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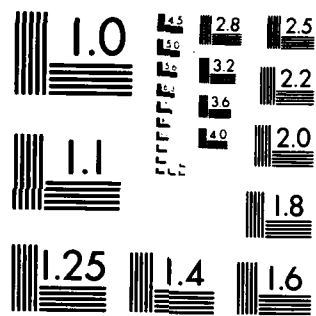
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AQUATIC PLANT CONTROL
RESEARCH PROGRAM

TECHNICAL REPORT A-83-5

EFFECTS OF ORGANIC AMENDMENTS
TO SEDIMENT ON FRESHWATER
MACROPHYTE GROWTH

by

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October 1983
Final Report

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REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER Technical Report A-83-5	2. GOVT ACCESSION NO. AD-A136972	3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle) EFFECTS OF ORGANIC AMENDMENTS TO SEDIMENT ON FRESHWATER MACROPHYTE GROWTH		5. TYPE OF REPORT & PERIOD COVERED Final report
		6. PERFORMING ORG. REPORT NUMBER
7. AUTHOR(s) John W. Barko, R. Michael Smart, M. Susan Hennington, Dwillette G. McFarland, Lee D. Ferguson		8. CONTRACT OR GRANT NUMBER(s)
9. PERFORMING ORGANIZATION NAME AND ADDRESS U. S. Army Engineer Waterways Experiment Station Environmental Laboratory P. O. Box 631, Vicksburg, Miss. 39180		10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS Aquatic Plant Control Research Program
11. CONTROLLING OFFICE NAME AND ADDRESS Office, Chief of Engineers, U. S. Army Washington, D. C. 20314		12. REPORT DATE October 1983
		13. NUMBER OF PAGES 32
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office)		15. SECURITY CLASS. (of this report) Unclassified
		15a. DECLASSIFICATION/DOWNGRADING SCHEDULE
16. DISTRIBUTION STATEMENT (of this Report) Approved for public release; distribution unlimited.		
17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)		
18. SUPPLEMENTARY NOTES Available from National Technical Information Service, 5285 Port Royal Road, Springfield, Va. 22161.		
19. KEY WORDS (Continue on reverse side if necessary and identify by block number) Aquatic environment Aquatic plants Freshwater biology Organic matter Sediment		
20. ABSTRACT (Continue on reverse side if necessary and identify by block number) The growth of three submersed macrophyte species (<i>Myriophyllum spicatum</i> , <i>Hydrilla verticillata</i> , and <i>Elodea canadensis</i>) and three partially emergent macrophyte species (<i>Sagittaria latifolia</i> , <i>Myriophyllum aquaticum</i> , and <i>Potamo- geton nodosus</i>) was examined on a nonamended sediment and on the same sediment amended by additions of five types of vegetative organic matter (two labile and three refractory). With individual amendments, the organic content of the sediment was increased from an initial value of (Continued)		

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20. ABSTRACT (Continued).

ca. 10 percent to a final value of 15 percent (low-level amendment) and from an initial value of ca. 15 percent to a final value of 20, 25, and 30 percent (high-level amendments).

At equal levels of organic matter addition (low-level amendment), macrophyte growth varied with the type of amendment and the species of aquatic macrophyte. Biomass accrual by emergent species as a group was generally greater on all sediments, and was less inhibited than that of submersed species on amended sediments. At the high levels of amendment, the growth of representative submersed and emergent species was severely inhibited on all amended sediments irrespective of amendment type.

The inhibitory influence on *Hydrilla verticillata* of sediment amended by additions of labile organic matter decreased with increasing sediment age relative to time of amendment. In contrast, sediments amended by additions of refractory organic matter remained inhibitory to a constant extent for at least 14 weeks following amendment.

Macrophyte growth on amended sediments was evaluated in relation to changes in interstitial water chemistry and shoot nutrient chemistry resulting from organic matter additions to sediment. Growth was unrelated to interstitial Fe, Mn, or PO_4 concentrations. However, a low level of N in both interstitial water and macrophyte shoots suggested possible N limitation of growth on sediments amended with refractory organic matter.

In another experiment, the inhibition of *H. verticillata* growth on sediment amended with refractory organic matter was determined to be unaffected by N additions to either the sediment, water, or both. These results, in combination with other nutritional considerations, suggested that growth inhibition did not involve nutrient limitation in this investigation.

Growth of all species was negatively correlated with average interstitial dissolved organic carbon (DOC) concentrations. Thus, differences in growth inhibition on amended sediments were perhaps attributable to treatment-related differences in interstitial DOC. Accumulation of phytotoxic, soluble organic carbon compounds during the anaerobic decomposition of organic amendments was suggested as a possible mechanism for growth inhibition. Organic accretion in sediments with increasing age was considered in relation to patterns of aquatic macrophyte distribution and succession in lacustrine systems.



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PREFACE

The study presented in this report was sponsored by the Department of the Army, Office of the Chief of Engineers (OCE) Directorate of Civil Works (DAEN-CW), through the U. S. Army Corps of Engineers (CE) Aquatic Plant Control Research Program (APCRP). Funds for the study were provided by DAEN-CW under Department of Army Appropriation No. 96X3122, Construction General. The APCRP is managed by the U. S. Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss. Technical Monitor for OCE was Mr. Lewis Darrell.

This work on the effects of different sediment characteristics on selected aquatic macrophyte species is a segment of the continuing effort of the APCRP to document some of the more important basic responses of problem aquatic species to various conditions in their environment. Dr. John W. Barko was the principal investigator for the work and prepared the report with the assistance of R. Michael Smart, M. Susan Hennington, Dwillette G. McFarland, and Lee D. Ferguson.

The authors wish to acknowledge Rex L. Chen and Derrick J. Bates of the Environmental Laboratory (EL) for their assistance in sediment and statistical analysis, respectively. Critical review comments, provided by S. R. Carpenter, University of Notre Dame, and B. Moss, University of East Anglia, were very helpful in revising an earlier version of the report. Additional suggestions were provided anonymously by a reviewer designated by the British Ecological Society.

This work was performed under the general supervision of Dr. John Harrison, Chief, EL, and the direct supervision of Mr. Donald L. Robey, Chief, Ecosystem Research and Simulation Division. Mr. J. Lewis Decell was manager of the APCRP.

Commander and Director of WES during this study was COL Tilford C. Creel, CE. Technical Director was Mr. F. R. Brown.

This report should be cited as follows:

Barko, J. W., et al. 1983. "Effects of Organic Amendments to Sediment on Freshwater Macrophyte Growth," Technical Report A-83-5, U. S. Army Engineer Waterways Experiment Station, CE, Vicksburg, Miss.

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EFFECTS OF ORGANIC AMENDMENTS TO SEDIMENT
ON FRESHWATER MACROPHYTE GROWTH

PART I: INTRODUCTION

Background

1. Among different aquatic systems and between locations within single systems, variations in the composition of bottom sediments strongly influence the growth and distribution of freshwater macrophytes (e.g., Pond 1905; Pearsall 1920; Wilson 1935; Misra 1938; Moyle 1945; Macan 1977; Sand-Jensen and S ndergaard 1979). However, there is little definitive information related to the underlying causes of such observations, and mechanisms accounting for sediment-macrophyte growth relationships have not been established.

2. Due to the capabilities of most submersed macrophytes to effectively mobilize a variety of nutrients from sediments (Patterson and Brown 1979; Barko and Smart 1981a, and literature cited therein) in combination with nutrient uptake from the water (Denny 1972; Barko 1982a), it is difficult to directly attribute sediment-related variations in submersed macrophyte growth to nutrition. Indeed, detailed nutritional investigations conducted in a wide variety of freshwater systems have generally failed to conclusively demonstrate specific nutrient limitation of submersed macrophyte growth (e.g., Peltier and Welch 1970; Carpenter and Adams 1977; Patterson and Brown 1979; Peverly 1980).

3. Alternatively, it has been suggested that the principal influence of substrate (i.e., sediment) upon the distribution of rooted aquatic macrophytes is due to its physical texture rather than its chemical composition (Sculthorpe 1967, p 53), though there is little evidence for this suggestion. Investigations conducted at the U. S. Army Engineer Waterways Experiment Station (WES), Environmental Laboratory, involving numerous sediments of wide-ranging texture have indicated no consistent relationship between texture (i.e., particle size

distribution) and the growth of submersed freshwater macrophytes (e.g., Barko and Smart 1980; Barko 1982a). This, of course, does not dismiss the possible importance of texture in conjunction with localized hydrodynamic conditions in determining macrophyte rooting success and resistance to erosion (cf. Haslam 1978, pp 40-70).

4. Previous investigations conducted at the WES Environmental Laboratory have suggested that the growth of some macrophyte species may be significantly retarded on highly organic sediments (Barko 1982a, b). In view of the potential importance of these findings to the specific question of sediment-related macrophyte growth and to the more general (yet related) question of aquatic ecosystem succession, it is of interest to examine the relationship between sediment organic matter and the growth of aquatic macrophytes in greater detail.

Purpose and Scope

5. The objective of this investigation was to examine the growth of a variety of freshwater macrophyte species on sediment experimentally amended by different additions of vegetative organic matter. Considerable effort was devoted to sediment chemistry and macrophyte tissue chemistry in an attempt to elucidate mechanistic relationships between the organic composition of sediments and the growth of rooted aquatic macrophytes.

6. Macrophytes investigated here include: *Sagittaria latifolia* Willd.; *Nyriophyllum aquaticum* (Vell.) Verde.; *Potamogeton nodosus* Poir.; *Nyriophyllum spicatum* L.; *Elodea canadensis* Rich. in Michx; and *Hydrilla verticillata* (L.f.) Caspary. Nomenclature follows Godfrey and Wooten (1979, 1981). The first two species (listed above) possess a partially emergent growth form. *Potamogeton nodosus* produces floating leaves that are structurally (Anderson 1978) and physiologically (Lloyd, Canvin, and Bristow 1977) similar to those of emergent plants. In this report, *P. nodosus* is considered with the former as an emergent species. The latter three species (listed above) possess a submersed growth form.

PART II: MATERIALS AND METHODS

Experimental Environment

7. This investigation was conducted in the greenhouse facility described in Barko and Smart (1981b). Macrophytes were grown on experimental sediments in large white fiberglass tanks, each with dimensions of 150 by 90 by 90 cm deep with a maximum volume of ca. 1200 l. Submersed macrophytes and *P. nodosus* were exposed to natural irradiance beneath neutral density shade fabric limiting maximum photosynthetically active radiation (PAR) to less than 50 percent full sunlight. No shading was provided for *S. latifolia* or *M. aquaticum*. Water temperature in the tanks was continuously maintained at $25^{\circ} \pm 1^{\circ}\text{C}$.

8. The solution used in the greenhouse tanks was formulated by additions of major ions as reagent-grade salts to deionized (reverse osmosis) water as in Barko, Hardin, and Matthews (1982). The pH and conductivity of the solution were initially 7.5 and $300 \mu\text{S} \cdot \text{cm}^{-1}$ (25°C), respectively. Both nitrogen (N) and phosphorus (P) were omitted from solution in order to minimize the growth of algae in the tanks. It was assumed that N, P, and micronutrients excluded from solution would be mobilized from sediments by roots (Barko and Smart 1981a).

Experimental Procedures

9. Surficial sediment was obtained by dredging from Lake Washington in Washington State. After thorough mixing, the sediment was divided into six separate quantities, five of which were amended by single additions of each type of organic matter (i.e., sediment amendments) described on the following page. The remaining sediment was not amended, and served as an experimental control during subsequent investigations. Hereafter, the nonamended sediment is referred to as NON, and amended sediments are referred to as ALG, MYR, CAT, OAK, and PIN in agreement with the designations listed in paragraph 10 of specific amendment types.

10. Sediment amendments were oven dried (100°C), ground in a Wiley

<u>Amendment</u>	<u>Form</u>	<u>Condition*</u>	<u>Designation</u>
Filamentous green alga (<i>Rhizoclonium</i>)	Whole thalli	Living	ALG-Amend
Submersed macrophyte (<i>Nyriophyllum</i>)	Leafy shoots	Living	MYR-Amend
Emergent macrophyte (<i>Typha</i>)	Leafy shoots	Dead (standing)	CAT-Amend
Hardwood tree (<i>Quercus</i>)	Leaves	Dead (litter)	OAK-Amend
Softwood tree (<i>Pinus</i>)	Needles	Dead (litter)	PIN-Amend

* Living materials were collected in a state of active growth in the spring. Dead materials, also collected in the spring, had overwintered in a moribund state.

mill to a particle size <0.7 mm, thoroughly mixed, and then rewet before addition to NON. Individual amendments were added to increase the organic content on NON from an initial value of ca. 10 percent to a final value of 15 percent (low-level amendment) and from an initial value of ca. 15 percent to a final value of 20, 25, and 30 percent (high-level amendments). Sediments were placed to a depth of ca. 10 cm in 1-l polyethylene containers providing a square surface ca. 80 cm² in area. Concurrently, subsamples of experimental sediments (NON and sediments at a low level of amendment) were placed into 500-ml centrifuge bottles, and thereafter maintained in darkness under water at 25°C for subsequent chemical determinations.

11. Macrophyte species included in the investigation were obtained from natural populations within the United States. Propagule type, number, and biomass of each species allocated during planting to individual sediment containers are summarized in Table 1. Three containers each of *S. latifolia* and *N. aquaticum* and six containers each of *P. nodosus*, *N. spicatum*, *H. verticillata*, and *E. canadensis* were prepared using NON and each of the amended sediments at a low level of organic matter addition. Additionally, four containers each of *P. nodosus* and *H. verticillata* were prepared using each of the amended sediments at high levels of organic matter addition. The emergent

Table 1
Propagule Type, Number, and Biomass of Each Species
Allocated to Sediment Containers

<u>Species</u>	<u>Propagule*</u>	<u>Propagule No.</u>	<u>Biomass, mg dry mass + standard error (n = 4)</u>
<i>S. latifolia</i>	Tuber	3	4.1 ± 0.20
<i>M. aquaticum</i>	Apical tip	4	1.2 ± 0.05
<i>P. nodosus</i>	Rhizome	3	0.4 ± 0.03
<i>M. spicatum</i>	Apical tip	4	0.2 ± 0.01
<i>H. verticillata</i>	Apical tip	4	0.1 ± 0.01
<i>E. canadensis</i>	Apical tip	4	0.1 ± 0.00

* Propagules were selected for uniformity in size and condition. Apical tips averaged 12 cm in length and were planted to a sediment depth of 6 cm.

species (*S. latifolia* and *M. aquaticum*) were positioned in tanks filled with solution to only one-half volume (depth 40 cm) to facilitate shoot emergence from the solution early during growth. All other species were positioned in tanks filled with solution to near-maximum volume (depth 82 cm). Planting was accomplished 2 weeks after the addition of sediment amendments. Additional unplanted sediment containers were maintained under conditions similar to those in the greenhouse tanks for a separate experiment initiated 8 weeks after amendment (details provided later in text).

12. The investigation included four related phases of experimentation (Experiments 1 through 4). Experiment 1 involved all macrophyte species grown on NON and on sediments amended at the low level of organic matter addition. Experiment 2 involved *H. verticillata* and *P. nodosus* grown on NON and on sediments amended at the high levels of organic matter addition. Experiment 3 involved *H. verticillata* grown on NON and on amended sediments (low level), which had been aged for a period of 8 weeks. Experiment 4 involved *H. verticillata* grown on NON and on CAT, OAK, and PIN (amended at the low level of organic matter

addition) under various conditions of nitrogen supply (described later in text).

13. Macrophyte growth during all phases of experimentation was limited to a period of 6 weeks, which in our greenhouse is adequate for the development of treatment-related differences in growth, while minimizing tissue deterioration associated with senescence. Differences in macrophyte growth were determined from estimates of total dry-weight biomass accrual (shoots + roots) according to Barko and Smart (1981a, b).

Analytical Procedures

14. The texture of NON was determined by size according to Day (1956). Size fractions of sediment amendments were determined by dry sieving. Organic matter in sediments and in sediment amendments was estimated from loss of oven-dry mass (100°C) after a 4-hr period of combustion at 550°C. 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. Nutrients in sediment amendments and in macrophyte biomass were determined following digestion in a mixture of H_2O_2 and H_2SO_4 using a procedure slightly modified (for volume differences) from Allen et al. (1974). Oxidation-reduction (redox) potential of sediments was determined using platinum electrodes, a calomel reference cell, and a millivolt meter. Electrodes were frequently cleaned and checked against solutions of known potential (Light 1972). All redox values were corrected to pH 7.0. The evolution of gaseous metabolic products from sediments was estimated in a Van Kessel apparatus using a Packard Model 419 gas chromatograph equipped with a thermal conductivity detector.

15. Sediment interstitial water was obtained from NON and from sediments at a low level of amendment by high-speed centrifugation at 4°C. Conductivity and pH determinations were followed directly by membrane filtration (0.45- μ m prewashed filters) in a nitrogen atmosphere to prevent the formation of precipitates. Dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) in filtrates were determined within

4 hr using a Beckman Model 915-A total organic carbon analyzer. Sub-samples of the filtrates were acidified (with 12 N HCl) to pH 2.0 and refrigerated for later analyses of nutrients.

16. Technicon autoanalyzers were used for N and P determinations, and a combination of flame photometry and DC argon plasma emission apparatus was used for other elements. The accuracy of analytical procedures used to obtain tissue nutrient concentrations was checked by including National Bureau of Standards reference tissues in all experimental sample sets. Experimental data were analyzed statistically using the Statistical Analysis System (Raleigh, North Carolina). Statements of significance made in the text refer to the 5 percent level or less of statistical confidence.

PART III: RESULTS

Sediment Environment

Nonamended (control) sediment

17. The Lake Washington sediment (NON) can be generally characterized as fine textured with a much greater silt than clay content (Table 2). Concentrations of nutrients in NON (Table 2) fall within, but toward the lower end of, ranges reported for other fine-textured sediments obtained from a variety of productive environments within the United States (cf. Barko and Smart 1979; Barko 1982a).

Table 2
Characterization of Nonamended Sediment (NON)

<u>Texture,* % dry mass</u>		<u>Sediment Nutrients,** mg · g dry mass⁻¹</u>			
Sand	22.5 ± 0.0	N	2.1 ± 0.0	Na	0.16 ± 0.00
Silt	67.5 ± 0.4	P	0.55 ± 0.00	K	0.54 ± 0.08
Clay	10.0 ± 0.0	Fe	15.5 ± 0.1	Ca	4.6 ± 0.0
		Mn	0.40 ± 0.01	Mg	4.5 ± 0.0

Note: Values provided are means ± standard error (n = 3).

* Sediment texture was measured by size and included organic as well as inorganic matter. Organic matter content was 10% of dry sediment mass.

** Sediment nutrient concentrations were determined following strong acidic digestion.

Sediment amendments

18. Specific nutrient levels and ash content in OAK, CAT, and PIN-Amends were generally much lower than in ALG and MYR-Amends (Table 3), reflecting the dead versus living condition, respectively, of the amendments at the time of their collection. Greater ratios of carbon to nitrogen in dead than in living amendments indicate the greater N content of the latter (particularly in MYR-Amend), and reflect differences in structural composition and resistance to decomposition (Godshalk and Wetzel 1978). The overall particle size (after grinding)

Table 3
Characteristics of Sediment Amendments

Nutrients	Concentrations in Amendments, mg · dry mass ⁻¹				
	ALG-Amend	MYR-Amend	CAT-Amend	OAK-Amend	PIN-Amend
N	10.9 ± 0.2	28.6 ± 0.2	5.7 ± 0.1	9.6 ± 0.2	4.5 ± 0.1
P	2.8 ± 0.0	2.9 ± 0.1	0.9 ± 0.0	1.3 ± 0.0	0.6 ± 0.0
K	22.7 ± 1.6	11.0 ± 0.0	1.1 ± 0.0	3.7 ± 0.1	1.1 ± 0.0
Na	1.6 ± 0.1	3.4 ± 0.1	0.5 ± 0.0	0.0 -	0.0 -
Ca	50.5 ± 7.4	36.1 ± 0.8	12.0 ± 0.2	12.9 ± 0.1	4.3 ± 0.1
Mg	6.3 ± 0.1	1.1 ± 0.0	0.8 ± 0.0	1.9 ± 0.0	0.8 ± 0.0
Fe	3.8 ± 0.1	2.9 ± 0.1	0.4 ± 0.0	0.2 ± 0.0	0.1 ± 0.0
Mn	5.4 ± 0.1	3.6 ± 0.1	0.6 ± 0.0	1.3 ± 0.0	0.8 ± 0.0
C:N*	31	13	79	45	98
Ash, %	29	21	4	8	5

Note: Values provided are means ± standard error (n = 3).

* Carbon to nitrogen ratio was calculated from mass concentrations and is dimensionless. Carbon was estimated as 0.465 × ash-free dry mass.

of dead amendments was greater than that of living amendments (data not presented). On the basis of these differences, organic matter derived from ALG and MYR is considered more labile than that derived from dead sources.

Sediment interstitial water

19. All amendments to the sediment resulted in dramatic changes in interstitial water chemistry when compared with NON (Figure 1). Deviations in most interstitial characteristics of amended sediments from the rather stable conditions of NON were greatest initially (2 weeks following amendment) and diminished with time. Regression analyses incorporating interstitial water data pooled across amended sediments indicate that DOC, conductivity, Fe, Mn, and PO₄-P were significantly intercorrelated. These intercorrelations suggest the operation of similar geochemical processes in amended sediments stimulated by additions of

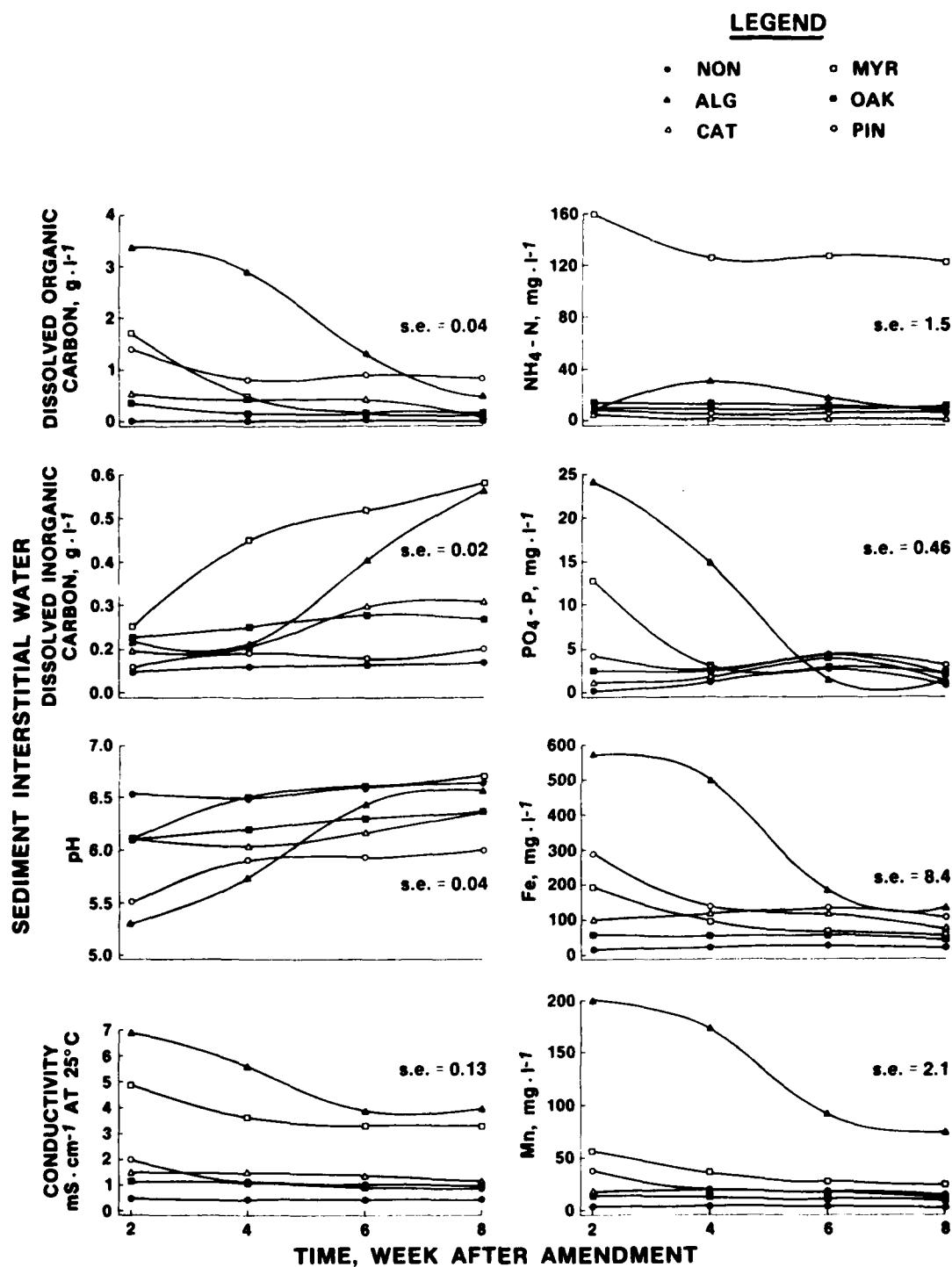


Figure 1. Chemical changes in the interstitial water of NON and of sediments amended at the low level of organic matter addition (see text). Curves were fit by computer (Spline function). Standard errors (s.e.) are pooled error estimates obtained from the analysis of variance

organic matter. These processes collectively increased soluble ion concentrations, and are likely to have involved metal complexation by organic compounds (Takkar 1969; Jackson 1975, and literature provided therein) as well as ion exchange reactions affected by pH and redox potential (Ponnamperuma 1972).

20. The pH of all amended sediments was initially low relative to NON, but progressively increased to values between 6.1 and 6.6, which were not appreciably different from the pH of NON at 8 weeks (Figure 1). This pattern of pH change with time is typical of that noted shortly after the submergence of soils (Ponnamperuma 1972). Initial reductions in the pH of amended sediments were probably caused by rapid accumulations of CO_2 and organic acids following amendment. Subsequent increases in pH roughly paralleled increasing DIC (presumably as bicarbonate) in the amended sediments. The DIC increased as DOC decreased in amended sediments, suggesting bicarbonate formation as a direct result of DOC decomposition (Matisoff, Fisher, and McCall 1981).

21. Among all of the chemical variables considered here in sediment interstitial water, $\text{NH}_4\text{-N}$ is the only one that cannot be related either directly or indirectly to DOC concentration. Conversely, N is the only element that bears any relationship in interstitial concentration to its concentration in amended sediments as a whole (calculated from known additions to NON). Concentrations of interstitial $\text{NH}_4\text{-N}$ are thus considered to reflect the balance between remineralization and microbial utilization (Ponnamperuma 1972). Amendments of low C:N organic matter (labile) apparently provided N in excess of microbial requirements, while amendments of higher C:N organic matter (refractory) resulted in partial depletion of interstitial N during microbial decomposition of sediment organic matter.

Sediment gas evolution

22. The evolution of carbon dioxide (CO_2) and methane (CH_4) from sediment with additions of labile organic matter (ALG and MYR) was generally greater than from the control and other amended sediments (Table 4). Whereas no detectable CH_4 was evolved from NON, CH_4 production in all amended sediments began within 2 weeks after organic matter addition.

Table 4
Gas Evolution from Experimental Sediments*

Sediment**	Gas Production Rate, $\mu\text{g} \cdot \text{g}$ dry sediment ⁻¹ · day ⁻¹		CH ₄ :CO ₂ , %
	CO ₂	CH ₄	
ALG	1570	470	30
MYR	1000	310	31
CAT	1080	190	18
PIN	520	90	17
OAK	150	15	10
NON	230	0	0

* Estimated over a 20-day period, beginning 2 weeks after addition of amendments to sediment.

** Sediments are arranged vertically downward in order of decreasing ratio of CH₄:CO₂.

Ratios of CH₄ to CO₂ evolved from sediment with additions of ALG and MYR were twofold to threefold greater than from the other sediments. Ethylene evolution was undetectable from any amended sediment or from the control sediment. Although soluble sulfide concentrations were not measured, sulfides were probably absent due to sufficient concentrations of iron to precipitate them from the interstitial water (Connel and Patrick 1968).

23. Methanogenesis is probably absent from anaerobic sediments until the redox potential (Eh) falls below -150 mV (Gambrell and Patrick 1978). Cappenberg (1974) found a maximum population of methane-producing bacteria between -250 and -300 mV. Sediment Eh values in the current investigation ranged from +50 to -150 mV with no consistent differences between control sediment and treatments. Because CH₄ was produced in the present investigation, Eh values appear anomalously high. Electrode potentials are biased to higher values when the true redox potential is controlled by substances (e.g., NH₄⁻, HCO₃⁻, CH₄) that are not electroactive at the surface of the platinum electrodes used to

measure Eh (Berner 1981). However, CH_4 evolution rates and ratios of CH_4 to CO_2 evolution suggest that the true redox potentials of sediment receiving organic matter additions may have been less than that of the control sediment, and that there were differences in true redox states.

Macrophyte Growth and Nutrition

Growth

24. At equal levels of organic matter addition (low-level amendment), macrophyte growth differed according to the type of amendment and the species of aquatic macrophyte in Experiment 1 (Figure 2). Growth inhibition was generally greatest on ALG, CAT, and PIN, and least on MYR and OAK sediments. Biomass accrual by emergent species as a group

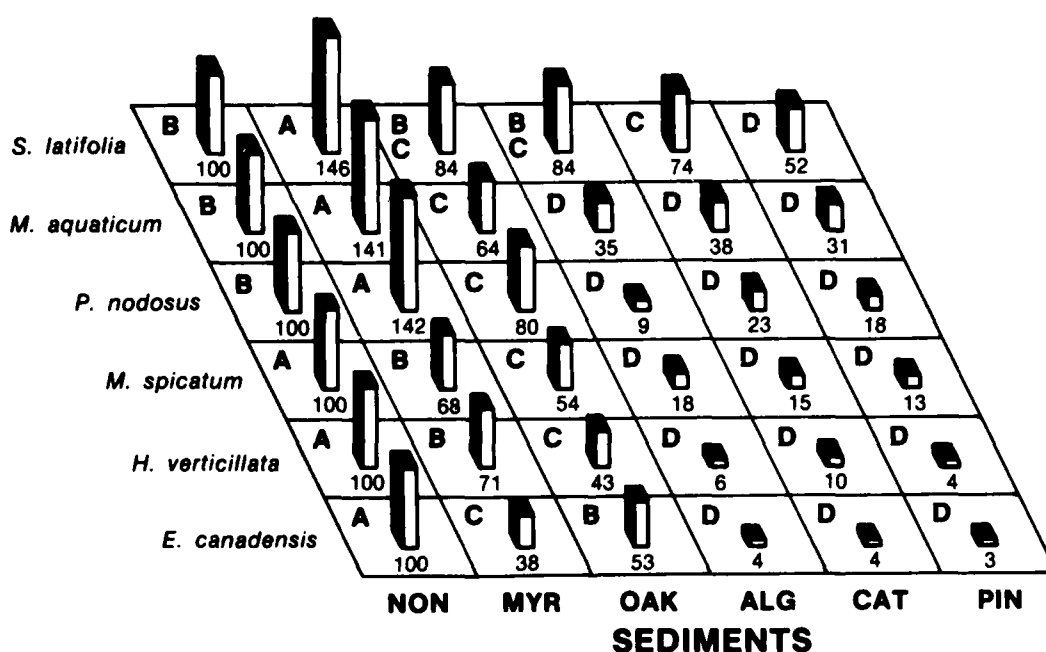


Figure 2. Total biomass response of individual species on NON and on sediments amended at the low level of organic matter addition in Experiment 1. Numerical values are expressed as percentages of the total biomass accrual obtained on NON. Biomass values within a species sharing the same letter do not differ significantly based on Duncan's multiple range test

(*S. latifolia*, *N. aquaticum*, and *P. nodosus*) was generally greater on all sediments, and was less inhibited than that of submersed species (*N. spicatum*, *H. verticillata*, and *E. canadensis*) on amended sediments. Curiously, biomass accrual by the emergent species was stimulated on MYR sediment.

25. At the high levels of amendment, the growth of *H. verticillata* and *P. nodosus* (representing submersed and emergent species, respectively) was severely inhibited on all amended sediments irrespective of amendment type in Experiment 2 (Figure 3). At levels of 20 percent organic matter and above, MYR and OAK sediments inhibited the growth of both species to a similar extent as ALG, CAT, and PIN at the low level of amendment (15 percent organic matter) in Experiment 1. No greater inhibition of growth in these species was obtained at sediment organic matter concentrations above 20 percent.

26. The possibility that the influence of organic matter addition on macrophyte growth might vary as sediments decreased in organic content with age was examined in Experiment 3 involving *H. verticillata* grown on control sediment and on sediment receiving 5 percent additions of organic matter 8 weeks previously. Less than 25 percent of the added organic matter was lost during aging, except for addition of algae where this loss approached 70 percent. The organic content of NON did not change appreciably during aging. Interstitial water chemistry at the start of this experiment was similar to that at the end of Experiment 1 (Figure 1).

27. Results of Experiments 1 and 3 for *H. verticillata* are contrasted in Figure 4. Growth on sediment receiving refractory organic matter did not differ with aging. In contrast, growth on sediment receiving labile organic matter was substantially greater after aging in Experiment 3. Rather than inhibiting growth as in Experiment 1, MYR sediment in Experiment 3 stimulated growth of *H. verticillata*.

Nutrition

28. Concentrations of N, P, Fe, and Mn in macrophyte shoots from Experiment 1 are contrasted among sediments and between macrophyte growth forms in Table 5. Major nutritional differences include:

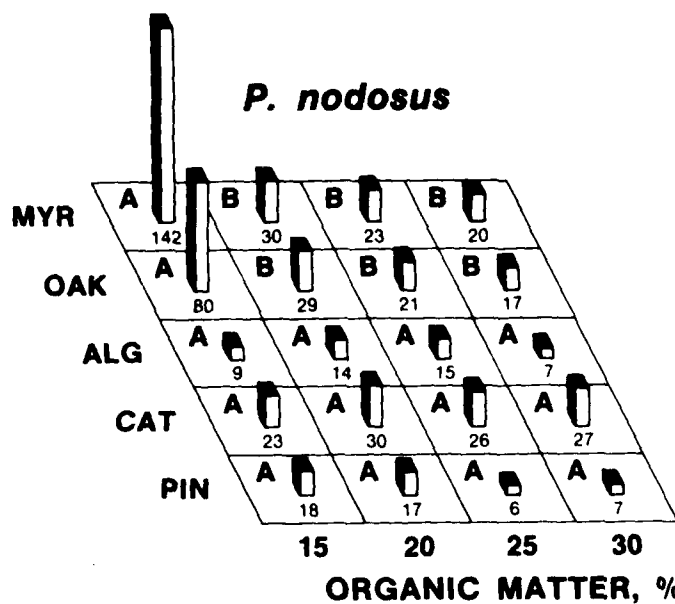
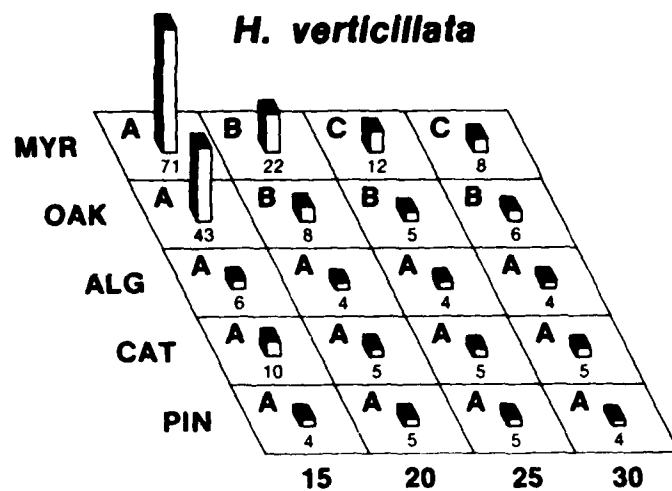


Figure 3. Total biomass response of *H. verticillata* and *P. nodosus* to different levels of organic amendments in Experiment 2. Numerical values are expressed as percentages of total biomass accrual on NON. Biomass values within amendment types sharing the same letter do not differ significantly based on Duncan's multiple range test

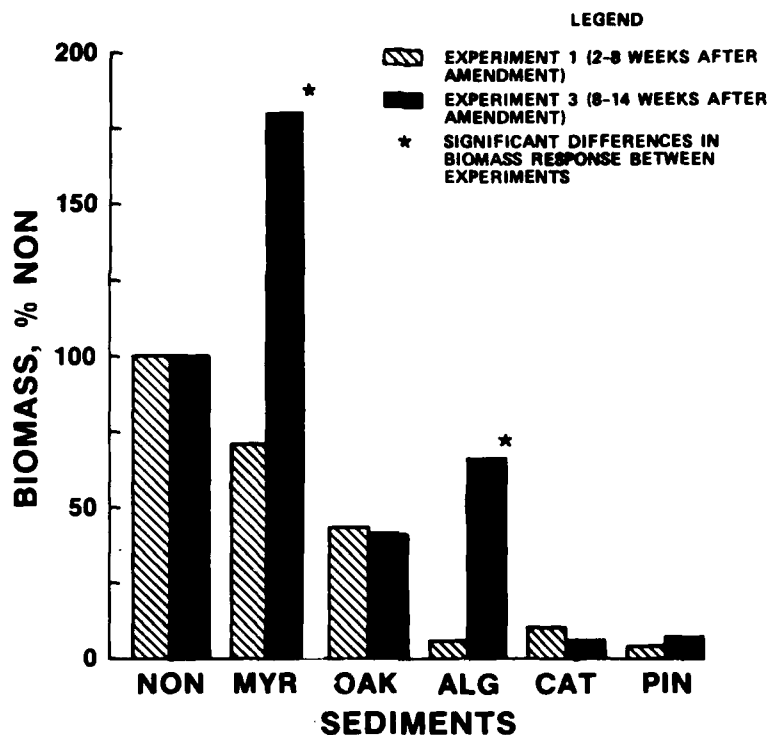


Figure 4. Total biomass response of *H. verticillata* during Experiments 1 and 3. Total biomass accrual is plotted as a percentage of that obtained on NON in each respective experiment

(a) greater Fe in submersed than in emergent macrophytes on all amended sediments, and (b) greater elevation of both Fe and Mn in submersed than in emergent macrophytes on amended sediment compared to NON. With few exceptions, variations in shoot N and P among sediments were minor. Concentrations of both of these elements were somewhat greater in emergent than in submersed macrophytes.

Table 5
Concentrations of N, P, Fe, and Mn in Shoots of Emergent and
Submersed Macrophytes Grown on Experimental Sediments*

Sediment**	Form†	Shoot Nutrients††, mg · g dry shoot mass ⁻¹			
		N	P	Fe	Mn
NON	E	8.2 ± 0.6	3.1 ± 0.2	0.11 ± 0.01	0.20 ± 0.03
	S	7.0 ± 0.7	2.1 ± 0.1	0.08 ± 0.01	0.06 ± 0.01
MYR	E	13.3 ± 0.9	3.2 ± 0.3	0.13 ± 0.01	0.18 ± 0.01
	S	20.1 ± 1.4	3.0 ± 0.2	0.26 ± 0.03	0.20 ± 0.02
OAK	E	8.5 ± 0.6	3.4 ± 0.3	0.17 ± 0.02	0.19 ± 0.02
	S	9.6 ± 0.5	2.3 ± 0.1	0.33 ± 0.03	0.12 ± 0.01
ALG	E	10.5 ± 0.8	2.5 ± 0.5	0.39 ± 0.11	0.37 ± 0.05
	S	6.3 ± 0.5	1.3 ± 0.1	0.78 ± 0.12	0.73 ± 0.19
CAT	E	6.6 ± 1.0	2.6 ± 0.6	0.21 ± 0.04	0.16 ± 0.02
	S	5.1 ± 0.4	1.3 ± 0.1	0.77 ± 0.10	0.30 ± 0.08
PIN	E	8.0 ± 1.2	2.2 ± 0.5	0.30 ± 0.08	0.15 ± 0.02
	S	5.8 ± 0.2	1.2 ± 0.1	0.86 ± 0.10	0.15 ± 0.03

* Growth was initiated 2 weeks after amendment at the low level (Experiment 1). Values provided are means ± standard error (n = 9). Values are representative of data pooled separately for emergent and submersed macrophyte growth forms.

** Sediments are arranged vertically downward in order of relatively increasing inhibition of macrophyte growth.

† Form E includes emergent macrophyte species. Form S includes submersed macrophyte species.

†† Shoot nutrients were determined after 6 weeks of growth on experimental sediments.

29. Considering possible relationships between macrophyte growth and shoot nutrition in Experiment 1, it is notable that the growth of submersed species correlates negatively with iron concentration in shoots, suggesting possible Fe toxicity associated with elevated Fe concentrations in sediment interstitial water (Jones and Etherington 1970; Jones 1973; Armstrong 1975). However, in Experiment 3, variations in the growth of *H. verticillata* were unrelated to shoot Fe concentration (data not presented). Moreover, levels of Fe in macrophyte shoots in all experimental phases of this investigation were not excessive in comparison with values reported for macrophytes in general (Hutchinson

1975). The same is also true for shoot Mn concentrations. Therefore, it is unlikely that growth inhibition in this investigation resulted from either Fe or Mn toxicity.

30. In comparison with suggested critical (i.e., growth limiting) values of tissue P for aquatic macrophytes (Gerloff and Krombholz 1966; Gerloff 1975; Barko and Smart 1979), shoot P concentrations in Table 5 indicate an adequate supply of this element for macrophyte growth in Experiment 1. However, on all sediment, with the exception of MYR, shoot N concentrations were very low, approaching generalized critical concentrations. In Experiment 3 the greater growth of *H. verticillata* on ALG compared to Experiment 1 coincided with a doubling in shoot N concentration. These results suggest a possible connection between N supply from sediment and macrophyte growth in this investigation.

31. To examine the possible relationship between N supply and macrophyte growth, Experiment 4 involving N additions to sediment and to solution was conducted. *Hydrilla verticillata* was grown on NON and at the low level of amendment on CAT, OAK, and PIN. These amended sediments were selected for experimentation because of their low concentrations of interstitial $\text{NH}_4\text{-N}$ and their apparent inability in previous experiments to sustain adequate N concentrations in macrophyte shoots. Treatments included (a) N addition to sediment, (b) N addition to solution, (c) N addition to sediment and solution, and (d) control (no addition of N). In treatments involving N additions, N was added to achieve $100 \text{ mg N} \cdot \ell^{-1}$ (as NH_4Cl) in sediment interstitial water and $5 \text{ mg} \cdot \ell^{-1}$ (as NH_4NO_3) in solution.

32. Nitrogen additions to sediment, solution, or both had no significant effect on the growth of *H. verticillata* (Figure 5). Results paralleled those obtained in Experiments 1 and 3. Therefore, it is unlikely that growth inhibition in *H. verticillata* was caused by inadequate N supply on CAT, OAK, and PIN in either this or previous experiments. Since N did not limit the growth of *H. verticillata* on NON in these experiments, it follows that sediment factors other than N must have been operative in stimulating the growth of this species on MYR relative to NON in Experiment 3.

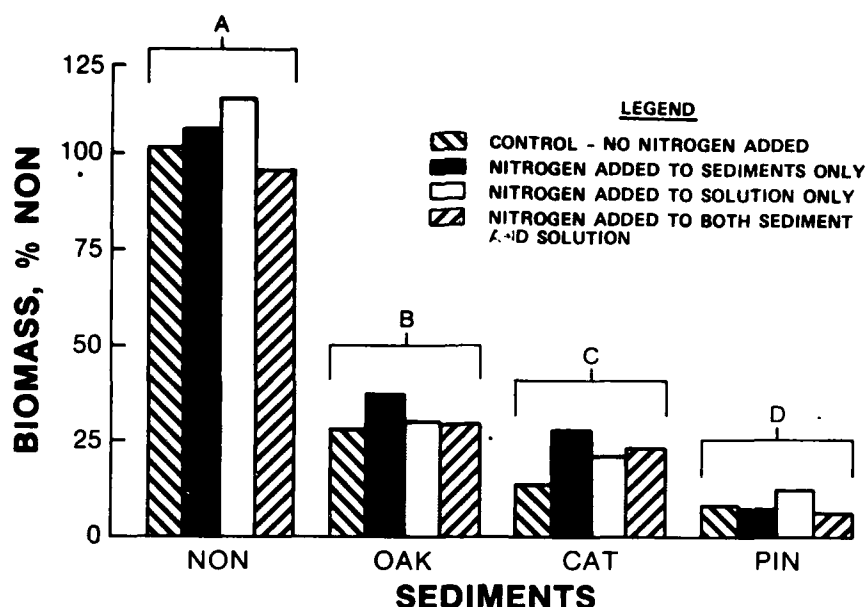


Figure 5. Total biomass response of *H. verticillata* in relation to inorganic nitrogen supply on NON and on sediments amended by additions of refractory organic matter in Experiment 4. Total biomass accrual is plotted as a percentage of that obtained on NON without added nitrogen (control). Effects of nitrogen additions on total biomass accrual are insignificant (from three-way analysis of variance). Different letters associated with biomass, averaged across nitrogen treatments within each sediment, indicate significant differences in biomass accrual (from Duncan's multiple range test)

Macrophyte Growth in Relation to Interstitial Water Chemistry

33. Arguments presented thus far suggest that concentrations of Fe, Mn, PO_4 , and NH_4 in the sediment interstitial water were unlikely to have affected the growth of *H. verticillata*. Values of interstitial water pH fell primarily within the range 6.0-7.0, considered typical for sediments (Baas Beeking, Kaplan, and Moore 1960). Conductivities, with possible exceptions in ALG and MYR, were not excessive (Ponnamperuma 1972, p 57). High concentrations of DIC in the interstitial water of

MYR sediment possibly stimulated growth of *H. verticillata* in Experiment 3 by facilitating increased photosynthetic rate (Sand-Jensen and Søndergaard 1979). However, with the emergent species on the same sediment, it is more likely that the much higher concentration of NH_4 compared to the same in other sediments (Figure 1) may have overcome depressed growth due to N limitation.

34. Macrophyte growth in all treatments, with the exception of sediment receiving additions of *Myriophyllum* organic matter, decreased with increasing concentrations of DOC in the sediment interstitial water. For all species, typified by the response of *H. verticillata* (Figure 6)

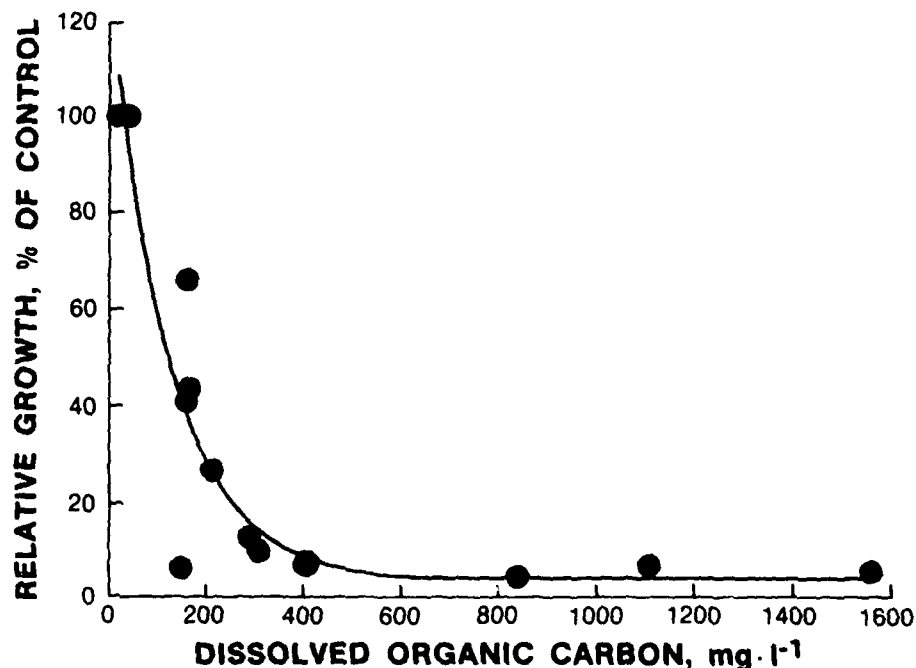


Figure 6. Relative growth (final dry weight) of *H. verticillata* in relation to the mean ($n = 3$) concentration of DOC in the interstitial water of control sediment (NON) and sediment receiving additions of algal, oak, *Typha*, and pine organic matter (Experiments 1, 3, and 4). Mean values ($n = 6$) for growth are percentages of dry weight obtained on control sediment. Curve was fit by computerized least squares procedures

at the 5 percent level of addition in Experiments 1, 3, and 4, growth exhibited a negative exponential decrease with increasing DOC (significant at the 0.1 percent level), where the latter was calculated from measurements made during the postrooting period of growth in each experiment. Treatments involving additions of MYR organic matter stimulated growth in some cases, for reasons unrelated to DOC (see above), and were therefore excluded from the analysis. The asymptotic nature of *H. verticillata* growth in relation to increasing DOC concentration parallels the response of this species, and *P. nodosus* as well, to increasing amounts of organic matter added to sediment (Figure 3).

35. Growth of *H. verticillata* was inhibited by approximately 90 percent on sediment with a DOC concentration $\geq 400 \text{ mg} \cdot \ell^{-1}$. From a less extensive data base it appears that the other submersed species investigated here were inhibited to approximately the same extent and emergent species to a lesser extent in relation to DOC concentration in the sediment interstitial water. While DOC concentrations of $300\text{--}500 \text{ mg} \cdot \ell^{-1}$ of sediments under open water are considered high (Golterman 1975, p 141), values in this range have been reported for sediments from lakes containing organic matter derived from adjacent cypress stands (Dooris and Martin 1980).

PART IV: DISCUSSION

36. Macrophytes modify the sediment environment through both their passive reception of allochthonous materials and their direct contribution of autochthonous primary production to the sediment (Wetzel 1979; Carpenter 1981). During the development of lacustrine systems, increasing proportions of sediment organic matter are derived from structurally complex emergent vegetation (Wetzel 1979). The littoral zone retains both soluble and particulate organic inputs from the watershed (Wetzel and Allen 1972; Mickle and Wetzel 1978). Due partially to the refractory nature of these materials (Godshalk and Wetzel 1977) and a decreasing availability of electron acceptors (Rich and Wetzel 1978), sediment organic matter accumulates at an increasing rate as lakes age. Increasing concentrations of interstitial DOC may occur as end products of anaerobic metabolism accumulate (Wetzel 1979).

37. A wide variety of soluble organic compounds, many of which derive from the anaerobic decomposition of cellulose and lignin, have been demonstrated to possess phytotoxic properties (Patrick, Toussoun, and Koch 1964; Guenzi and McCalla 1966; Yoshida 1975; Drew and Lynch 1980). These compounds, in combination with other potential phytotoxins (metals, gases, and soluble sulfides) in anaerobic sediments, produce a seemingly hostile environment for plant growth (Armstrong 1975, 1978).

38. It has been suggested that the capacity of aquatic macrophytes to survive the presence of phytotoxins in sediments may be largely dependent upon oxygen transport from shoots to roots since oxygen (in addition to supporting root respiration) contributes to the detoxification of the rhizosphere (Armstrong 1978). In nearly all vascular macrophytes, internal ventilation is facilitated by the presence of a lacunar system, i.e., a network of internal air spaces (Williams and Barber 1961). Lacunar volume varies considerably among macrophyte species, being generally more extensive in emergent than in submersed growth forms (Sculthorpe 1967; Hutchinson 1975).

39. Transport of atmospheric oxygen in emergent macrophytes is

generally considered to occur by molecular diffusion (Teal and Kanwisher 1966; Hutchinson 1975; Armstrong 1978) or by pressurized mass flow (Dacey 1980, 1981). However, strictly submersed macrophytes having no direct contact with the atmosphere may be less able to oxidize their rhizosphere than emergent macrophytes.* Thus, the ability of submersed macrophytes to detoxify the sediment environment may be relatively limited in comparison with that of emergent macrophytes.

40. It is interesting that the succession of aquatic plant communities (submerged to floating leaved to emergent) in lakes parallels the accumulation of organic matter in sediments (Pearsall 1920; Wilson 1941; Walker 1972; Wetzel 1979). In addition, plant community composition, as well as the spatial distribution of individual species, varies with sediment organic content (Pearsall 1920; Misra 1938; Moyle 1945; Macan 1977). Although many other factors such as decreasing depth (Pearsall 1920; Wilson 1941) and shading by phytoplankton (Jupp and Spence 1977) or by epiphytes (Phillips, Eminson, and Moss 1978; Sand-Jensen and S ndergaard 1981) have been implicated in the succession of aquatic plant communities, differential tolerance to increasing levels of organic matter in sediments may contribute to the decline of submerged species, thereby favoring the invasion of emergent species.

* Personal Communication, February 1982, S. R. Carpenter, Assistant Professor, University of Notre Dame, Indiana.

PART V: CONCLUSIONS AND RECOMMENDATIONS

41. Sediment organic matter can greatly inhibit the growth of submersed macrophytes and, to a lesser extent, that of emergent species. The inhibitory property of sediment organic matter was associated here either directly or indirectly with high concentrations of soluble organic compounds in the interstitial water. Sediments receiving additions of refractory organic matter retained macrophyte growth-inhibiting properties for a longer period than those receiving additions of labile organic matter. The extent of macrophyte growth inhibition was determined by the type as well as the amount of organic matter incorporated into sediment.

42. Organic matter concentration in freshwater sediments extends over a broad range, reflecting differences in climate, basin morphology, basin age, and vegetative characteristics of the watershed. Effects on macrophyte growth of sediments loaded naturally with organic matter need to be examined in detail. Physiological mechanisms of growth inhibition (or stimulation) by organic matter need to be characterized. It is important first to determine which fractions of total sediment organic matter possess growth-affecting properties, and then to attempt the characterization of specific constituents.

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