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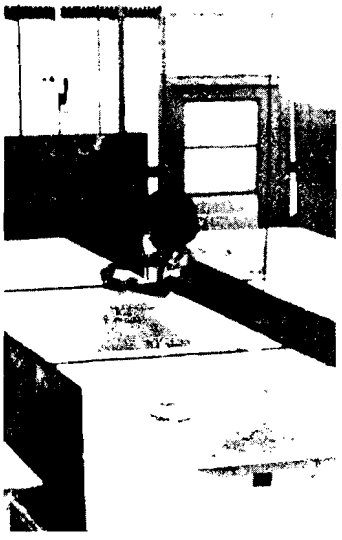

ENVIRONMENTAL LABORATORY

**AQUATIC PLANT CONTROL RESEARCH PROGRAM**

TECHNICAL REPORT A-86-1

# EFFECTS OF SEDIMENT COMPOSITION ON GROWTH OF SUBMERSED AQUATIC VEGETATION


by

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Experiments with two submersed aquatic macrophytes, *Myriophyllum spicatum* L. and *Hydrilla verticillata* (L.f.) Royle, grown on 40 different sediments from 17 geographically widespread North American lakes, indicated tenfold and twentyfold declines in growth with increasing sediment organic matter up to a concentration of about 20 percent dry sediment mass. Poor growth was obtained also on inorganic sediments with a sand fraction exceeding 75 percent dry

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sediment mass. Diminished growth on organic sediments occurred at low values of sediment density, and on sands at high values of sediment density. Differential centrifugation of organic sediment, facilitating an increase in sediment density with no change in organic matter content, stimulated *Hydrilla* growth, indicating that sediment density rather than organic matter content was most influential in regulating growth.

Macrophyte growth and nutrient accumulation in shoots were closely correlated, but essentially unrelated to concentrations of nutrients in shoots. The magnitude (r value) and statistical significance of correlations between nutrients in macrophyte shoots and sediments varied appreciably, depending on the form of shoot nutrient data (concentration or accumulation) and the type (interstitial water or total) and basis (mass or volume) of sediment nutrient data. Growth and nutrient accumulation were highly correlated with sediment nutrient densities (concentration/sediment volume) indicating close connections among growth, nutrition, and sediment density.

Additions of phosphorus and iron in combination to organic sediments with nitrogen supplied in the overlying solution resulted in significant growth increases in *Hydrilla*, suggesting that diminished growth on unfavorable sediments was caused by multiple nutrient limitation. It is postulated that nutrient uptake on low density organic sediments was limited by long diffusion distances. Limited rates of nutrient diffusion and exchange in coarse-textured sediments may have contributed, in addition to low nutrient status, to their poor ability to support macrophyte growth. Thus, mechanisms of growth limitation on sands and organic sediments appear to be similar, both involving nutrition.

It is further postulated that variations in the ability of different aquatic macrophytes to cope with infertility or other factors associated with unfavorable sediment composition may influence the species composition of aquatic macrophyte communities. Changes in the organic/inorganic composition of sediments may contribute fundamentally to vegetational change in aquatic systems.

# PREFACE

The studies reported here were sponsored by the Department of the Army, Office of the Chief of Engineers (OCE) Directorate of Civil Works (DAEN-CW), through the US Army Corps of Engineers (CE) Aquatic Plant Control Research Program (APCRP). Funds were provided by DAEN-CW under Department of the Army Appropriation No. 96X3122 Construction General. The APCRP is managed by the US Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss. Technical Monitor for OCE was Mr. Carl Brown.

Principal investigator for these studies was Dr. John W. Barko, Environmental Laboratory (EL), WES. Experimental design, data analysis, and interpretation were provided by Dr. Barko and Mr. R. Michael Smart. Technical assistance was provided by Mmes. Susan Hennington, Dwilette G. McFarland, and Ramona H. Warren. The report was prepared by Dr. Barko. Critical reviews were provided by Dr. Gordon L. Godchalk, University of Southern Mississippi, and Dr. Robert R. Twilley, University of Maryland. Assistance in sediment collection was provided by Drs. T. R. Batterson, S. R. Carpenter, S. Hardin, M. J. Klug, K. A. Langeland, K. W. McLeod, S. Painter, M. A. Perkins, and J. E. Titus. The report was edited by Ms. Jamie W. Leach of the WES Publications and Graphic Arts Division.

This investigation was performed under the general supervision of Dr. John Harrison, Chief, EL, and Mr. Donald L. Robey, Chief, Ecosystem Research and Simulation Division (ERSD), and the direct supervision of Dr. Thomas L. Hart, Chief, Aquatic Processes and Effects Group (APEG). Manager of the APCRP was Mr. J. Lewis Decell.

COL Allen F. Grum, USA, was Director of WES during the preparation and publication of this report. Dr. Robert W. Whalin was Technical Director.

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CONTENTS

# EFFECTS OF SEDIMENT COMPOSITION ON GROWTH OF SUBMERSED AQUATIC VEGETATION

## PART I: INTRODUCTION

1. Since the turn of the century it has been recognized that the nature of bottom sediments affects the growth of rooted submersed aquatic vegetation (cf. reviews by Sculthorpe 1967, Hutchinson 1975). Associated mechanisms, however, have not been clearly established, and it remains difficult to predict or manage the growth of these plants without a better understanding of the influence of specific sediment factors. The recognized importance of roots in the nutrition of submersed macrophytes (Denny 1972, 1980; Bristow 1975; Barko and Smart 1981a; Smart and Barko 1985) suggests a possible connection between growth and sediment nutrient availability. Alternatively, the influence of sediments on submersed aquatic vegetation may be due to physical properties rather than chemical composition (Sculthorpe 1967, Haslam 1978, Denny 1980).

2. Different macrophyte species appear to vary in their responses to sediment conditions (Barko and Smart 1980, 1983), which may influence the species composition of aquatic macrophyte communities. Macrophyte community composition and the spatial distribution of individual species have been correlated with sediment organic matter content (Pearsall 1920, Misra 1938, Macan 1977). Moreover, there is an apparent association during lake aging between increasing sediment organic matter and the decline of rooted submersed aquatic vegetation (Walker 1972, Wetzel 1979, Carpenter 1981). These observations suggest that the effect of sediment on submersed macrophytes may be in part related to sediment organic matter content. Earlier it was demonstrated that additions of organic matter to a fine-textured inorganic sediment can substantially reduce the growth of submersed macrophytes (Barko and Smart 1983), but the mechanisms involved, or their applicability to growth on unaltered sediments, remain unknown.

3. Here, based on an extensive investigation involving 40 sediments from 17 geographically widespread North American lakes, broad variations in the growth of *Hydrilla verticillata* (L.f.) Royle and *Myriophyllum spicatum* L. on sediments of different texture and organic matter content are reported. This report is provided to better elucidate relationships between growth of

submersed macrophytes and sediment composition. Additionally, the role of sediment composition as a factor contributing to macrophyte succession and other types of vegetational change in aquatic systems is considered.

## PART II: MATERIALS AND METHODS

### Sediment Collection

4. Sites of sediment collection (Table 1) were selected to span a broad range in sediment texture and organic matter content. At each site surficial sediments were obtained with a small hand-held dredge. Sediment samples (about 24 ℓ) from each site were sieved (2-mm plastic mesh) to remove debris, thoroughly mixed, then placed to a depth of about 10 cm in 1-ℓ, square polyethylene containers (80 $cm^2$) for later planting. Subsamples were placed in 500-ml centrifuge bottles for subsequent physical and chemical analyses. Sediments were equilibrated for several weeks in darkness under water at 25° C prior to the initiation of macrophyte growth experiments.

### Experimental Environment and Procedures

5. Growth experiments were conducted under partially controlled environmental conditions in a greenhouse. This facility, housing 18 large (1,200 ℓ) macrophyte culture tanks and ancillary equipment, is described elsewhere (Barko and Smart 1981b). Light was reduced, using neutral-density shade fabric, to 50 percent ambient daylight (about 1,000 $\mu E/m^2/sec$ during midsummer), and water temperature was maintained at 25° ± 1° C. Solution chemistry was nearly identical to that described in Table 1 of Smart and Barko (1985), except for the addition of $Ca(NO_3)_2$. The solution contained (in milligrams per litre): 32.2 $Ca^{+2}$, 6.8 $Mg^{+2}$, 16.0 $Na^{+1}$, 6.0 $K^{+1}$, 26.9 $SO_4^{-2}$, 44.2 $Cl^{-1}$, 22.1 $NO_3^{-1}$, and 51.8 $HCO_3^{-1}$. Phosphorus and micronutrients were excluded from solution to minimize algal growth in the case of the former, and because of difficulties in maintaining solubility of the latter. It was assumed that these elements excluded from solution would be obtained from sediments by root uptake (Denny 1980, Barko and Smart 1981a, Huebert and Gorham 1983, Smart and Barko 1985).

6. There was one primary experiment including both *Hydrilla* and *Myriophyllum* grown on all sediments, and several secondary experiments including only *Hydrilla* grown under specifically manipulated conditions (explained later in text). Plant growth in all experiments was examined in replicate (n = 4 to 6) over 5-week periods of growth. The entire investigation was conducted over

a 3-year period, with experimentation restricted primarily to the "growing season" (March through November). Growth was estimated from measurements of final dry weight total biomass (shoots plus roots). The contribution of initial mass from planted apical tips (15 cm in length, 4 per container) to growth was negligible. Losses of plant biomass and associated nutrients during the experiments due to senescence were likewise negligible.

## Sediment and Plant Tissue Analyses

7. Particle size (texture) of the sediments was determined by the hydrometer method of Patrick (1958). Sediment moisture and density were determined gravimetrically by drying known volumes at 105° C. Dried sediment samples were combusted at 550° C to estimate total organic matter content from weight loss on ignition. Total sediment carbon and inorganic carbon were determined directly using a Leco carbon analyzer. Humus fractions (fulvic and humic acids) were quantified spectrophotometrically following a series of acid-base extractions of wet sediment (Stevenson 1982). Sediment interstitial water was separated by high speed centrifugation at 4° C, with conductivity and pH determined immediately. Subsamples of the supernatants were filtered (0.45 μm, prewashed millipore) in an atmosphere of nitrogen to prevent oxidative precipitation of metals. Dissolved organic carbon and dissolved inorganic carbon were determined by infrared gas analysis (Beckman model 915-A total organic carbon analyzer). Subsamples of the filtrates were acidified to pH 2 with 12 M HCl and refrigerated for later nutrient analyses.

8. Total sediment nitrogen was determined by Kjeldahl digestion (Bremner 1965). Other nutrients (see below) in the total sediment were determined following dissolution of sediment ash in HCl and $HNO_3$, using a plant digestion procedure (Allen et al. 1974) modified slightly for differences in nutrient concentrations for application to sediment. Nutrients in plant shoots were determined following digestion in a mixture of $H_2O_2$ and $H_2SO_4$ (Allen et al. 1974).

9. Analyses of N and P were performed colorometrically using Technicon Auto-Analyzer II procedures. Other nutrients (Na, K, Ca, Mg, Fe, and Mn) were determined by flame photometry. Tissue Ca concentrations were somewhat variable due to differential precipitation on leaf surfaces, and are not reported here. The accuracy of analytical procedures (typically > 95 percent) for

total sediment and plant tissues was verified by including National Bureau of Standards reference materials in experimental sample sets. Analytical precision was ±5 percent or less (expressed as a coefficient of variation). Statistical analyses were performed using the Statistical Analyses System (Raleigh, N. C.). Statements of statistical significance in the text without specific indication of probability level refer to $p \leq 0.05$.

## PART III: RESULTS

### Sediment Composition

10. Sediments exhibited broad ranges in physical and chemical composition (Table 2; Appendices A-C). Texture varied from predominantly fine-grained silts and clays to coarse-grained sands. Sediment density increased with increasing sand content and decreased with increasing organic matter. Moisture content closely paralleled organic matter content and was related inversely to sediment density. Humus fractions (fulvic and humic acids), non-humic organic matter, and total Kjeldahl nitrogen (TKN) were all positively and significantly correlated with total organic matter ($r > 0.80$, $p < 0.01$). Independent estimates of total organic matter and total organic carbon were in very close agreement ($r = 0.99$, $p < 0.001$). Organic carbon comprised 53 ± 1 percent (std. error, $n = 40$) of sediment organic matter, which is comparable to the estimate of 58 percent C in the organic matter of soils (Allen et al. 1974).

11. Concentrations of all nutrients considered in the total sediment were inversely correlated significantly with sand content. Nutrient concentrations in the interstitial water, however, were essentially unrelated to sand content. Sediment organic matter had little influence on total nutrient concentrations in the sediment, except for TKN (noted above) and P, both of which were positively correlated with organic matter. In contrast, low concentrations of most nutrients in the interstitial water and, consequently, low values of conductivity were associated with high sediment organic matter content. The range in sediment pH was minor compared with that of natural waters, and on the average pH approximated neutrality.

12. Concentrations of Ca, Mg, Fe, and Mn were individually correlated positively and significantly between interstitial water and total sediment. In contrast, there was no relationship between water and sediment for N, P, Na, or K. Total sediment Ca and inorganic C were closely related ($r = 0.98$, $p < 0.001$) as stoichiometric constituents (3.6 Ca to 1 C) of $CaCO_3$. Dissolved organic C and dissolved inorganic C were weakly but significantly correlated respectively with total organic C ($r = -0.36$, $p < 0.05$) and total inorganic C ($r = 0.39$, $p < 0.05$).

## Macrophyte Growth

13. Total biomass of both species generally decreased with increasing organic matter up to 20 percent, and at greater values was rather uniformly reduced to the lower end of growth ranges, tenfold and twentyfold in *Myriophyllum* and *Hydrilla* (Figure 1). At relatively low values of organic matter (<10 percent), sediments with greater than 75 percent sand (triangles in Figure 1) also provided poor macrophyte growth. In both species, shoot biomass was closely related to total biomass ($r > 0.98$, $p < 0.001$), and shoot length increased directly with increasing shoot mass ($r > 0.85$, $p < 0.01$). The ratio of root-to-shoot biomass varied over an approximately twofold greater range in *Myriophyllum* (0.08 to 0.42) than in *Hydrilla* (0.02 to 0.23), and in both species was inversely related to growth ($r < -0.76$, $p < 0.01$). Thus, plant stature and biomass allocation, in addition to total biomass, were affected by sediment composition.

14. Diminished growth of macrophytes on inorganic "sands" (i.e., >75 percent sand by weight) occurred at high values of sediment density (ca. 0.9 to 1.3 g/ml), and on "organic" sediments (>20 percent organic matter) at low values of sediment density (ca. <0.2 g/ml). Thus macrophyte growth was reduced at both ends of the density spectrum. Over the range of 0 to 20 percent organic matter, sediment density declined sharply with increasing organic matter content, but remained unchanged at greater values of organic matter (Figure 2). Outlying data points in this figure reflect the apparently anomolous influence of high sand fractions on the density of organic sediments (refer to DRPT-3 and -4 in Appendix A). On fine-textured sediments over the range of 0 to 20 percent organic matter, macrophyte growth was negatively related to sediment organic matter content ($r < -0.66$, $p < 0.01$), and positively related to sediment density ($r > 0.78$, $p < 0.01$).

15. In close agreement with data reported for marsh soils (Gosselink, Hatton, and Hopkinson 1984) sediment density was virtually independent of organic density, which was nearly constant (ca. 0.05 g/ml), and was determined almost entirely by mineral density (Figure 3). Mineral mass contributed directly to the density of sediments with an organic matter content of less than about 20 percent. Above this value, however, the density of mineral mass was overshadowed by the volume imparted by organic matter as sediment density approximated that of organic matter. The nearly constant ratio of mass to

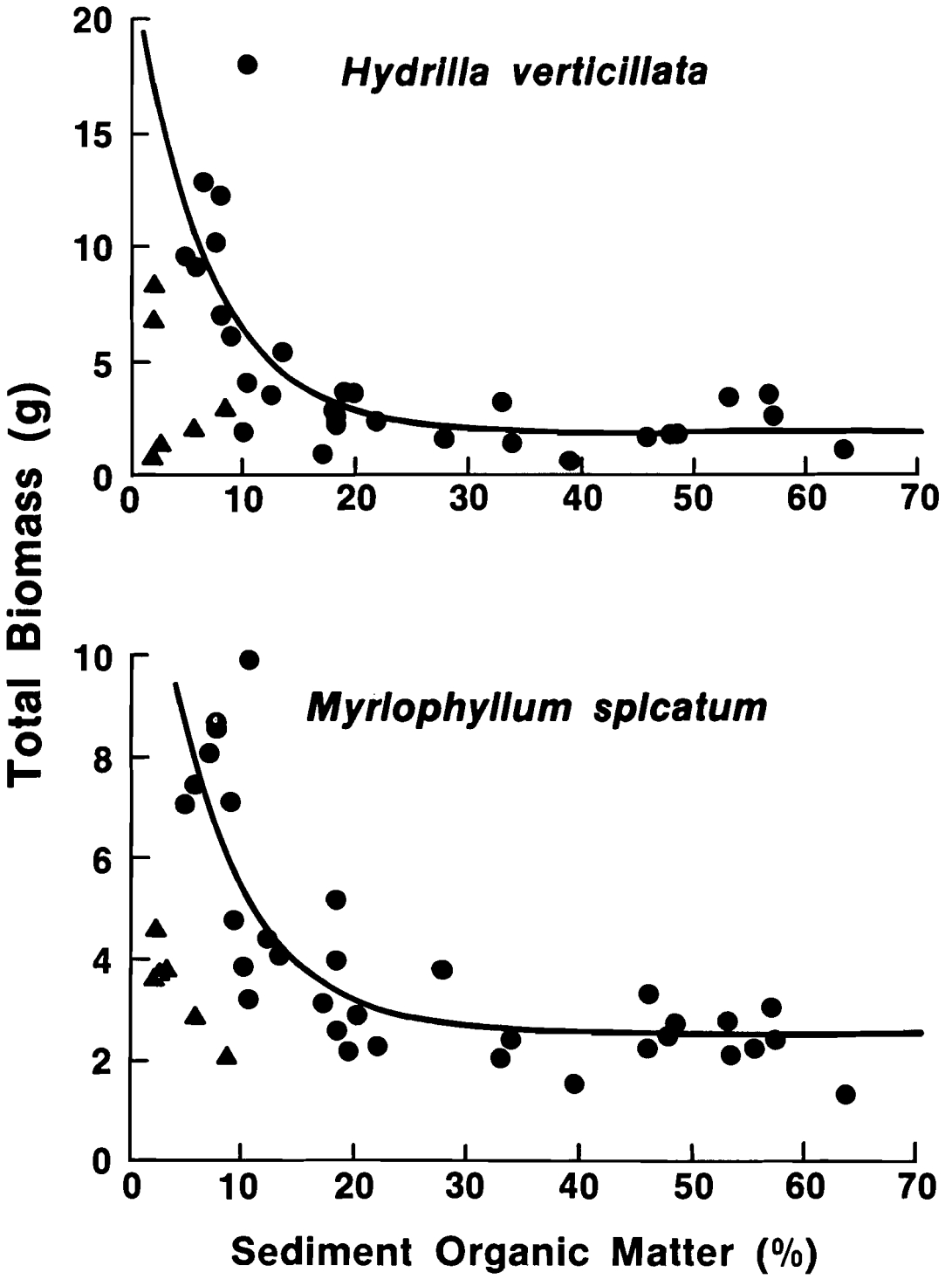


Figure 1. Relationship between growth as total dry weight biomass (n = 4) of *Hydrilla* and *Myriophyllum* and sediment organic matter content (n = 2). Triangles designate sediments containing <75 percent sand, which were excluded from curve fitting. Curve was fit by computerized least squares procedure and is included for contrast only

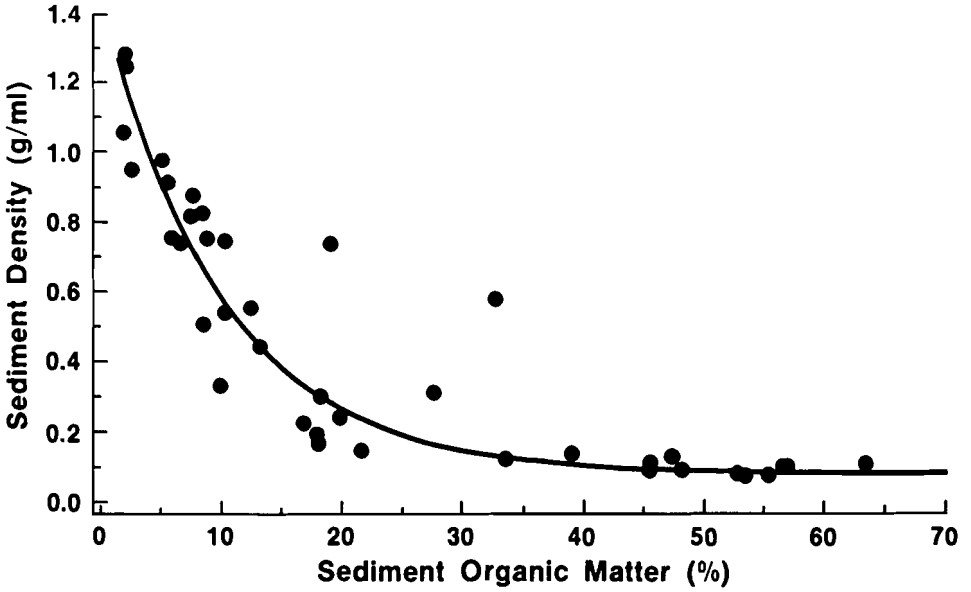


Figure 2. Relationship between sediment density (n = 2) and sediment organic matter content (n = 2) for 40 sediments from North American lakes. Curve was fit by computerized least squares procedure and is included for contrast only

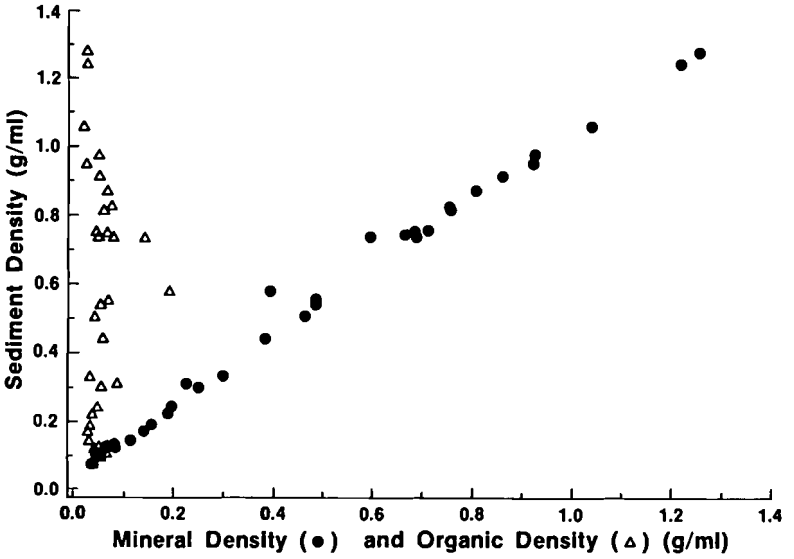


Figure 3. Relationships between sediment density (n = 2), mineral density (n = 2), and organic density (n = 2) for 40 sediments from North American lakes. Closed circles designate mineral densities. Open triangles designate organic densities. Mineral and organic densities were partitioned from weight loss on ignition (550° C). Intersection between mineral density and organic density corresponds to organic matter ≥ 20 percent

volume of organic matter accounts for the absence of change in sediment density with organic matter increasing beyond about 20 percent, and may be linked also with the rather uniform depression of macrophyte growth noted here on highly organic sediments.

16. In order to more directly examine the influences of sand (high sediment density) and organic matter (low sediment density) on macrophyte growth, a separate experiment involving sediment manipulations was conducted. Manipulations included additions of a fine-textured inorganic sediment from Lake Washington (WASH-1) in increments of 0, 20, and 40 percent by volume, to a washed builders' sand (97 percent sand) and to a composite organic sediment (53 percent organic matter). At the maximum level of addition, the organic matter content was reduced to 25 percent dry mass in the organic sediment, and the sand fraction to 75 percent dry mass in the sand. With additions of WASH-1 sediment, the growth of *Hydrilla* increased dramatically overall, threefold on the organic sediment, and sevenfold on the sand (Figure 4). These increases in growth accompanied an increase in sediment density from 0.10 to 0.23 g/ml in the former and a decrease in density from 1.43 to 1.23 g/ml in the latter. Notably, the growth of *Hydrilla* was stimulated in this experiment even though the organic sediment remained "organic" and the sand remained a "sand."

17. In the above experiment, changes in sediment mineralogy and overall nutrient content (unmeasured) due to sediment additions were undoubtedly coupled with changes in measured sediment variables (density, texture, and organic matter). Accordingly, results were potentially influenced by changes in sediment nutrient content, and in the case of the organic sediment, by changes in organic content. This inability to differentiate between the effects of changes in sediment density, nutrients, and organic matter prompted the conduct of an additional experiment designed to evaluate previous results more fully.

18. The composite organic sediment (as above, but without sediment additions) was differentially centrifuged, thus providing four statistically discrete fractions with respect to sediment density. Sediment organic matter content and total nutrient content were unaffected by centrifugation. Centrifugation with concomitant increases in sediment density resulted in significant increases in the growth of *Hydrilla*. This increase in growth approximately paralleled the effect achieved over a similar range in density

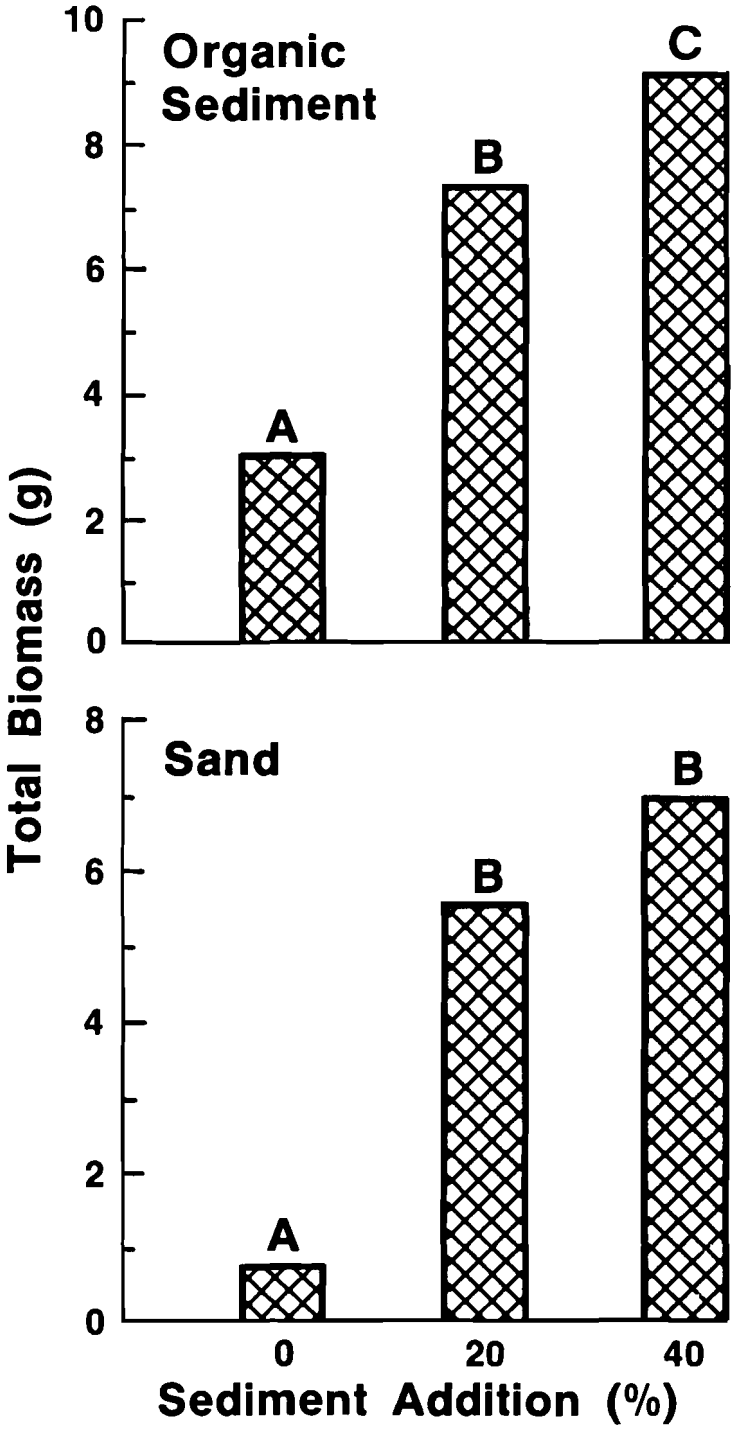


Figure 4. Effects of additions of fine-textured inorganic sediment to both an organic sediment and to a sand on the growth as total dry weight biomass of *Hydrilla*. Vertical bars represent means (n = 4). Values sharing the same letter within sediments do not differ significantly ($p < 0.05$) from one another (Duncan's multiple range test)

by additions of fine-textured inorganic sediment (Figure 5). Increased growth on centrifuged sediments was presumably independent of changes in sediment mineralogy, organic matter content, and mass nutrient content (nutrient mass per sediment mass) since the sediment matrix remained unchanged. Nutrient density (nutrient mass per sediment volume) did change, however, increasing proportionately with increasing sediment density.

## Macrophyte Nutrition

19. Relationships between shoot nutrient concentrations and macrophyte growth were generally very poor (Figure 6). Only N, P, and to a lesser extent K and Fe concentrations were associated with growth. Ranges in concentrations of most nutrients differed only moderately between species. Exceptions included P and Na, which varied respectively over ca. threefold and tenfold greater ranges in *Myriophyllum* than in *Hydrilla*. For most nutrients greatest variability in concentration occurred under conditions of least growth. Except for a single value of P in *Hydrilla*, nutrient concentrations exceeded critical values (i.e., growth-limiting concentrations) established for

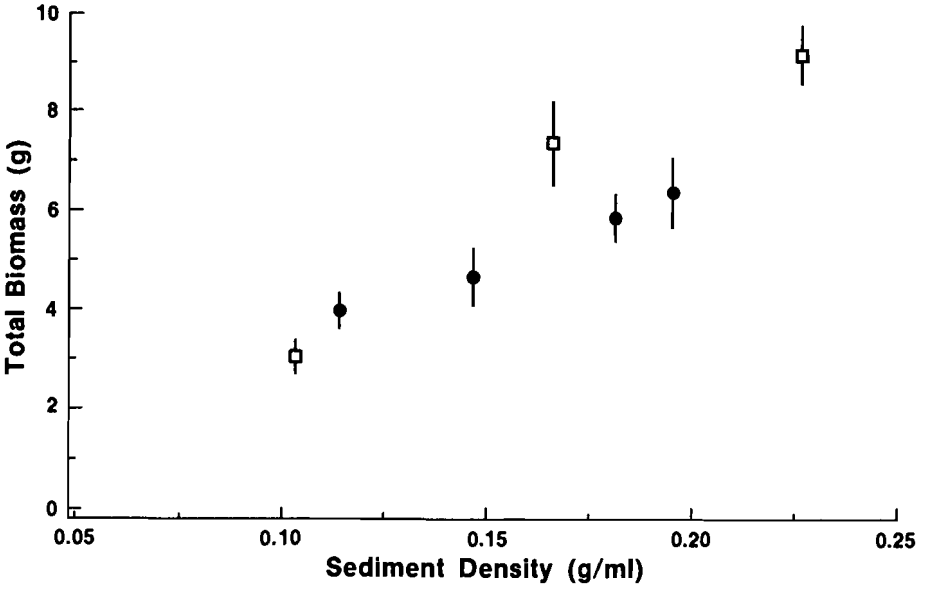


Figure 5. Relationship between growth as total dry weight biomass of *Hydrilla* and the density of amended organic sediment. Amendments included additions of fine-textured inorganic sediment (open squares) and centrifugation (closed circles). Values of biomass are means (n = 4) ± one standard deviation. Variation in sediment density among replicates (n = 2) was negligible

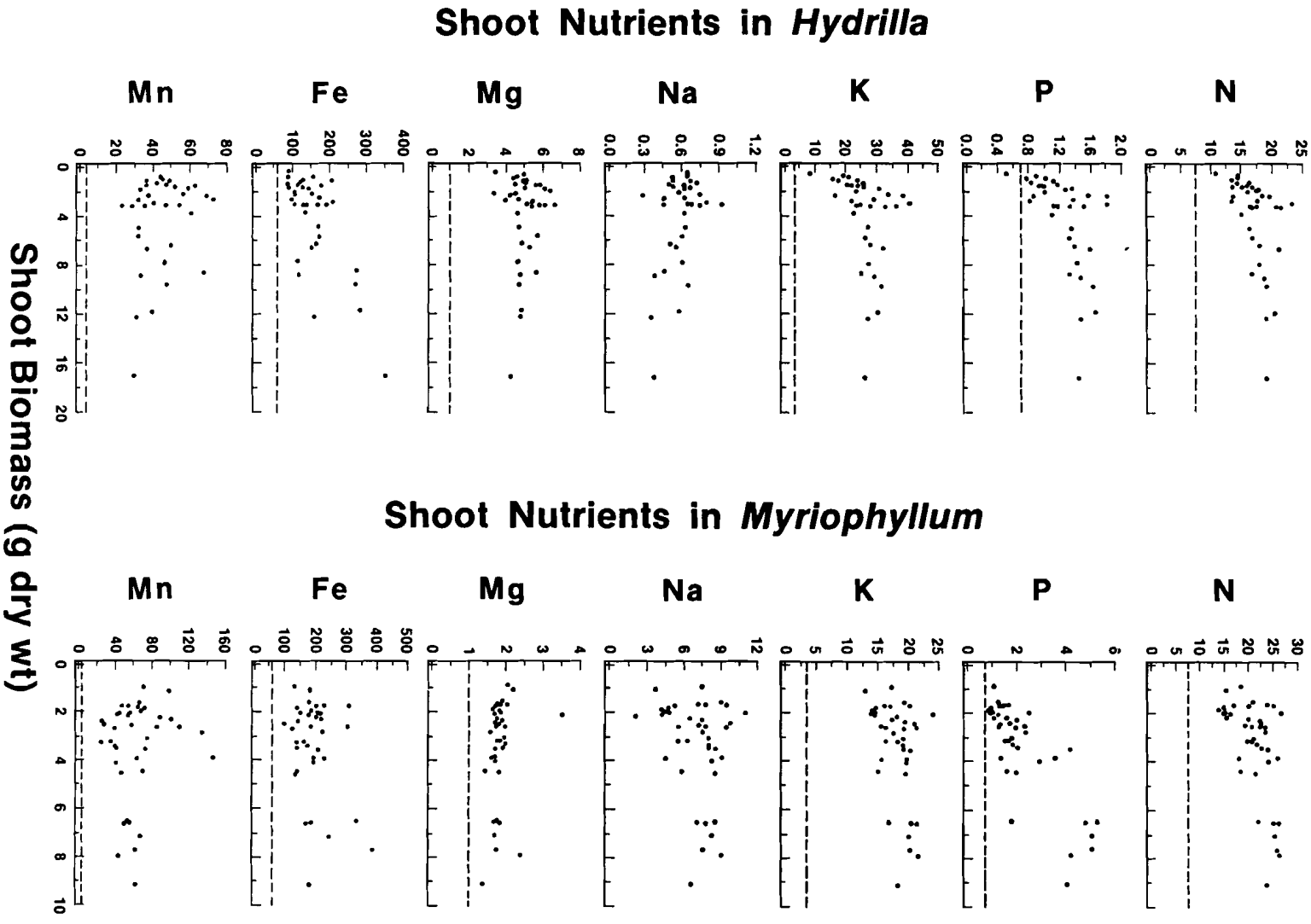


Figure 6. Relationships between nutrient concentrations and growth (shoot biomass) of *Hydrilla* and *Myriophyllum*. Nutrient concentrations (µg/g for Fe and Mn and mg/g for other nutrients) are averages (n = 2). Dashed horizontal lines represent critical concentrations, i.e., growth-limiting values (see text). Critical Na concentration is unknown

*Myriophyllum spicatum* and *Elodea occidentalis* (Pursh) St. John (Gerloff 1975).

20. Nutrient accumulation coefficients (Table 3) represent growth-weighted averages of shoot nutrient concentrations from regression analyses, and thus approximately mirror respective concentration ranges in Figure 6. These did not vary appreciably between species except for P, Na, and Mg. Whereas accumulation in plant shoots of all nutrients was essentially unrelated to shoot nutrient concentrations, accumulation was highly correlated with growth (Table 3). This reflects the greater responsiveness of growth than tissue nutrient concentrations to sediment conditions. Identical results were obtained from analyses of nutrient accumulation in sediment addition and centrifugation experiments.

21. The magnitude (r value) and statistical significance of correlations between nutrients in macrophyte shoots and in sediments varied appreciably, depending on the form of shoot nutrient data (concentration or accumulation), and the type (interstitial water or total), and basis (mass or volume) of sediment nutrient data considered (Table 4). Relationships with shoot nutrient accumulation were generally better than those with shoot nutrient concentration. However, with few exceptions (notably Fe and Mn) shoot nutrient concentration and accumulation were rather poorly related to nutrient concentration in the interstitial water. Correlations were improved by considering nutrients in the total sediment, particularly on the basis of volume. Accumulation of all nutrients with the exception of N (a component of organic matter) was highly correlated with respective sediment nutrient concentrations expressed on the basis of volume (as sediment nutrient densities). Owing to the close relationship between macrophyte growth and nutrient accumulation (noted above), growth as well was highly correlated with sediment nutrient densities (Table 5), indicating close connections among growth, nutrition, and sediment density in this investigation.

22. In order to examine directly the possibility that sediment nutrient availability affected macrophyte growth, a series of experiments involving additions of P and Fe to organic sediments was conducted. These elements were selected for addition because of their possibly reduced availability in organic sediments and their absence from solution in this particular investigation. Six organic sediments were obtained for experimental purposes from separate collections over a 2-year period at or near sites of original collection in lakes Buckhorn, Chemung, Chenango, and Seminole. Phosphorus and Fe

were added to selected sediments separately and in combination as $CaHPO_4$ at 0.1 g/ℓ wet sediment and as $Fe_2O_3$ at 5.0 g/ℓ wet sediment, respectively. Added P approximated tenfold that, which as the only source, would be required to sustain 10 g of *Hydrilla* growth. Added Fe was approximately equivalent to 20 percent of that in Lake Washington sediment (WASH-1). In these experiments neither texture, sediment organic matter content, nor sediment density were affected by manipulations.

23. *Hydrilla* did not respond to the addition of Fe alone, and responded to the addition of P alone on only one of four sediments (Table 6). The growth of this species increased significantly, however, on sediments amended by P in combination with Fe. Significant increases in nutrient accumulation were coupled with growth increases, but occurred also in response to the addition of P alone with no increase in growth on ORG-2 sediment. Additions of P alone generally promoted increased accumulation of multiple nutrients, reflecting increased shoot nutrient concentrations. In contrast, addition of Fe alone resulted in increased Fe accumulation (only on ORG-6 sediment), but had no effect on the accumulation of other nutrients. Where growth was stimulated by nutrient additions, it can be inferred that accumulation of added nutrients resulted in growth increases.

24. In a related experiment the effects on *Hydrilla* growth of N in solution (a characteristic of all previous designs in this investigation) was examined with and without addition of combined P and Fe to ORG-6 sediment (as described above). Nitrogen in solution had no effect on *Hydrilla* growth on the unamended sediment, but significantly increased growth on the same sediment amended by P and Fe addition (Figure 7). Without N in solution, the combined addition of P and Fe had no effect on *Hydrilla* growth. From this it appears that growth responses to nutrient additions (Table 6) probably would not have occurred without N in solution.

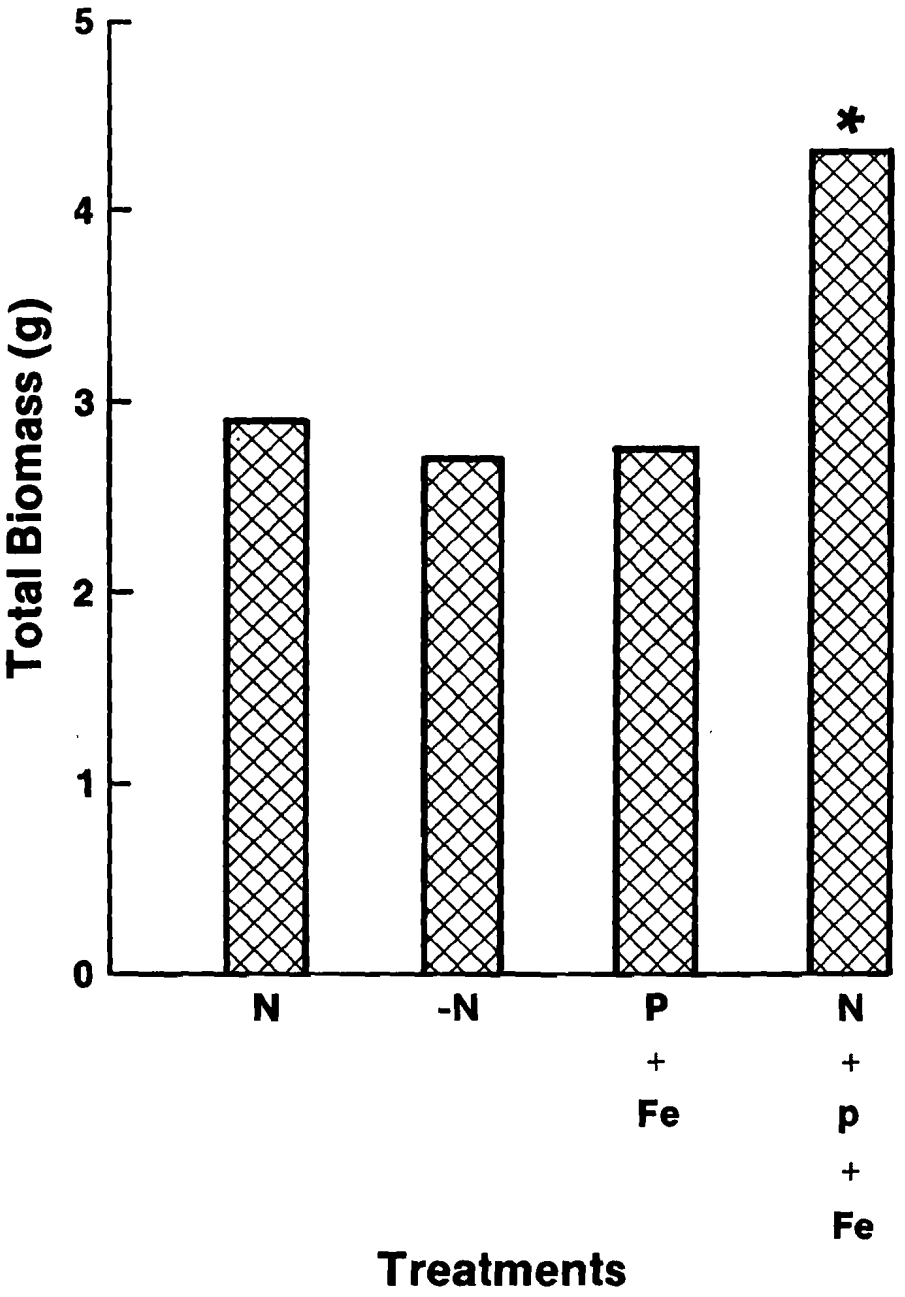


Figure 7. Effects of N in solution with and without additions of combined P and Fe (see text) to an organic sediment on the growth as total dry weight biomass of *Hydrilla*. Biomass values are means (n = 6). Nitrogen in solution without P and Fe addition to sediment was the experimental control. From Dunnett's test, growth response to treatments was statistically significant ($p < 0.05$) only in the N solution with addition of P and Fe to sediment

## PART IV: DISCUSSION

### Mechanisms of Growth Regulation

25. This investigation indicates that, under otherwise uniform environmental conditions, the growth of *Hydrilla* and *Myriophyllum* is relatively poor on low density, highly organic sediments and on high density sands. While numerous other environmental factors are clearly involved in affecting submersed macrophyte growth (e.g. Spence 1967, 1982; Wetzel 1983; Barko, Adams, and Clesceri 1986), sediment organic matter content and texture are important in affecting the growth potential of submersed aquatic vegetation on different sediments.

26. The influence of sediment composition on the productivity and distribution of aquatic macrophytes was originally recognized many years ago in the studies of Pond (1905), Pearsall (1920), and Misra (1938). As in the present investigation, these authors demonstrated a negative relationship between high sediment organic matter content and the growth of submersed macrophytes. Extremely sandy sediments have been generally recognized as supporting poor macrophyte growth. Numerous studies conducted during the last decade in a broad variety of aquatic systems have confirmed that sediment composition does exert a major influence on the growth of submersed aquatic vegetation (e.g. Moeller 1975, Schiemer and Prosser 1976, Unni 1977, Anderson 1978, Sand-Jensen and Søndergaard 1979, Kiørboe 1980, Danell and Sjoberg 1982, Wheeler and Giller 1982).

27. Diminished growth of submersed macrophytes on highly organic sediments has been difficult to explain because of the complexity of potentially interacting mechanisms. Growth inhibition by phytotoxins under anaerobic conditions (Armstrong 1975, Yoshida 1975, Drew and Lynch 1980) represents one possible mechanism. Additionally, root metabolism may be affected by inadequate oxygen supply (Armstrong 1978, Crawford 1982). Another possibility is nutrient limitation due to nutrient complexation with organic matter (Wali, Gruendling, and Blinn 1972; Jackson and Schindler 1975; Sikora and Keeney 1983).

28. It was earlier postulated that inhibitory organic compounds associated with high concentrations of dissolved organic carbon in the interstitial water of sediments might suppress macrophyte growth (Barko and Smart 1983),

but no evidence for this was found here. Some degree of protection from potential phytotoxins on the part of certain submersed macrophyte species may be provided by oxygen release from roots (Tessenow and Baines 1978; Carpenter, Elser, and Olson 1983; Penhale and Wetzel 1983). Thus, growth inhibition by products of anaerobic decomposition in organic sediments (e.g. Dooris and Martin 1980) is perhaps less common than earlier envisioned.

29. Combined results of experiments involving specific nutrient additions (Table 6, Figure 7) indicate convincingly that diminished growth on organic sediments in this investigation was caused in large part by a general (i.e., multiple) nutrient inadequacy. Diminished growth on sands, owing to their inherently infertile nature, can probably also be attributed to nutritional causes (Appendices B and C; see also Sand-Jensen and Søndergaard 1979, Kiørboe 1980). Indeed, the increased growth of *Hydrilla* achieved on sand as well as on organic sediment by addition of fine-textured inorganic sediment (Figure 4) can be viewed as a response to multiple nutrient enrichment. Results of the few nutrient enrichment studies conducted to date with submersed aquatic vegetation, both fresh water and marine, appear to support this contention that multiple nutrients are involved in growth limitation on unfavorable sediments (Moeller 1983; Roberts, Orth, and Moore 1984 and literature cited therein).

30. Whereas it can perhaps be argued that nutrient limitation in the present investigation was a product of study design (i.e., due to exclusion of P and Fe from solution), it is our conviction based on a substantial body of evidence (reviewed in Smart and Barko 1985) that these elements, and in addition N, are normally acquired by rooted aquatic vegetation directly from sediments. Nutrients can be absorbed by shoots as well as by roots (Denny 1972, 1980; Waisel, Agami, and Shapira 1982; Barko 1982). However, shoot uptake is unlikely to contribute significantly to macrophyte N, P, and Fe nutrition, due to the normally much greater availability of these nutrients in sediments than in the open water of aquatic systems. In reality, aqueous nutrient concentrations far below those required for effective uptake by shoots (Bole and Allan 1978; Waisel, Agami, and Shapira 1982) can be expected to stimulate the growth of attached algae, phytoplankton, and other microorganisms, causing severe suppression of submersed macrophyte growth due to the decreased availability of light, among other possible factors (e.g. Jupp and Spence 1977; Phillips,

Eminson and Moss 1978; Sand-Jensen and Søndergaard 1981; Sand-Jensen and Borum 1984; Twilley et al. 1985).

31. Sediment density or factors related to it clearly affected macrophyte nutrition and growth in the present investigation, and in this regard we postulate that density regulated the nutrient uptake and consequently macrophyte growth by influencing nutrient diffusion distances. In reviewing the subject of nutrient acquisition by higher terrestrial plants (Nye and Tinker 1977, Chapin 1980, Clarkson and Hanson 1980), it is apparent that diffusion to roots is usually the rate-limiting step in nutrient uptake. Structural and functional similarities between roots of aquatic plants and those of terrestrial plants (Sculthorpe 1967, Bristow 1975) suggest that the same principle of rate limitation applies to aquatic vegetation. The implication here is that nutrient uptake on low density, high porosity organic sediments was limited by long diffusion distances. Indeed, increased density, with presumably decreased diffusion distances, resulted in the enhanced growth of *Hydrilla* on centrifuged organic sediment (Figure 5).

32. Sediment density increased with increasing sand, but with a concomitant reduction in nutrient content. Macrophyte growth on sands was presumably diminished here due to low nutrient availability. Sandy sediments are typically low in organic matter, thus accounting for the disparity between macrophyte growth on "sands" and fine-textured sediments of low organic matter content (Figure 1). Limited rates of nutrient diffusion and exchange in coarse-textured sediments may, in addition to low nutrient status, contribute to their poor ability to support the growth of submersed macrophytes.

## Nutritional Considerations

33. In contrast with results from nutrient enrichment experiments, concentrations of nutrients in shoots (Figure 6) indicated essentially no limitation of macrophyte growth by nutrients, which we consider to be particularly misleading. The utility of tissue nutrient analysis, as a diagnostic technique (Gerloff and Krombholz 1966, Gerloff 1975) in evaluating macrophyte nutrition, is unfortunately hampered severely by its reliance on very limited and somewhat variable (cf. Bates 1971) growth-limiting criteria (i.e., critical nutrient concentrations). Another serious drawback is the implicit assumption of limitation by a single element. In experimental systems where a

single nutrient is clearly deficient and its critical concentration is precisely known, results from tissue nutrient analysis can be instructive (e.g. Barko 1982). However, in systems where a variety of nutrients potentially affect macrophyte growth, these analyses can be relied upon only to provide information on the seasonal periodicity of nutrient uptake (cf. Moeller 1978, Carpenter and Adams 1977, Kimball and Baker 1982).

34. Macrophyte nutrient accumulation and growth were closely coupled in this investigation, which is typical in higher plants (Clarkson and Hanson 1980) and evidenced routinely in seasonal evaluations of submersed macrophyte growth and nutrition in a variety of aquatic environments (e.g., Moeller 1978, Carpenter and Adams 1977, Peverly 1985). From results of enrichment experiments (Table 6, Figures 4 and 7) in combination with data on nutrient accumulation (Table 3 and unpublished data), it is suggested that growth was governed by the availability in sediments of P and Fe, and that the accumulation of other nutrients including N, provided in solution and presumed to be nonlimiting here, reflected demand for nutrients created by growth.

35. Relationships among macrophyte growth, nutrient accumulation, and nutrient concentrations either in the interstitial water or the total sediment (on a mass basis) were relatively poor. Nutrients in the sediment interstitial water represent a readily available pool, but probably constitute only a small fraction of total sediment nutrients available to rooted macrophytes. Attempts at relating the growth and nutrition of submersed macrophytes to total or extractable sediment nutrients (on a mass basis) have been generally unsuccessful (e.g., Kern Hansen and Dawson 1978, Kulshreshtha and Gopal 1982, Lee and Stewart 1983), and identical difficulties have been encountered in studies of salt marsh vegetation as well (e.g., Nixon and Oviatt 1973; Broome, Woodhouse, and Seneca 1975; DeLaune, Buresh, and Patrick 1979).

36. Assuming that the nutrition of rooted aquatic macrophytes is more responsive to sediment volume (affected by density) than to sediment mass, it has been suggested that expression of sediment nutrient concentrations on a volume basis (as nutrient densities) may be more meaningful than as more commonly expressed on a mass basis (DeLaune, Buresh, and Patrick 1979; Gosselink, Hatton, and Hopkinson 1984 and literature cited therein). Results of the present investigation in combination with the above indicate that expression of sediment nutrients as nutrient densities may be preferable in aquatic systems, where in contrast to terrestrial systems, sediment organic matter content, and

consequently sediment density, are highly variable. A singularly important advantage to expressing sediment nutrient concentrations as nutrient densities is that it integrates the influences of sand (high density, low nutrient content) and organic matter (low density, high nutrient content) on nutrient availability.

## Sediment as a Factor in Vegetational Change

37. *Hydrilla* appears to be more sensitive than *Myriophyllum* to sediment composition (Figure 1). Root-to-shoot ratios in both species increased with decreasing sediment fertility, as has been noted in other submersed macrophyte species as well (e.g. Denny 1972, Anderson 1978, Sand-Jensen and Søndergaard 1979, Aioi 1980). However, in *Hydrilla* the range in this ratio was about half that in *Myriophyllum*. A high ratio of root-to-shoot biomass is characteristically associated with plants growing in infertile environments (Aung 1974, Chapin 1980), and in terrestrial systems has been recognized as a strategy for maximizing the volume of soil occupied by root surfaces (Clarkson and Hanson 1980). Accordingly, the greater ability of some aquatic macrophyte species to allocate proportionately more growth into root formation on unfavorable sediments may provide a competitive advantage.

38. Submersed macrophytes in general appear to be replaced in lakes by nutritionally more conservative floating-leaved and emergent life forms with typically greater root-to-shoot biomass ratios (Westlake 1963, 1965) as sediment organic matter accumulates (Walker 1972; Wetzel 1979; Carpenter 1981, 1983). This pattern, which is apparently reversible by wave action or inorganic sedimentation (Pearsall 1920), may reflect in part the lesser tolerance of submersed compared with emergent macrophytes to unfavorable nutritional conditions. In nature, variations in the ability of different macrophyte life forms to cope with infertility or other factors associated with unfavorable sediment composition may influence the species composition and successional development of aquatic macrophyte communities.

39. The pattern of explosive initial growth followed by precipitously declining abundance, which frequently characterizes the invasion of lacustrine systems by adventive species (Carpenter 1980), suggests a particularly high degree of sensitivity on the part of these submersed macrophytes to environmental change. Major declines in rooted submersed aquatic vegetation have

been reported worldwide (e.g. Sculthorpe 1967, Bayley et al. 1978, Carpenter 1980, Orth and Moore 1983), but none have been adequately explained. Possible contributing factors include shading by phytoplankton and/or epiphytes (Jupp and Spence 1977; Phillips, Eminson, and Moss 1978; Sand-Jensen and Søndergaard 1981, Sand-Jensen and Borum 1984), combined effects of eutrophication (Moss 1983), reproductive failure (Twilley et al. 1985), allelopathy (Szczepanski 1977), and disease (Bayley et al. 1978). Any of these factors, alone or in combination, may promote submersed macrophyte declines. In this connection, it is proposed that unfavorable sediment composition, as it directly affects macrophyte nutrition, may also be a contributory factor.

40. We are aware of one documented occurrence of a decline in rooted submersed macrophytes following a major loading of organic matter due to watershed disturbance (Kight 1980, cf. Barko 1982). Conversely, the growth of submersed macrophytes on organic sediments may be stimulated by additions of inorganic sediment (Figure 4). Sediment composition may be modified by aquatic plants themselves directly by sediment nutrient uptake (e.g. Wali, Gruendling, and Blinn 1972; Prentki 1979, Barko and Smart 1980) and contributions of their own remains to the sediment (Walker 1972; Wetzel 1979; Carpenter 1981, 1983), and indirectly by collecting externally loaded materials (Mickle and Wetzel 1978a, b, 1979, Patterson and Brown 1979).

## PART V: CONCLUSIONS

41. The growth of submersed macrophytes is relatively poor on both highly organic sediments and sands compared with that on fine-textured inorganic sediments. Poor growth on sands is related to high sediment density, and on organic sediments to low sediment density. Mechanisms of growth regulation on sand and organic sediments are similar, both involving nutrition. High concentrations of organic matter in sediments affect negatively the growth of submersed macrophytes, by reducing sediment density and the associated availability of essential nutrients (notably N, P, and Fe). These elements are likewise low in available concentrations in sandy sediments.

42. Sediment composition in freshwater systems varies over a broad range, reflecting differences in climate, basin morphology, basin age, and vegetative characteristics of the watershed. Whereas sediment composition is an intrinsic component of the regional environment, it is potentially amenable to manipulation. Various sediment covers, including sand, gravel, and plastic liners, have been used in attempts to control the production of submersed macrophytes by altering sediment texture and reducing sediment nutrient uptake. Alternatively, dredging has been employed to both remove nutrient-rich sediments and to expose nutrient-poor underlying substrata, e.g., sand and gravel. Considered collectively, such efforts have indicated reductions in macrophyte productivity, and, in nearly all cases, dramatic shifts in the species composition of submersed macrophyte communities.

43. In view of major findings of this investigation, it is suggested that watershed disturbances, direct mechanical disturbances of bottom sediments, or autogenic processes affecting the inorganic/organic composition of sediments (and thus, sediment density and fertility) may contribute fundamentally to vegetational changes in aquatic systems. Better information on these changes will increasingly allow greater flexibility in managing submersed aquatic vegetation.

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Table 1

Identification and Location of Lakes from Which Bottom Sediments Were Obtained

| Lake* | Designation** | Location | Sites† |
|---|---|---|---|
| Deer Point | DRPT | Florida, USA | 4 |
| Kerr | KERR | Florida, USA | 2 |
| Rodman | RDMN | Florida, USA | 2 |
| Okeechobee | OKBE | Florida, USA | 2 |
| Seminole | SEML | Georgia, USA | 5 |
| Parr Pond | PARR | South Carolina, USA | 2 |
| Brown's | BRNL | Mississippi, USA | 2 |
| Openwood | OPEN | Mississippi, USA | 1 |
| Farm Pond | FARM | Mississippi, USA | 1 |
| Chenango | CHEN | New York, USA | 2 |
| Duck | DUCK | Michigan, USA | 2 |
| Wintergreen | WINT | Michigan, USA | 2 |
| Chemung | CHEM | Ontario, Canada | 2 |
| Buckhorn | BUCK | Ontario, Canada | 2 |
| Mendota | MEND | Wisconsin, USA | 1 |
| Wingra | WING | Wisconsin, USA | 4 |
| Washington | WASH | Washington, USA | 4 |

* The term "lake" is used in a general context. Sampled lakes included natural water bodies and reservoirs.

** Designations are abbreviated lake names used extensively in the text.

† The "Sites" column is the number of sediment sampling sites in each lake.

Table 2

Physical and Chemical Characteristics of Selected Lake Sediments*

| Characteristic | Min. | Max. | Mean |
|---|---|---|---|
| Total sediment | | | |
| Texture, % | | | |
| Sand | 2 | 95 | 40 |
| Silt | 1 | 77 | 44 |
| Clay | 3 | 65 | 17 |
| Density, g/ml | 0.07 | 1.29 | 0.46 |
| Moisture, % | 27 | 93 | 67 |
| Organic matter, % | | | |
| Total | 2 | 63 | 24 |
| Humic matter (fulvic + humic) | 0.1 | 21.4 | 5.9 |
| Nonhumic matter | 1.2 | 49.2 | 18.4 |
| Organic carbon (TOC) | 0.5 | 34.0 | 12.1 |
| Nutrients, mg/g | | | |
| Inorganic carbon (TIC) | 1.0 | 82.0 | 13.8 |
| Total Kjeldahl nitrogen (TKN) | 0.3 | 24.1 | 7.8 |
| Phosphorus (P) | 0.2 | 4.9 | 1.8 |
| Sodium (Na) | 0.05 | 1.53 | 0.36 |
| Potassium (K) | 0.04 | 6.36 | 1.58 |
| Calcium (Ca) | 0.1 | 331 | 44.9 |
| Magnesium (Mg) | 0.0 | 27.1 | 3.8 |
| Iron (Fe) | 1.0 | 49.8 | 16.7 |
| Manganese (Mn) | 0.0 | 1.43 | 0.36 |
| Interstitial water | | | |
| Conductivity, µS/cm | 171 | 1,618 | 679 |
| pH | 5.8 | 7.1 | 6.7 |
| Dissolved constituents, mg/ℓ | | | |
| Organic carbon (DOC) | 14 | 133 | 41 |
| Inorganic carbon (DIC) | 3 | 205 | 85 |
| Ammonium - N ($NH_4$-N) | 1.6 | 45.6 | 16.8 |
| Orthophosphate - P ($PO_4$-P) | 0.04 | 9.36 | 1.15 |
| Sodium (Na) | 1.7 | 89.0 | 16.7 |
| Potassium (K) | 0.7 | 22.0 | 6.0 |
| Calcium (Ca) | 12 | 133 | 77 |
| Magnesium (Mg) | 1.2 | 82.5 | 19.6 |
| Iron (Fe) | 0.0 | 71.0 | 11.1 |
| Manganese (Mn) | 0.0 | 22.5 | 2.9 |

* All units of mass are based on sediment dry weight except moisture, which is based on wet weight. Descriptive statistics were calculated from mean values (n = 2) for 40 sediments. Min. = minimum value. Max. = maximum value. Mean = average (n = 40).

Table 3

Correlations Between Nutrient Accumulation (Mass × Concentration) and Growth in *Hydrilla* and *Myriophyllum**

| Nutrient | Species | Accumulation Coefficient** | Relationship With Growth (r) |
|---|---|---|---|
| N | *Hydrilla* | 19.4 ± 0.3 | 0.99 |
| | *Myriophyllum* | 26.3 ± 0.7 | 0.98 |
| P | *Hydrilla* | 1.54 ± 0.03 | 0.99 |
| | *Myriophyllum* | 5.08 ± 0.33 | 0.93 |
| K | *Hydrilla* | 27.8 ± 0.8 | 0.98 |
| | *Myriophyllum* | 20.4 ± 0.6 | 0.98 |
| Na | *Hydrilla* | 0.42 ± 0.03 | 0.93 |
| | *Myriophyllum* | 8.03 ± 0.43 | 0.95 |
| Mg | *Hydrilla* | 4.57 ± 0.12 | 0.99 |
| | *Myriophyllum* | 1.64 ± 0.10 | 0.94 |
| Fe | *Hydrilla* | 0.28 ± 0.02 | 0.92 |
| | *Myriophyllum* | 0.30 ± 0.03 | 0.83 |
| Mn | *Hydrilla* | 0.04 ± 0.00 | 0.91 |
| | *Myriophyllum* | 0.05 ± 0.00 | 0.79 |

* Accumulation coefficients (mg/g dry weight) are slopes from linear regressions of shoot nutrient accumulation (mg) on shoot growth (g dry weight). Correlation coefficients (r) from regressions are significant at $p < 0.001$ ($n = 40$ sediments).

** Variance is provided as a standard error ($n = 40$).

Table 4

Correlations of Shoot Nutrient Concentration and Nutrient Accumulation (Mass × Concentration) in *Hydrilla* and *Myriophyllum* With Sediment Nutrient Concentration in the Interstitial Water (IW) and in the Total Sediment (Based on Mass and Volume).[a] Values are Correlation Coefficients (r).[b] n = 40 Sediments

| | | Concentration-Related Correlations | | | Accumulation-Related Correlations | | |
|---|---|---|---|---|---|---|---|
| | | | Total Nutrients | | | Total Nutrients | |
| Nutrient | Species | IW Nutrients | Mass Basis | Volume Basis | IW Nutrients | Mass Basis | Volume Basis |
| N | *Hydrilla* | 0.34* | -0.41* | 0.17 | 0.25 | -0.49* | -0.16 |
| | *Myriophyllum* | 0.25 | -0.59* | -0.10 | 0.29 | -0.54* | -0.22 |
| P | *Hydrilla* | 0.14 | 0.05 | 0.49* | 0.01 | -0.01 | 0.80* |
| | *Myriophyllum* | -0.04 | -0.03 | 0.91* | 0.03 | -0.03 | 0.91* |
| K | *Hydrilla* | 0.14 | -0.01 | 0.08 | 0.07 | 0.46* | 0.67* |
| | *Myriophyllum* | 0.18 | 0.31 | 0.42* | 0.24 | 0.55* | 0.76* |
| Na | *Hydrilla* | -0.19 | -0.37* | -0.46* | 0.20 | 0.35* | 0.67* |
| | *Myriophyllum* | 0.26 | 0.08 | 0.19 | 0.51* | 0.56* | 0.81* |
| Mg | *Hydrilla* | -0.26 | -0.20 | -0.07 | 0.25 | 0.45* | 0.61* |
| | *Myriophyllum* | 0.08 | 0.11 | 0.11 | 0.61* | 0.67* | 0.77* |
| Fe | *Hydrilla* | 0.42* | 0.35* | 0.51* | 0.49* | 0.45* | 0.67* |
| | *Myriophyllum* | 0.37* | 0.04 | 0.19 | 0.52* | 0.27 | 0.53* |
| Mn | *Hydrilla* | 0.15 | 0.33* | 0.05 | 0.44* | 0.32 | 0.71* |
| | *Myriophyllum* | 0.50* | 0.26 | 0.33* | 0.58* | 0.34* | 0.72* |

[a] Concentrations based on mass represent nutrient mass per sediment mass (mg/g). Those based on volume (nutrient densities) represent nutrient mass per sediment volume (mg/ml), and were calculated as products of concentration and sediment density.

[b] Significant correlations ($p < 0.05$) are identified with an asterisk.

Table 5

Correlations Between Macrophyte Growth and Sediment Nutrient Densities (Concentrations/Sediment Volume). Values are Correlation Coefficients (r).[a] n = 40 Sediments

| Species | Correlations with Sediment Nutrient Density | | | | | | |
|---|---|---|---|---|---|---|---|
| | N | P | K | Na | Mg | Fe | Mn |
| *Hydrilla* | -0.20 | 0.79* | 0.67* | 0.84* | 0.60* | 0.80* | 0.70* |
| *Myriophyllum* | -0.23 | 0.78* | 0.72* | 0.85* | 0.62* | 0.78* | 0.63* |

[a] Significant correlations ($p < 0.001$) are identified with an asterisk.

Table 6

Effects of Specific Nutrient Additions to Organic Sediments (>20% Organic Matter) on Growth as Total Dry Weight Biomass (n = 4 to 6) and Shoot Nutrient Accumulation (n = 2 to 3) in Hydrilla

| Sediment | Treatment Addition | Growth Response,[a] g dry mass | | Shoot Nutrient Accumulation,[a] mg | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Control | | | | Treatment | | | |
| | | Control | Treatment | N | P | K | Fe | N | P | K | Fe |
| ORG-1 | P | 1.59 | 1.64 | 23.5 | 1.8 | 28.4 | -- | 35.5 | 5.2 | 61.9 | -- |
| ORG-2 | P | 2.83 | 3.13 | 46.1 | 3.3 | 66.3 | -- | 66.1* | 7.0* | 103.3* | -- |
| ORG-3 | P | 3.11 | 3.29 | 54.1 | 5.2 | 67.0 | -- | 69.7 | 8.5 | 116.9 | -- |
| ORG-4 | P | 1.37 | 2.48* | 23.7 | 1.4 | 27.1 | -- | 64.1* | 7.5* | 102.3* | -- |
| ORG-5 | Fe | 2.62 | 2.23 | 36.4 | 1.8 | 40.1 | 3.2 | 27.6 | 1.9 | 42.2 | 3.4 |
| ORG-6 | Fe | 5.21 | 5.14 | 97.3 | 7.6 | 152.8 | 7.4 | 94.7 | 7.9 | 135.8 | 22.2* |
| ORG-5 | P + Fe | 2.62 | 6.23* | 36.4 | 1.8 | 40.1 | 3.2 | 114.7* | 10.6* | 170.6* | 10.0* |
| ORG-6 | P + Fe | 5.21 | 7.86* | 97.3 | 7.6 | 152.8 | 7.4 | 151.5* | 12.4* | 193.7* | 17.1* |

[a] Values are means. Treatment values designated with an asterisk differ significantly ($p < 0.05$) according to Student's T-Test from control value counterparts.

APPENDIX A:

PHYSICAL CHARACTERISTICS AND ORGANIC MATTER COMPOSITION OF 40 DIFFERENT SEDIMENTS*

| Lake | Sediment | Texture | | | Moisture | Density | Organic Matter | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Sand | Silt | Clay | | | Total | Fulvic | Humic | Nonhumic** |
| BRNL | 1 | 5 | 77 | 18 | 40 | 0.98 | 5.2 | 0.0 | 0.0 | 5.2 |
| | 2 | 5 | 77 | 18 | 48 | 0.74 | 6.8 | 0.2 | 0.1 | 6.5 |
| BUCK | 1 | 25 | 65 | 10 | 90 | 0.11 | 45.7 | 8.1 | 6.2 | 31.4 |
| | 2 | 27 | 53 | 20 | 93 | 0.07 | 55.5 | 7.6 | 7.6 | 40.3 |
| CHEM | 1 | 20 | 63 | 17 | 92 | 0.08 | 53.0 | 6.3 | 3.6 | 43.1 |
| | 2 | 25 | 65 | 10 | 90 | 0.11 | 63.4 | 9.6 | 4.6 | 49.2 |
| CHEN | 1 | 17 | 65 | 18 | 88 | 0.12 | 33.6 | 2.1 | 1.1 | 30.4 |
| | 2 | 20 | 68 | 12 | 87 | 0.13 | 39.1 | 3.4 | 1.8 | 33.9 |
| DRPT | 1 | 11 | 24 | 65 | 78 | 0.24 | 19.8 | 1.5 | 2.9 | 15.4 |
| | 2 | 20 | 50 | 30 | 91 | 0.09 | 45.7 | 7.4 | 6.5 | 31.8 |
| | 3 | 81 | 10 | 9 | 53 | 0.58 | 32.8 | 5.4 | 14.9 | 12.5 |
| | 4 | 86 | 5 | 9 | 46 | 0.74 | 19.1 | 4.6 | 12.0 | 2.5 |
| DUCK | 1 | 76 | 16 | 8 | 43 | 0.82 | 8.5 | 0.8 | 1.2 | 6.5 |
| | 2 | 27 | 51 | 22 | 93 | 0.07 | 53.4 | 4.2 | 2.7 | 46.5 |
| FARM | 1 | 10 | 75 | 15 | 41 | 0.82 | 7.5 | 0.9 | 1.0 | 5.6 |
| KERR | 1 | 71 | 10 | 19 | 75 | 0.30 | 18.3 | 0.9 | 1.5 | 15.9 |
| | 2 | 33 | 30 | 37 | 88 | 0.13 | 47.5 | 4.9 | 8.7 | 33.9 |
| MEND | 1 | 47 | 43 | 10 | 40 | 0.87 | 7.6 | 0.1 | 0.0 | 7.5 |
| OKBE | 1 | 94 | 1 | 5 | 32 | 1.06 | 1.9 | 0.2 | 0.2 | 1.5 |
| | 2 | 95 | 2 | 3 | 38 | 0.95 | 2.7 | 0.3 | 0.5 | 1.8 |
| OPEN | 1 | 2 | 68 | 30 | 49 | 0.75 | 6.0 | 0.2 | 0.1 | 5.8 |
| PARR | 1 | 90 | 7 | 3 | 27 | 1.28 | 2.1 | 0.3 | 0.6 | 1.2 |
| | 2 | 27 | 20 | 53 | 65 | 0.44 | 13.2 | 1.0 | 1.4 | 10.9 |
| RDMN | 1 | 57 | 24 | 19 | 73 | 0.31 | 27.6 | 4.8 | 5.2 | 17.6 |
| | 2 | 76 | 15 | 9 | 57 | 0.55 | 12.4 | 1.8 | 2.4 | 8.2 |
| SEML | 1 | 25 | 50 | 25 | 91 | 0.09 | 48.1 | 3.8 | 4.3 | 40.0 |
| | 2 | 85 | 12 | 3 | 38 | 0.91 | 5.6 | 0.8 | 1.0 | 3.9 |
| | 3 | 47 | 40 | 13 | 59 | 0.54 | 10.4 | 1.4 | 3.6 | 5.4 |
| | 4 | 77 | 15 | 8 | 28 | 1.25 | 2.2 | 0.1 | 0.1 | 1.9 |
| | 5 | 70 | 20 | 10 | 48 | 0.75 | 8.9 | 1.1 | 0.5 | 7.3 |
| WASH | 1 | 22 | 68 | 10 | 48 | 0.74 | 10.4 | 2.2 | 2.1 | 6.1 |
| | 2 | 30 | 45 | 25 | 91 | 0.10 | 57.0 | 9.5 | 8.6 | 38.9 |
| | 3 | 30 | 55 | 15 | 91 | 0.10 | 56.7 | 10.2 | 11.2 | 35.3 |
| | 4 | 61 | 29 | 10 | 55 | 0.51 | 8.6 | 0.6 | 0.4 | 7.5 |
| WING | 1 | 29 | 59 | 12 | 71 | 0.33 | 9.9 | 0.1 | 0.0 | 9.8 |
| | 2 | 11 | 76 | 13 | 84 | 0.17 | 18.0 | 0.5 | 0.3 | 17.3 |
| | 3 | 9 | 77 | 14 | 80 | 0.22 | 16.9 | 0.3 | 0.3 | 16.3 |
| | 4 | 9 | 75 | 16 | 83 | 0.19 | 17.9 | 0.2 | 0.2 | 17.2 |
| WINT | 1 | 25 | 56 | 19 | 93 | 0.07 | 52.8 | 4.4 | 4.3 | 44.1 |
| | 2 | 10 | 75 | 15 | 86 | 0.14 | 21.6 | 0.7 | 0.2 | 20.8 |

* Values for total organic matter, density, and moisture are averages (n = 2). Average coefficients of variation for replicated variables were less than 1%. All others are single observations. Units are mass percentages except for density (g/ml). Units of mass are based on sediment dry weight except for moisture, which is based on wet weight.

** Nonhumic matter was computed as total organic matter - (humic + fulvic) matter.

APPENDIX B:

INTERSTITIAL WATER CHEMISTRY FOR 40 DIFFERENT SEDIMENTS*

| Lake | Sediment | Conductivity | pH | DOC | DIC | $NH_4$-N | $PO_4$-P | Na | K | Ca | Mg | Fe | Mn |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BRNL | 1 | 0.95 | 7.0 | 33 | 73 | 5.1 | 0.8 | 81.0 | 3.3 | 78 | 31.0 | 20.0 | 3.9 |
| | 2 | 1.34 | 6.8 | 40 | 185 | 19.6 | 0.6 | 71.0 | 8.2 | 124 | 47.0 | 51.5 | 14.5 |
| BUCK | 1 | 0.36 | 6.6 | 25 | 50 | 6.1 | 0.7 | 3.9 | 5.2 | 63 | 4.5 | 1.3 | 0.8 |
| | 2 | 0.33 | 6.6 | 23 | 43 | 6.7 | 0.6 | 3.8 | 5.5 | 55 | 4.1 | 0.2 | 0.4 |
| CHEM | 1 | 0.86 | 6.8 | 33 | 123 | 45.6 | 9.4 | 5.3 | 4.8 | 120 | 10.0 | 0.1 | 1.4 |
| | 2 | 0.62 | 6.9 | 18 | 90 | 12.6 | 0.2 | 6.1 | 4.7 | 118 | 8.6 | 0.1 | 0.5 |
| CHEN | 1 | 0.71 | 6.8 | 35 | 105 | 19.7 | 0.7 | 4.0 | 5.1 | 124 | 10.0 | 0.6 | 1.1 |
| | 2 | 0.55 | 7.0 | 23 | 75 | 9.6 | 0.0 | 2.4 | 1.1 | 94 | 15.0 | 0.1 | 0.4 |
| DRPT | 1 | 0.45 | 7.0 | 23 | 58 | 3.5 | 0.1 | 8.4 | 2.1 | 70 | 12.0 | 12.5 | 0.2 |
| | 2 | 0.59 | 6.8 | 25 | 90 | 12.6 | 0.0 | 7.4 | 3.6 | 102 | 9.6 | 5.5 | 0.7 |
| | 3 | 0.37 | 6.0 | 133 | 55 | 22.9 | 0.1 | 7.1 | 5.4 | 50 | 2.8 | 2.0 | 0.0 |
| | 4 | 0.30 | 5.9 | 118 | 45 | 15.9 | 0.1 | 6.6 | 3.2 | 43 | 2.6 | 1.9 | 0.0 |
| DUCK | 1 | 0.40 | 6.3 | 53 | 53 | 13.6 | 0.1 | 3.8 | 5.4 | 45 | 10.0 | 7.5 | 2.4 |
| | 2 | 0.31 | 6.8 | 15 | 50 | 6.9 | 0.3 | 2.8 | 3.6 | 37 | 10.5 | 5.8 | 1.9 |
| FARM | 1 | 1.07 | 6.5 | 83 | 180 | 16.9 | 1.5 | 5.8 | 14.0 | 118 | 53.0 | 70.0 | 11.5 |
| KERR | 1 | 0.41 | 5.8 | 23 | 3 | 1.6 | 0.1 | 17.0 | 1.1 | 42 | 14.0 | 2.7 | 0.3 |
| | 2 | 0.37 | 6.3 | 14 | 13 | 2.4 | 0.3 | 23.0 | 1.7 | 31 | 11.0 | 0.7 | 0.0 |
| MEND | 1 | 1.62 | 7.0 | 45 | 205 | 33.9 | 1.7 | 75.0 | 10.5 | 133 | 82.5 | 11.0 | 3.0 |
| OKBE | 1 | 1.47 | 7.1 | 68 | 170 | 36.5 | 2.8 | 89.0 | 20.0 | 131 | 59.5 | 0.1 | 0.1 |
| | 2 | 0.99 | 6.9 | 23 | 125 | 21.0 | 3.9 | 30.0 | 22.0 | 133 | 27.0 | 0.1 | 0.1 |
| OPEN | 1 | 0.35 | 6.8 | 22 | 49 | 3.5 | 0.3 | 1.7 | 7.3 | 33 | 10.0 | 23.0 | 4.2 |
| PARR | 1 | 0.98 | 6.9 | 110 | 90 | 44.7 | 0.1 | 2.7 | 2.0 | 12 | 1.5 | 18.0 | 5.4 |
| | 2 | 0.47 | 6.9 | 40 | 55 | 4.1 | 0.1 | 13.5 | 3.0 | 31 | 8.0 | 71.0 | 8.4 |
| RDMN | 1 | 0.64 | 6.8 | 40 | 80 | 9.0 | 1.2 | 12.5 | 3.7 | 110 | 13.5 | 0.1 | 0.1 |
| | 2 | 0.71 | 6.7 | 43 | 98 | 18.2 | 2.5 | 8.8 | 16.0 | 106 | 15.0 | 0.9 | 0.6 |
| SEML | 1 | 0.17 | 6.5 | 16 | 24 | 6.9 | 0.1 | 2.6 | 1.5 | 19 | 1.1 | 4.6 | 2.5 |
| | 2 | 0.58 | 6.8 | 38 | 78 | 27.8 | 0.1 | 4.0 | 10.0 | 69 | 3.4 | 22.5 | 13.5 |
| | 3 | 0.61 | 7.0 | 23 | 83 | 7.2 | 0.0 | 4.8 | 2.9 | 105 | 3.6 | 20.5 | 22.5 |
| | 4 | 0.91 | 6.9 | 130 | 50 | . | . | . | . | . | . | . | . |
| | 5 | 0.54 | 7.0 | 25 | 75 | 10.0 | 0.1 | 2.0 | 0.7 | 90 | 3.8 | 18.0 | 1.9 |
| WASH | 1 | 0.65 | 6.7 | 43 | 75 | 29.2 | 1.3 | 9.6 | 4.6 | 49 | 15.5 | 28.0 | 5.2 |
| | 2 | 0.18 | 6.5 | 30 | 13 | 5.9 | 1.5 | 7.1 | 1.7 | 14 | 4.2 | 1.7 | 0.2 |
| | 3 | 0.37 | 6.7 | 25 | 48 | 9.8 | 1.2 | 6.9 | 3.4 | 38 | 10.0 | 10.0 | 0.7 |
| | 4 | 0.68 | 6.5 | 35 | 98 | 37.5 | 2.3 | 8.2 | 8.0 | 33 | 15.0 | 19.0 | 2.7 |
| WING | 1 | 0.96 | 7.0 | 30 | 135 | 22.2 | 0.5 | 25.0 | 4.8 | 99 | 48.5 | 0.1 | 0.5 |
| | 2 | 0.98 | 6.9 | 33 | 130 | 25.6 | 1.8 | 24.0 | 3.7 | 110 | 40.0 | 1.9 | 0.4 |
| | 3 | 0.95 | 6.9 | 28 | 125 | 18.3 | 0.7 | 27.0 | 5.7 | 101 | 46.5 | 0.0 | 0.4 |
| | 4 | 0.92 | 7.0 | 30 | 120 | 20.3 | 1.5 | 24.0 | 3.7 | 100 | 43.5 | 0.0 | 0.5 |
| WINT | 1 | 0.83 | 7.0 | 30 | 115 | 25.0 | 3.8 | 6.9 | 13.5 | 96 | 31.0 | 0.0 | 0.3 |
| | 2 | 0.63 | 6.9 | 25 | 78 | 15.1 | 1.6 | 5.5 | 8.3 | 70 | 25.5 | 0.0 | 0.5 |

* Values are averages (n = 2). Average coefficients of variation (in %) were 1.6 for conductivity, 0.2 for pH, 8.6 for dissolved organic carbon (DOC), 6.9 for dissolved inorganic carbon (DIC), 2.2 for $NH_4$-N, 6.2 for $PO_4$-P, 1.4 for Na, 1.7 for K, 2.8 for Ca, 1.6 for Mg, 12.4 for Fe, and 7.5 for Mn. Units are mg/ℓ except for conductivity (mS/cm at 25°C) and pH.

APPENDIX C:

TOTAL SEDIMENT CHEMISTRY FOR 40 DIFFERENT SEDIMENTS*

| Lake | Sediment | Carbon** Inorg | Org | Total | TKN† | P | Na | K | Ca | Mg | Fe | Mn |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BRNL | 1 | 8 | 5 | 13 | 0.7 | 2.1 | 0.5 | 4.7 | 6.4 | 12.4 | 34.0 | 0.7 |
| | 2 | 8 | 13 | 21 | 1.5 | 2.1 | 1.2 | 4.2 | 8.6 | 13.3 | 33.2 | 0.7 |
| BUCK | 1 | 1 | 230 | 231 | 17.1 | 2.8 | 0.3 | 1.1 | 8.1 | 2.2 | 19.9 | 0.4 |
| | 2 | 1 | 290 | 291 | 20.4 | 3.2 | 0.3 | 1.9 | 7.9 | 2.9 | 25.1 | 0.4 |
| CHEM | 1 | 24 | 270 | 294 | 20.0 | 4.6 | 0.2 | 1.6 | 98.9 | 2.9 | 12.8 | 0.6 |
| | 2 | 19 | 340 | 359 | 23.8 | 2.9 | 0.2 | 1.2 | 81.7 | 2.5 | 11.1 | 0.4 |
| CHEN | 1 | 46 | 180 | 226 | 11.6 | 1.8 | 0.3 | 2.1 | 171.4 | 2.9 | 16.3 | 0.4 |
| | 2 | 26 | 210 | 236 | 12.8 | 2.3 | 0.2 | 2.9 | 102.4 | 3.3 | 16.5 | 0.2 |
| DRPT | 1 | 2 | -- | -- | 5.1 | 2.2 | 0.6 | 3.2 | 2.3 | 2.4 | 34.3 | 0.1 |
| | 2 | 1 | 230 | 231 | 12.8 | 3.4 | 0.2 | 1.2 | 3.8 | 1.2 | 15.5 | 0.2 |
| | 3 | 1 | 215 | 216 | 7.2 | 1.3 | 0.1 | 0.1 | 2.4 | 0.2 | 1.9 | 0.0 |
| | 4 | 1 | 93 | 94 | 3.7 | 0.7 | 0.1 | 0.1 | 0.5 | 0.1 | 1.0 | 0.0 |
| DUCK | 1 | 1 | 42 | 43 | 2.8 | 0.7 | 0.1 | 1.0 | 0.3 | 1.2 | 7.0 | 0.2 |
| | 2 | 1 | 280 | 281 | 20.5 | 3.2 | 0.2 | 2.6 | 0.9 | 2.6 | 23.3 | 0.7 |
| FARM | 1 | 1 | 30 | 31 | 2.5 | 1.7 | 0.3 | 3.7 | 0.2 | 2.1 | 22.7 | 0.3 |
| KERR | 1 | 1 | 100 | 101 | 6.2 | 0.9 | 0.2 | 1.1 | 0.2 | 0.9 | 14.1 | 0.1 |
| | 2 | 1 | 260 | 261 | 12.8 | 2.0 | 0.4 | 1.6 | 0.7 | 2.0 | 24.7 | 0.1 |
| MEND | 1 | 25 | 26 | 51 | 1.9 | 1.6 | 0.5 | 2.0 | 52.0 | 27.1 | 16.0 | 0.4 |
| OKBE | 1 | 1 | 8 | 9 | 1.0 | 0.4 | 0.2 | 0.3 | 0.9 | 0.3 | 2.5 | 0.0 |
| | 2 | 1 | 13 | 14 | 1.4 | 0.3 | 0.2 | 0.3 | 0.7 | 0.2 | 2.6 | 0.0 |
| OPEN | 1 | 1 | 5 | 6 | 1.3 | 2.2 | 0.5 | 6.4 | 0.1 | 4.0 | 49.8 | 0.5 |
| PARR | 1 | 1 | 11 | 12 | 0.4 | 0.3 | 0.1 | 0.1 | 0.0 | 0.0 | 5.4 | 0.2 |
| | 2 | 1 | 37 | 38 | 2.7 | 2.4 | 0.2 | 2.2 | 0.2 | 0.4 | 45.8 | 0.5 |
| RDMN | 1 | 2 | 110 | 112 | 7.5 | 1.7 | 0.2 | 0.4 | 10.5 | 1.6 | 15.6 | 0.1 |
| | 2 | 1 | 66 | 67 | 4.1 | 0.9 | 0.1 | 0.4 | 0.6 | 0.4 | 6.6 | 0.1 |
| SEML | 1 | 1 | 240 | 241 | 14.7 | 1.8 | 0.2 | 0.8 | 1.5 | 0.6 | 16.9 | 1.1 |
| | 2 | 1 | 31 | 32 | 2.1 | 0.2 | 0.1 | 0.0 | 0.0 | 0.0 | 3.4 | 0.2 |
| | 3 | 1 | 56 | 57 | 2.7 | 0.9 | 0.1 | 0.3 | 0.8 | 0.3 | 13.9 | 1.4 |
| | 4 | 1 | 6 | 7 | 0.3 | 0.4 | 0.2 | 0.9 | 0.0 | 0.3 | 12.5 | 0.3 |
| | 5 | 1 | 42 | 43 | 2.1 | 0.4 | 0.1 | 0.4 | 0.3 | 0.2 | 12.6 | 0.2 |
| WASH | 1 | 1 | 64 | 65 | 2.4 | 1.8 | 1.2 | 2.0 | 1.8 | 6.2 | 33.7 | 0.6 |
| | 2 | 2 | 270 | 272 | 14.5 | 1.4 | 0.5 | 1.0 | 3.1 | 3.2 | 14.7 | 0.3 |
| | 3 | 1 | 270 | 271 | 10.2 | 1.7 | 0.5 | 1.0 | 5.3 | 3.1 | 32.3 | 0.3 |
| | 4 | 1 | 40 | 41 | 3.1 | 1.1 | 1.2 | 1.4 | 2.1 | 3.3 | 20.4 | 0.3 |
| WING | 1 | 82 | 35 | 117 | 4.0 | 1.2 | 0.3 | 1.0 | 331.4 | 8.9 | 5.3 | 0.5 |
| | 2 | 66 | 80 | 146 | 7.2 | 2.2 | 0.3 | 1.6 | 248.4 | 10.2 | 7.5 | 0.5 |
| | 3 | 73 | 77 | 150 | 7.1 | 1.7 | 0.2 | 1.5 | 210.3 | 7.9 | 7.3 | 0.4 |
| | 4 | 62 | 73 | 135 | 7.5 | 1.8 | 1.5 | 1.8 | 172.3 | 7.9 | 8.8 | 0.4 |
| WINT | 1 | 7 | 270 | 277 | 21.9 | 4.2 | 0.2 | 2.0 | 24.8 | 3.7 | 13.9 | 0.2 |
| | 2 | 56 | 110 | 166 | 9.7 | 4.9 | 0.1 | 1.2 | 231.3 | 5.3 | 6.7 | 0.4 |

* Values are single observations. Units are mg/g sediment dry weight.

** Organic carbon was computed as the difference between total and inorganic carbon.

† TKN = total Kjeldahl nitrogen.