition of macrophyte communities

35

during the natural or man-induced successional development of aquatic systems.

51.   A concerted effort has been undertaken by the Aquatic Plant Control Research Program to manage aquatic macrophytes in systems where they grow to nuisance proportions. The investigations reported herein increase the fundamental knowledge based upon which plant management and related predictive capabilities continue to be refined. To a considerable extent, the environment dictates where and what types of nuisance aquatic plant problems will occur. As relationships between various characteristics of the aquatic environment and the growth of macrophytes become better defined, it may be possible to amend macrophyte community composition in favor of preferred species.

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