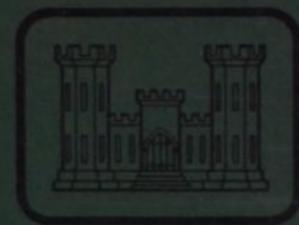


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PLANT-MEDIATED PHOSPHORUS MOBILIZATION FROM SEDIMENTS: POTENTIAL INFLUENCE ON FRESHWATER PHOSPHORUS CYCLING

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ABSTRACT (Continued)

exclusively from the sediments. Phosphorus absorption and translocation into shoots (i.e., mobilization) was substantial, and in some cases suggested a greater than 1000-fold turnover of interstitial water $\text{PO}_4\text{-P}$ over a 3-month period.

In reservoirs, or in localized portions of reservoirs (e.g., coves and embayments), that are shallow and subjected to relatively minor areal water loads, P mobilization by aquatic plants is likely to play an important role in P cycling, possibly enhancing algal productivity. Even in deep impoundments, there are frequently numerous shallow coves in which rooted plants may significantly affect localized nutrient conditions. The mobilization of sediment P by submersed plants represents an important aspect of the P cycle, and may affect the overall metabolism of lacustrine systems.

SUMMARY

The mobilization of sediment phosphorus (P) by three submersed freshwater plant species was investigated on five different reservoir sediments. The study was conducted under controlled environmental conditions in lucite columns that enabled the separation of sediment and plant roots from the overlying P-free "complete" nutrient solution. The species investigated (Egeria densa, Hydrilla verticillata, and Myriophyllum spicatum) had minor root systems (on a biomass basis), but were demonstrated to be fully capable of deriving their P nutrition exclusively from the sediments. Phosphorus absorption and translocation into shoots (i.e., mobilization) was substantial, and in some cases suggested a greater than 1000-fold turnover of interstitial water PO_4-P over a 3-month period. Sediment P mobilization, a function of both plant growth and tissue P concentration, differed considerably among plant species and sediments. Phosphorus release from the species investigated appears to be primarily dependent upon tissue decay rather than excretory processes. Since losses of biomass from submersed plants and subsequent tissue decay are continuous in aquatic systems, these plants potentially provide a persistent source of sediment derived P to other ecosystem components.

Nutrients (including P) sedimented in reservoirs represent a potentially vast source of supply to the overlying water. The mobilization of nutrients by submersed plants is a potentially important mechanism whereby sediment nutrients can be recycled. Algae in most aquatic systems, including reservoirs, appear to be limited by the supply of P. In these systems, additions of P through plant-mediated processes can result in increased rates of algal growth.

In reservoirs, or in localized portions of reservoirs (e.g., coves and embayments), that are shallow and subjected to relatively minor areal water loads, P mobilization by aquatic plants is likely to play an important role in P cycling, possibly enhancing algal productivity. Even in deep impoundments, there are frequently numerous shallow coves in which rooted plants may significantly affect local nutrient conditions.

PREFACE

Funding for the investigation was provided by the Environmental and Water Quality Operational Studies (EWQOS) Program, sponsored by the Office, Chief of Engineers, and managed by the U. S. Army Corps of Engineers (CE) Waterways Experiment Station (WES), Vicksburg, Mississippi. The work described in this report was performed in EWQOS Work Unit IIA.3.

General supervision and managerial assistance were provided by Drs. R. L. Eley and R. M. Engler, Division and Branch Chiefs, respectively, in the Ecosystem Research and Simulation Division of the Environmental Laboratory (EL). Coprincipal investigators were Dr. J. W. Barko and Mr. R. M. Smart. Excellent technical assistance was obtained from Ms. D. G. Hardin, Mr. G. W. Hartline, Ms. M. S. Matthews, and Mr. R. G. Rhett. This report was written by Dr. Barko, Mr. Smart, and Ms. Matthews and Hardin. Additional support was provided by the EL Analytical Laboratory Group. Dr. R. H. Kennedy provided many helpful discussions during the course of the study and also reviewed this report. The Division and Branch Chiefs named above assisted in a similar capacity. Chief of the EL was Dr. J. Harrison. Program Manager of EWQOS was Dr. J. L. Mahloch.

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The Commanders and Directors of the WES during the study and preparation of the report were COL J. L. Cannon, CE, and COL N. P. Conover, CE. Technical Director was Mr. F. R. Brown.

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PLANT-MEDIATED PHOSPHORUS MOBILIZATION FROM SEDIMENTS:
POTENTIAL INFLUENCE ON FRESHWATER PHOSPHORUS CYCLING

PART I: INTRODUCTION

1. Nutrients sedimented in reservoirs represent a potentially vast source of supply to the overlying water. Various mechanisms of nutrient release from sediments have been identified as contributing to the "internal nutrient loading" of aquatic systems (cf Cooke et al. 1977). One of these mechanisms, phosphorus release by rooted submersed plants, has been demonstrated to be a significant component of the phosphorus cycle in estuaries (McRoy et al. 1972). The occurrence of this mechanism in freshwater systems also has been suggested on the basis of results of several recent investigations of the nutrition of freshwater submersed plants (see for example, DeMarte and Hartman 1974, Bristow 1975).

2. The effect of nutrients released from higher plants on algal growth depends primarily on the nutritional requirements of the algae. Considering the overwhelming amount of evidence that phosphorus (P) is the predominant algal growth-limiting nutrient in most freshwater systems (Schindler 1977), algal productivity appears to be predominantly controlled by P supply.

3. Since the development of empirical methods of predicting the trophic status of P-limited aquatic systems from P loading data (cf Vollenweider 1975), attempts have been made to reduce rates of eutrophication by reducing external inputs of P. The restoration of Lake Washington (Edmondson 1972) is a frequently cited example of the beneficial effects of reduced P input. However, reductions in external P supply through sewage treatment, diversion, and other means can only be immediately effective in aquatic systems in which internal mechanisms of P supply are relatively unimportant. Shapiro et al. (1975) suggest that mechanisms of internal nutrient supply (including plant-mediated sediment P cycling) become increasingly important in lakes that have become eutrophic over a long period of time. The same may also be

true for reservoirs that have been subjected to high rates of sedimentation even for relatively short periods of time. In such situations, the control of internal mechanisms of nutrient supply may become necessary to reduce the occurrence of algal blooms. Thus, it is important that these internal mechanisms are better understood.

4. In this report, the mobilization of sediment P by three freshwater submersed plants (Egeria densa, Hydrilla verticillata, and Myriophyllum spicatum) is comparatively evaluated on five different reservoir sediments. The objectives in the study were twofold: to evaluate the magnitude of P absorption exclusively from reservoir sediments by submersed plants in relation to their specific P requirements, and to quantify the ability of these plant species to release P into their surrounding environment. Portions of the results of this investigation are also considered elsewhere, for fundamental evaluation of the potential influence of submersed plants on the P cycle and metabolism of lacustrine systems (Barko and Smart 1980b), and for application to the eutrophication problem in Lake Wingra, Wisconsin, U.S.A. (Barko and Smart 1979b). Aspects of this work appropriate for CE-wide implementation are planned for separate publication in which other processes of internal P cycling are comparatively discussed.

PART II: METHODS

5. The investigation was conducted in a controlled environment chamber at temperatures maintained between 18 and 20°C. Light was supplied during a 14-hr photoperiod each day from Sunbrella Fixtures (Chagrin Falls, Ohio) containing a combination of Multi-Vapor and Lucalox (sodium vapor) high intensity lamps. Spectral Radiometer determinations indicated no difference between the quality of this artificially supplied light and natural sunlight. Photosynthetically active radiation was provided at a rate of approximately 350 $\mu\text{einsteins}/\text{m}^2 \cdot \text{sec}$.

6. Experimental columns used in the investigation (Figure 1) had a total volume of 20 ℓ . Each column consisted of two 150 cm tall concentric cylindrical lucite sleeves fitted and sealed over a 30-cm tall sediment container. The inner sleeve restricted the areal expansion of plants to 132 cm^2 , and could be removed, scraped of attached algae, and replaced if necessary. Filtered and humidified air was added continuously to each of the columns providing gentle mixing and equilibration with the air.

7. Sediments were dredged from sublittoral locations in four reservoirs having a past history of high nutrient inputs and one (DeGray) with low nutrient inputs. These reservoirs were Ashtabula, North Dakota; Branched Oak, Nebraska; DeGray, Arkansas; Papillion (site 16), Nebraska; West Thompson, Connecticut. After thorough mixing of each sediment, texture, organic matter, total P, and interstitial water $\text{PO}_4\text{-P}$ were determined using the procedures described in Barko and Smart (1979a).

8. Sediments were placed in the sediment containers and allowed to settle for several weeks. At that time the sediment surfaces were sealed with paraffin to a thickness of approximately 1 cm. The seal contained four 1.6-cm diameter openings to facilitate later planting.

9. Apical shoots, 15 cm in length, of each plant species were clipped from greenhouse cultured stock. Leaves were stripped from the lower 10 cm before the shoots were inserted into the sediment, allowing 5 cm of leafy shoot to emerge. Containers of each sediment were planted

with four shoots of each species and replicated four times. Three containers of each sediment remained unplanted to serve as controls. Containers were placed into large tanks to allow time for rooting and replacement of damaged shoots. The tanks contained 50 mg/l CaCO_3 in deionized water buffered to pH 7. After 2 weeks all shoots had commenced active growth. The sediment containers then were removed from the tanks, and prepared for introduction into the columns.

10. Openings in the paraffin seals of both the control and experimental sediment containers were closed with a low temperature (36.5°C) melting point wax (eicosane, Eastman-Kodak Co., Rochester, New York) before the columns were assembled and filled with a P-free nutrient solution. The nutrient solution used in the study was modified Bold's Basal Medium (Nichols and Bold 1965) made up from glass-distilled water and reagent grade chemicals. Modifications included the deletion of P and a 1:10 dilution of all other constituents except Ca, which was added as CaCO_3 to adjust the alkalinity to 1 meq/l. The pH of the solution was adjusted to 7.0.

11. The columns (including controls) were all uniformly inoculated with a mixed algal culture. Algal growth in the columns was visually noted and used as a rough indicator of P release from the plants. Every 2 weeks the solutions were subsampled (250 ml volume) for total P determination using a modification of the persulfate digestion method described in Gales, Julian, and Kroner (1966). Depending upon apparent algal density, at least 50 percent of the solution was replaced after each sampling. Solution levels were incrementally increased to keep pace with the upward growth of the plants in the columns.

12. Phosphorus analyses were performed by the Analytical Laboratory Group of the Environmental Laboratory using Technicon Autoanalyzer procedures that enabled an 8 $\mu\text{g}/\text{l}$ lower limit of P detection. Phosphorus in the control columns, representing extraneous and non-plant related sources of P introduction, was subtracted from values of P determined in the planted columns. The very low values of P (usually less than detection) determined in the controls and the complete lack of visible algae attested to the P-free integrity of the experimental apparatus.

13. During the study, the columns were inspected daily for plant damage, and fragments were immediately retrieved. These materials were dried, stored, and combined with the harvested biomass at the end of the study. The purpose in removing these materials was to minimize P release into the columns due to tissue decay. This enabled the unobstructive evaluation of the extent of intrinsic mechanisms of P release (i.e., excretion) from the plants.

14. After 3 months of study, the columns were dismantled, and attached algae were removed by scraping the inner columns. Algae thus collected were resuspended in 750 ml of glass-distilled water and digested as described earlier. Plants were harvested by clipping the shoots at the paraffin surface. No attempt was made to remove algal epiphytes, which were subsequently treated as plant mass. Root mass was removed from the sediment by washing over a 1-mm sieve. All plant materials were dried at 80°C to constant weight and ground in a Wiley mill. Subsamples were digested with a hydrogen peroxide-sulfuric acid mixture, slightly modified from Allen et al. (1974). Phosphorus analyses were subsequently performed on Technicon Autoanalyzers.

PART III: RESULTS

Sediment Comparisons

15. Sediments used in the investigation are characterized in Table 1 by texture, organic matter, total P, and interstitial water PO_4 -P. These sediments are texturally diverse, ranging from a predominantly sandy sediment (W. Thompson) to two totally fine-textured sediments (Branched Oak and DeGray). Branched Oak and Papillion reservoirs are located in the same watershed, which may explain their textural similarity. Clay contents differ considerably among the sediments, but apparently these differences do not affect total P concentrations, which are nearly identical. Total P falls within the low to intermediate portion of the range reported for most eutrophic lakes (see for example, Williams et al. 1971; Slater and Boag 1978). Organic matter contents are remarkably similar among the sediments, and fall within the range presented by Boyd (1970) for reservoir sediments in the southern United States. Interstitial water PO_4 -P concentrations range from 0.03 to 0.22 mg/l, and are similar to values reported for other eutrophic sediments (Barko and Smart 1979a).

Plant Growth and Biomass Distribution

16. On the basis of shoot height (Figure 2) growth rates of both Hydrilla and Myriophyllum diminished considerably toward the end of the study. Indeed, Myriophyllum appeared to initiate senescence during the last 2 weeks. In deference to the above, the growth of Egeria remained nearly constant throughout the study. In general, sediment-related differences in shoot heights within a species are indicative of similar differences in shoot biomass (Table 2). However, other morphological parameters such as branch number and internodal branch spacing (which were not routinely determined in this investigation) may also relate to shoot biomass.

17. At the end of the study, the shoot biomass of Myriophyllum and

Egeria were comparable, and both exceeded that of Hydrilla (Table 2). Based on observations made in the plant culturing facility, and the data of Van, Haller, and Garrard (1978), Hydrilla appears to grow better at higher water temperatures than those maintained during this study (18-20°C). Therefore, low water temperature may partially explain the relatively poorer growth of Hydrilla. Differences in shoot biomass of the three species demonstrated no consistent pattern among sediments. Whereas the growth of Egeria was statistically comparable on all sediments, the growth of Hydrilla and Myriophyllum was poor on Ashtabula and W. Thompson, respectively.

18. The generally low root:shoot biomass ratios (Table 2) indicate the minor contributions of roots to the total biomass of these submergent species. On all sediments, Myriophyllum had higher ratios of root:shoot biomass than the other species. The significantly higher biomass ratios for Hydrilla on Ashtabula and for Myriophyllum on W. Thompson reflect the relatively unfavorable growth of these species on these two sediments. High ratios of root:shoot biomass suggest the possible influence of metabolic stress on aboveground to belowground biomass distribution (Barko and Smart 1978, 1979a). It is interesting that the unknown sediment-related stress factors in this investigation affected plant growth in a species-specific fashion.

Sediment P Mobilization

19. Plant tissue P concentrations (Table 3) were high. Indeed, some of the higher values are comparable to shoot P concentrations obtained by Ryan, Riemer, and Toth (1972) for several submersed plants under fertilized conditions. With the exception of the relatively low P concentration of Myriophyllum on W. Thompson, all concentrations in Table 3 exceed 1.3 mg/g dry plant weight, suggested as a generalized critical P concentration for submersed plants (Gerloff and Krombholz 1966). More recently, a somewhat lower critical P concentration of 0.79 mg/g dry shoot weight was estimated for Myriophyllum spicatum (Carpenter and Adams 1977). Specific critical P concentrations

for Egeria densa and Hydrilla verticillata are not available, but probably do not exceed the generalized value previously given for submersed plants. Based on the foregoing information, it appears that plant growth was not limited by P supply on any of the five sediments.

20. The amounts of P absorbed from sediments and translocated to shoots (i.e., mobilized) by the plants (Table 4) differed among species and sediments. The greater mobilization of sediment P by Myriophyllum and Egeria compared to P mobilization by Hydrilla reflects the greater biomass of the former two species (Table 2). In contrast, variations in P mobilization among sediments primarily reflect differences in tissue P concentrations (Table 3).

21. With few exceptions, cumulative P released from the plant shoots (Figure 3) during the investigation represented less than 10 percent of total P mobilized (Table 4). Because of the precautions taken to minimize tissue decay during experimentation, the P released from Egeria and Myriophyllum should be considered to approximate P excretion. However, this approximation does not apply to Hydrilla, which continuously shed its lower leaves. These leaves were too small to be effectively removed from the columns, and thus provided a sustained source of P through tissue decay. Phosphorus released from Hydrilla, particularly on Ashtabula, exceeded P released by the other species on all sediments.

22. The generally high turnover values for interstitial water (IW) PO_4 -P (Table 5) emphasize the substantial nature of P mobilization by the plants during this investigation. Turnover was highest on Papillion, where the mobilization of P was greatest, in spite of this sediment's low IW PO_4 -P concentration (Table 1). In contrast, P turnover was less on W. Thompson, which had an equally low concentration of IW PO_4 -P. Phosphorus turnover on Ashtabula and DeGray was generally least because of their higher IW PO_4 -P concentrations, which however, did not enhance P mobilization. High turnover values in Table 5 substantiate the results of Li et al. (1972, 1974) indicating that the exchange of P between sediment particles and the surrounding water can be very rapid.

PART IV: DISCUSSION

Evaluation of Sediment P Absorption by Submersed Plants

23. In this investigation all three plant species were clearly able to derive their P nutrition exclusively from the sediments; furthermore, rates of P translocation from roots to shoots were adequate to maintain substantial biomass production. On an areal basis, net shoot production of Egeria and Myriophyllum ranged from approximately 540 to 1120 g dry weight/m², which is within the range of annual net production reported by Likens (1975) for submersed plants on fertile sites. For the reasons given earlier, shoot production of Hydrilla biomass was less.

24. Root production by these species was minimal, but this obviously did not impair P absorption. Nutrient uptake by roots is much more likely to be dependent upon root surface area, internal anatomy, and physiological transport mechanisms than upon root biomass. The lack of a well developed root system in submersed as compared to emergent aquatic plants has led some investigators to consider them to be of secondary importance to shoots in nutrient uptake (cf Sculthorpe, 1967). The lack of definitive information on the relative importance of nutrient absorption by shoots versus roots has obscured the influence of submersed plants on lacustrine nutrient cycles.

25. Recent investigations of differential P uptake by shoots versus roots of submersed plants (Bristow 1975, Bole and Allan 1978) have indicated the predominance of roots in P absorption. Working with Myriophyllum spicatum, Bole and Allan (1978) recently demonstrated almost exclusive P uptake from sediments by roots while shoots were simultaneously exposed to concentrations of PO₄-P up to 0.5 mg/l in the water. Jupp and Spence (1977) documented the occurrence of submersed plant-limiting phytoplankton blooms at a PO₄-P concentration of 0.05 mg/l, an order of magnitude less than the concentration cited above. Therefore, it is possible that submersed plants are competitively excluded from aquatic systems having aqueous P concentrations

high enough to allow significant uptake by shoots. In aquatic systems where rooted submersed plants do exist, they probably derive their P nutrition predominantly from sediments.

Influence of Submersed Plants on the P Cycle
in Aquatic Systems

26. Phosphorus mobilized from sediments by submersed plants represents a potentially important P recycling mechanism in aquatic systems. Releases of P from plant tissues can occur through both excretory and decay processes. In deference to the results of McRoy et al. (1972), demonstrating quantitatively significant excretion of P from Zostera marina, very little P was excreted from the plants studied in this investigation. However, the results of this investigation are in full agreement with the recent findings of Peverly and Brittain (1978) and Smith (1978) who independently demonstrated minimal P excretion from Myriophyllum spicatum in their laboratory investigations. The magnitude of phosphorus excretion from submersed plants may differ with shoot morphology and anatomy; this could possibly explain the different results obtained with Zostera (op cit).

27. The principle means of P release from the three species herein investigated appears to be tissue decay. In nature, losses of biomass from submersed plants are continuous and thereby provide a persistent and potentially important source of sediment-derived P to other components of aquatic systems. Considering the importance of biomass turnover, Westlake (1975) estimated the annual net production of submersed plants at 1.20 to 1.25 times their seasonal maximum biomass. Indeed, the turnover of Myriophyllum spicatum through tissue sloughing and decay during the growing season alone has been demonstrated to exceed peak seasonal biomass (Adams and McCracken 1974). Therefore, the P released from aquatic plants during decomposition potentially exceeds their tissue P content at peak biomass.

28. Phosphorus release from decaying plant tissues appears to be very rapid and quantitatively important (Nichols and Keeney 1973; Solski

1962, as cited in Wetzel 1975; Kistritz 1978). The rapidity of P release may be due to early microbial colonization of plant tissues. For example, the leaves of Potamogeton have been demonstrated to become progressively damaged by their attached microflora (Howard-Williams, Davies, and Cross 1978) thus promoting leaching and preparing them for immediate exposure upon death to rapid bacterial and fungal attack. This scenario is very likely common to most submergent plants.

Application to CE Reservoirs

29. With 25 percent areal coverage by plants and complete decomposition of shoot biomass, total P mobilized from the reservoir sediments during this 3-month study could provide an internal source of P supply (in g/m^2 of water surface \cdot yr) ranging from approximately 0.60 to 1.05 for Egeria, 0.10 to 0.50 for Hydrilla, and 0.15 to 1.60 for Myriophyllum. The greater values for Egeria and Myriophyllum are comparable to external P loadings into many eutrophic aquatic systems (including reservoirs) and exceed "acceptable P" loadings into systems with an areal water load of less than 40 m/yr (Vollenweider 1976). Compared to critical P loading values for the reservoirs considered herein (Table 6), P mobilization by submersed plants with an areal coverage of as little as 10 percent could be important in three out of the five reservoirs.

30. In reservoirs, or in localized portions of reservoirs (e.g., coves and embayments), that are shallow and subject to relatively minor areal water loads, P mobilization by aquatic plants may play an important role in P cycling. Even in very large and deep impoundments, there are frequently numerous shallow coves in which plants may significantly affect localized nutrient conditions.

31. Many CE reservoirs have vegetatively well developed littoral zones and associated wetlands. Indeed, recent surveys (Leidy and Jenkins 1978, Thornton et al.)* have indicated that a substantial

* Unpublished data.

number of CE reservoirs possess morphometric and geomorphic features conducive to the development of rooted aquatic plant communities. Thus, in many CE impoundments, the mobilization of sediment P by rooted aquatic plants could be important in cycling P into the water column, thereby partially sustaining excessive rates of phytoplankton productivity.

PART V: CONCLUSIONS AND RECOMMENDATIONS

32. Based on the results of this investigation the following generalized conclusions are made:

- a. The submersed plants, Egeria densa, Hydrilla verticillata, and Myriophyllum spicatum are able to obtain their P nutrition exclusively from the sediment through P uptake by roots. Rates of P absorption by roots and translocation into shoots (i.e., mobilization) appear adequate to meet or exceed the requirements of the plant tissues for P during periods of rapid biomass production.
- b. In aquatic systems where submersed plants are prevalent, most of their P is probably derived from the sediment rather than the water.
- c. Very little P appears to be lost from living plant tissues through intrinsic excretory processes. For the three species investigated, the amount of P excreted represented less than 10 percent of total P mobilized from the sediments in most cases.
- d. Large amounts of P mobilized from sediments by rooted submersed plants are potentially contributed to the open water sectors of aquatic systems through processes of biomass turnover and decay.
- e. For algae in most aquatic systems, limited by the supply of P, additions of P to the water column by submersed plant-mediated mechanisms can result in increased rates of algal growth.
- f. In reservoirs, or in localized portions of reservoirs that are shallow and subjected to relatively minor areal water loads, P mobilization by aquatic plants may play an important role in P cycling and in promoting algal growth.

33. Based on the aforementioned conclusions, the following generalized recommendations are made:

- a. Aquatic plants should be considered as a potentially important source of P supply to other components (including algae) of aquatic systems.
- b. In applying methods of aquatic plant control, the potential effects of nutrients (particularly P) released from decaying plant tissues need to be considered.

- c. The role of plant-mediated sediment P cycling in regulating algal blooms needs to be evaluated in comparison with other internal mechanisms of P supply (e.g., thermocline migration). This will be possible as internal nutrient cycling processes become better understood.
- d. Other important aquatic plants, particularly those that differ anatomically and morphologically from the species considered in this investigation, need to be evaluated in regard to their ability to mobilize sediment nutrients. This will be accomplished during the second phase of experimentation in this work unit. Results will be reported in 1980.

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Table 1

Reservoir Sediment Characterizations: Texture, Organic Matter,
Total Phosphorus (P), and Interstitial Water PO₄-P

Parameter	Sediment Source and Characterization, Mean (Standard Error)*				
	Ashtabula	Branched Oak	DeGray	Papillion	W. Thompson
Texture, % dry wt					
sand	27.2 (0.8)	0.0 (9.0)	0.0 (0.0)	0.8 (0.8)	60.0 (0.0)
silt	22.5 (0.0)	20.0 (0.0)	33.3 (0.8)	25.8 (1.7)	2.5 (0.0)
clay	48.3 (0.8)	80.0 (0.0)	66.7 (0.8)	73.3 (0.8)	37.5 (0.0)
Organic matter, % dry wt	6.5 (0.6)	6.5 (0.2)	6.6 (0.7)	5.8 (0.4)	5.8 (0.3)
Total P, g/kg dry wt	0.61 (0.01)	0.65 (0.03)	0.69 (0.01)	0.60 (0.01)	0.66 (0.03)
Interstitial water PO ₄ -P, mg/l	0.22 (0.03)	0.07 (0.01)	0.19 (0.01)	0.03 (0.00)	0.03 (0.00)

* Means and standard errors are based on three replications.

Table 2

Shoot Biomass and Root:Shoot Biomass Ratios

<u>Species</u>	<u>Biomass Category</u>	<u>Reservoir Sediment Source - Biomass Measurements*</u>				
		<u>Ashtabula</u>	<u>Branched Oak</u>	<u>DeGray</u>	<u>Papillion</u>	<u>W. Thompson</u>
<u>Egeria densa</u>	Shoot, g dry wt	11.0 a	10.9 a	10.4 a	12.2 a	9.3 a
	Root:Shoot, %	2.2 a	1.5 a	1.7 a	2.3 a	1.4 a
<u>Hydrilla verticillata</u>	Shoot, g dry wt	0.7 a	4.3 b	2.8 b	5.2 b	3.4 b
	Root:Shoot %	6.1 a	1.3 b	3.6 b	1.4 b	1.6 b
<u>Myriophyllum spicatum</u>	Shoot, g dry wt	14.7 a	13.8 ab	10.1 bc	11.8 ab	7.1 c
	Root:Shoot, %	10.0 a	8.5 a	12.4 a	13.7 a	23.8 b

* Values are means based on four replications. Values within a row sharing the same letter do not differ at the 5-percent level of significance determined using Duncan's multiple range test; others differ at the 5-percent level or less.

Table 3

Phosphorus Concentrations in Plant Shoots

<u>Species</u>	<u>Reservoir Sediment Source - P Concentrations, mg/g(dry plant wt)*</u>				
	<u>Ashtabula</u>	<u>Branched Oak</u>	<u>DeGray</u>	<u>Papillion</u>	<u>W. Thompson</u>
<u>Myriophyllum spicatum</u>	3.4 a	6.1 b	3.5 a	5.6 b	1.0 c
<u>Egeria densa</u>	3.7 ac	5.0 b	4.3 ab	4.1 ac	3.3 c
<u>Hydrilla verticillata</u>	6.7 a	5.9 a	5.9 a	4.0 b	3.4 b

* Values are means of four replications. Values within a row sharing the same letter do not differ at the 5-percent level of significance determined using Duncan's multiple range test; others differ at the 5-percent level or less.

Table 4

Comparisons of Shoot Phosphorus (P) Contents and Associated P Released in
Relation to P Mobilized on Different Reservoir Sediments

Species	P Category	Sediment Source - P, mg/column**				
		Ashtabula	Branched Oak	DeGray	Papillion	W. Thompson
<u>Egeria densa</u>	Released P* (% of total)	2.0 ab (5)	2.6 a (5)	2.9 a (6)	2.7 a (5)	1.4 b (4)
	Shoot P content (% of total)	39.9 ac (95)	53.2 b (95)	43.3 ab (94)	50.2 ab (95)	30.7 c (96)
	Total P mobil- ized	41.9 ac	55.8 b	46.2 ab	52.9 ab	32.1 c
<u>Hydrilla verticillata</u>	Released P* (% of total)	1.7 a (29)	1.8 a (7)	1.4 a (9)	1.5 a (7)	1.3 a (11)
	Shoot P content (% of total)	4.2 a (71)	24.9 b (93)	15.0 c (91)	19.6 bc (93)	10.4 ac (89)
	Total P mobil- ized	5.9 a	26.7 b	16.0 c	21.1 bc	11.7 ac

(Continued)

* Represents cumulative P determined in column water plus P removed from column walls.

** Values are means of four replications. Values within a row sharing the same letter do not differ at the 5-percent level of significance determined using Duncan's multiple range test; others differ at the 5-percent level or less.

Table 4 (Concluded)

Species	P Category	Sediment Source - P, mg/column**				
		Ashtabula	Branched Oak	DeGray	Papillion	W. Thompson
<u>Myriophyllum spicatum</u>	Released P* (% of total)	0.3 a (1)	1.1 ab (1)	0.7 a (2)	2.5 b (4)	0.2 a (3)
	Shoot P content (% of total)	47.8 a (99)	84.2 b (99)	35.4 a (98)	66.1 c (96)	6.8 d (97)
	Total P mobil- ized†	48.1 a	85.3 b	37.1 a	68.6 c	7.0 d

† These values for Myriophyllum are slightly lower than values presented in Barko and Smart (1979b) where root P content was included in total.

Table 5

Plant-Mediated Turnover of PO_4 -P in ReservoirSediment Interstitial Water

Species	Sediment Source - Turnover Values*				
	Ashtabula	Branched Oak	DeGray	Papillion	West Thompson
<u>Egeria densa</u>	84	429	122	1058	535
<u>Hydrilla verticillata</u>	12	205	42	422	195
<u>Myriophyllum spicatum</u>	96	656	95	1372	117

* Turnover values are ratios of total P absorbed from sediments and translocated to shoots (i.e., mobilized) in relation to PO_4 -P content of sediment interstitial water. Turnover values are dimensionless.

Table 6

Critical Phosphorus (P) Loadings for Selected Reservoirs

<u>Reservoir</u>	<u>P Mobilization* at 10% Coverage, g/m²/yr</u>	<u>Critical P Loadings, g/m²/yr**</u>	
		<u>Permissible</u>	<u>Excessive</u>
Ashtabula	0.25	0.23	0.44
Branched Oak	0.43	0.14	0.28
DeGray	0.25	0.32	0.60
Papillion	0.36	0.26	0.45
W. Thompson	0.13	2.20	4.50

* Values represent averages for the three plant species.

** Determined using Vollenweider loading curve (Vollenweider 1975) and appropriate mean depth and hydraulic residence time data.

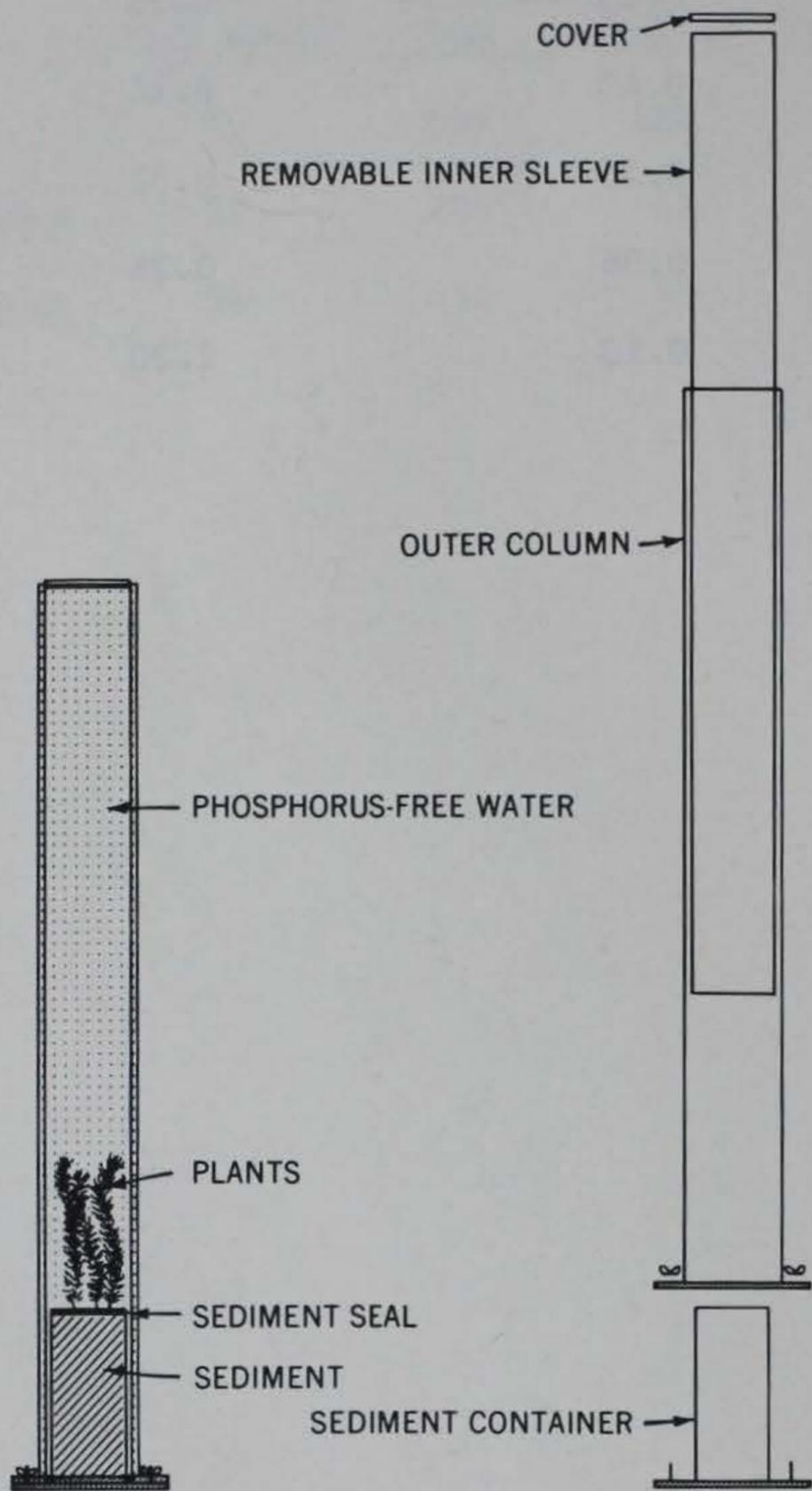


Figure 1. Columns used in evaluating sediment phosphorus mobilization

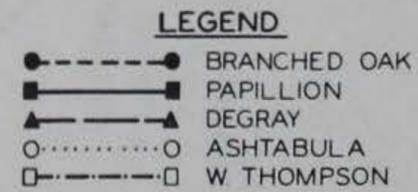
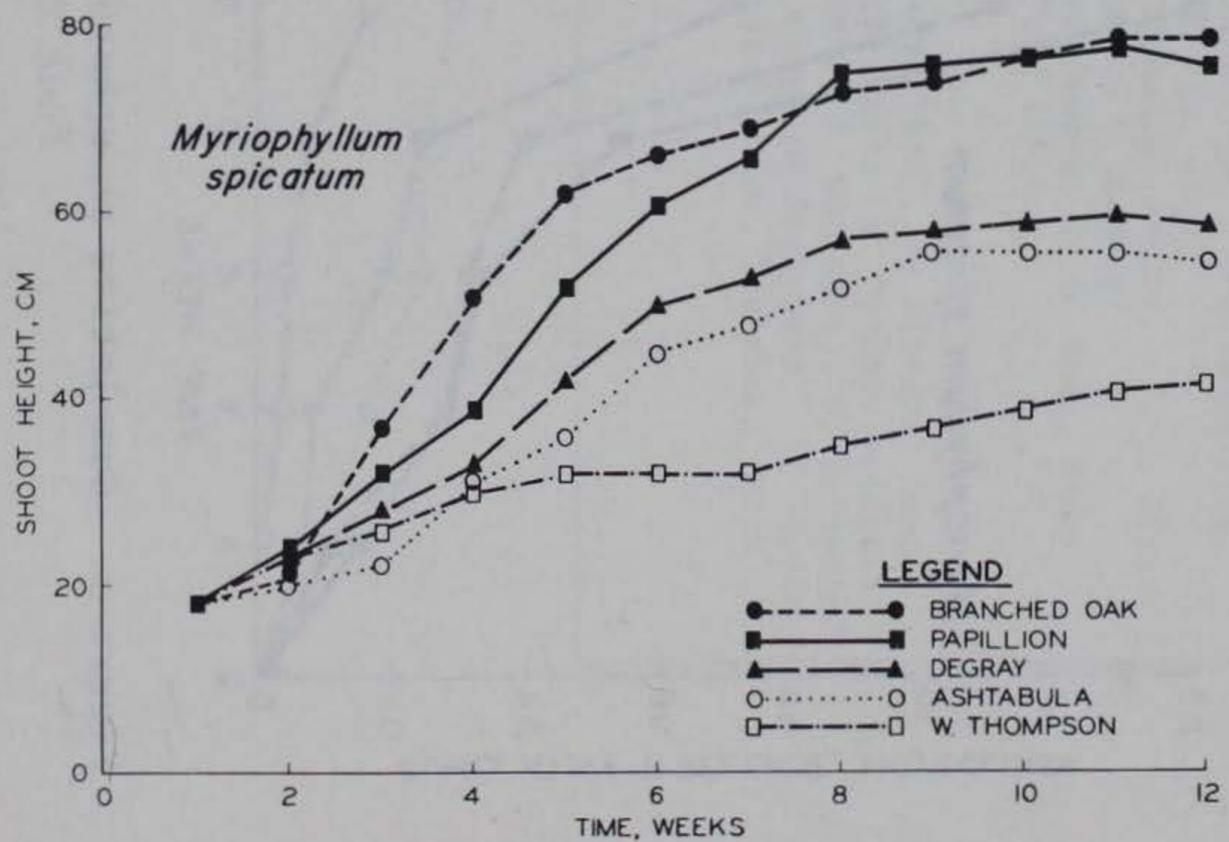
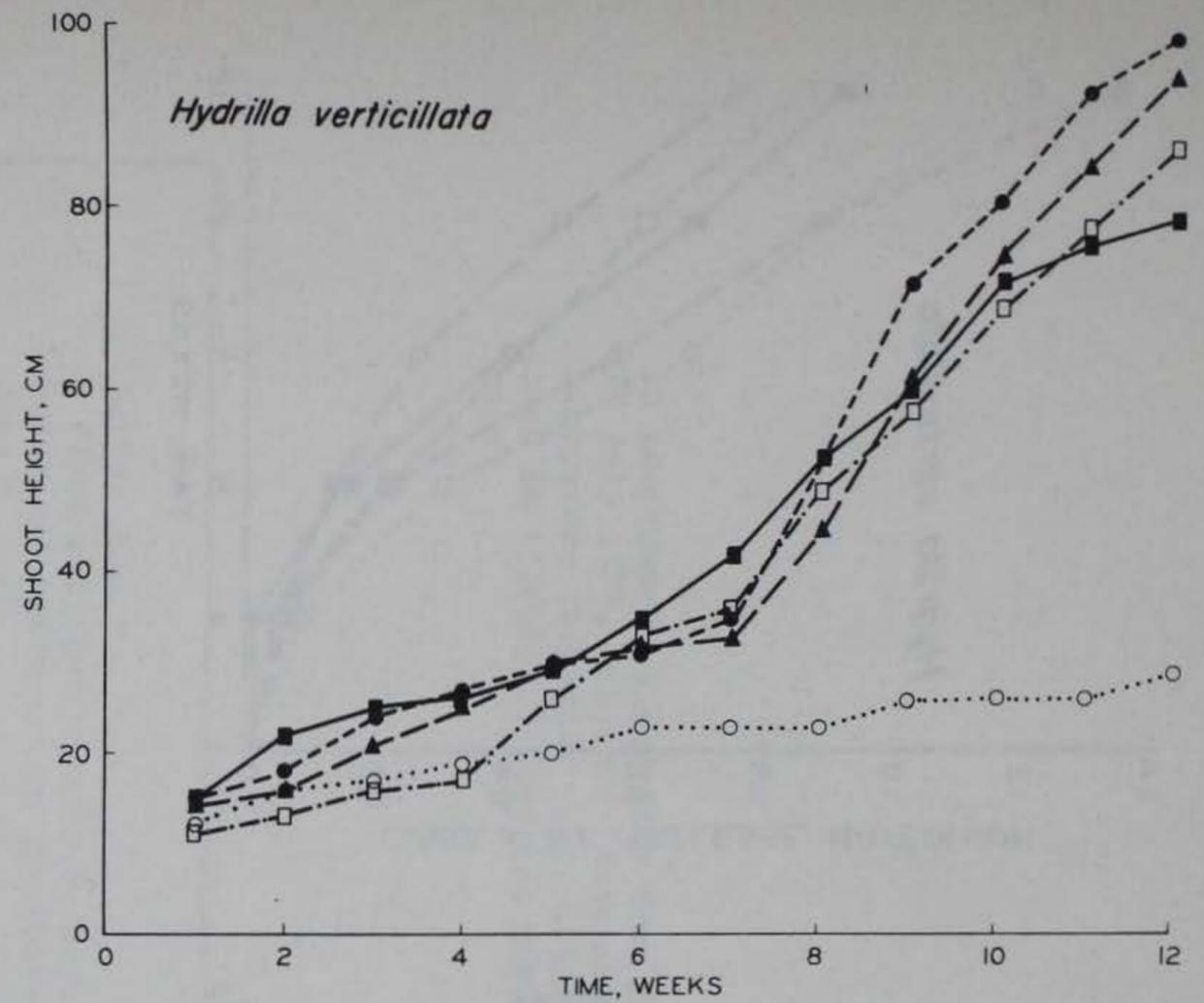
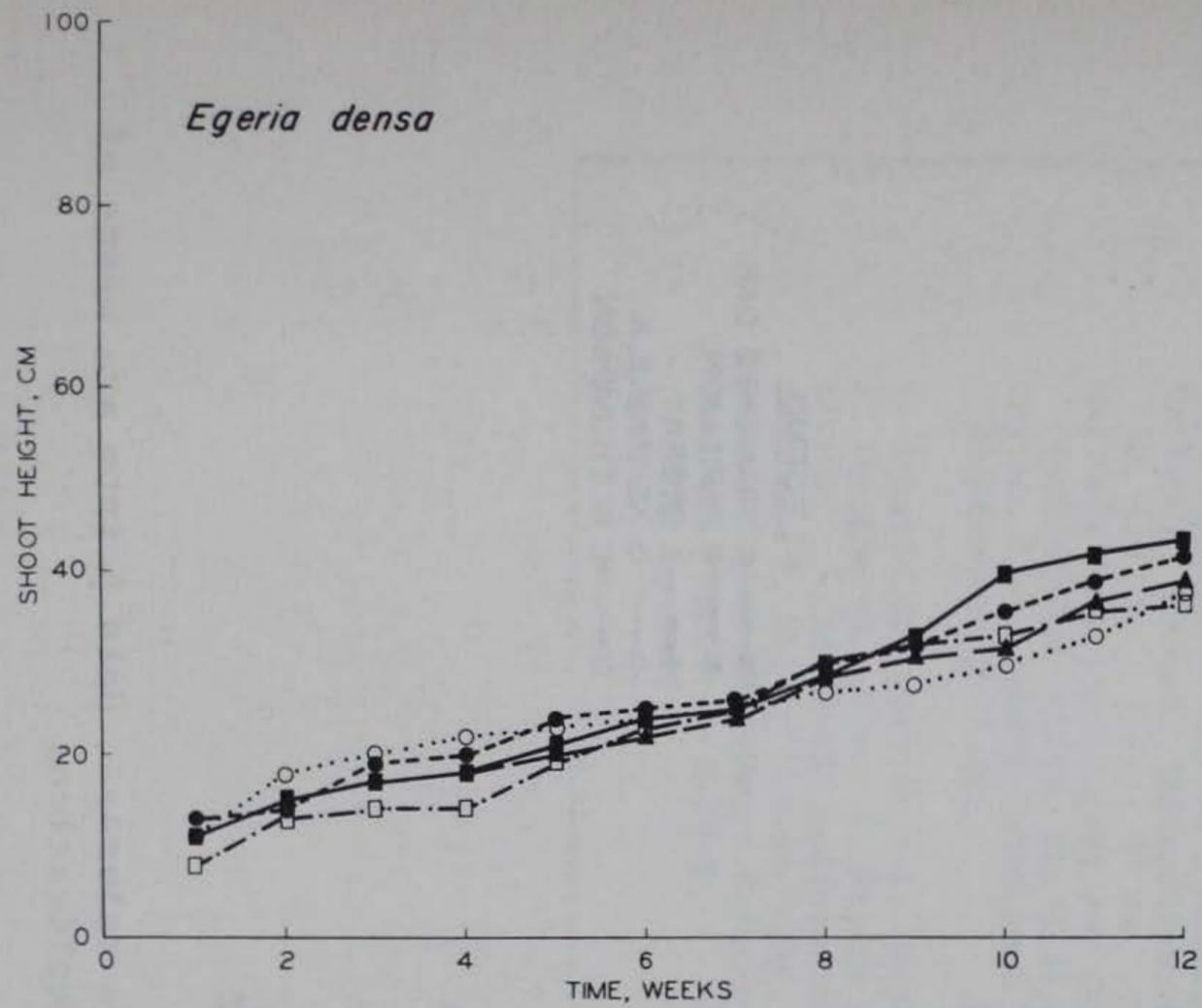


Figure 2. Shoot height. Data points are means of four replications

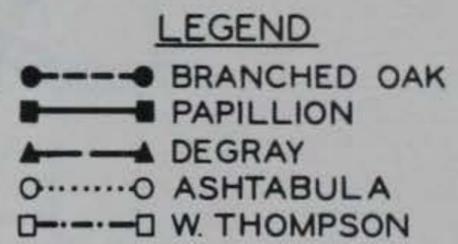
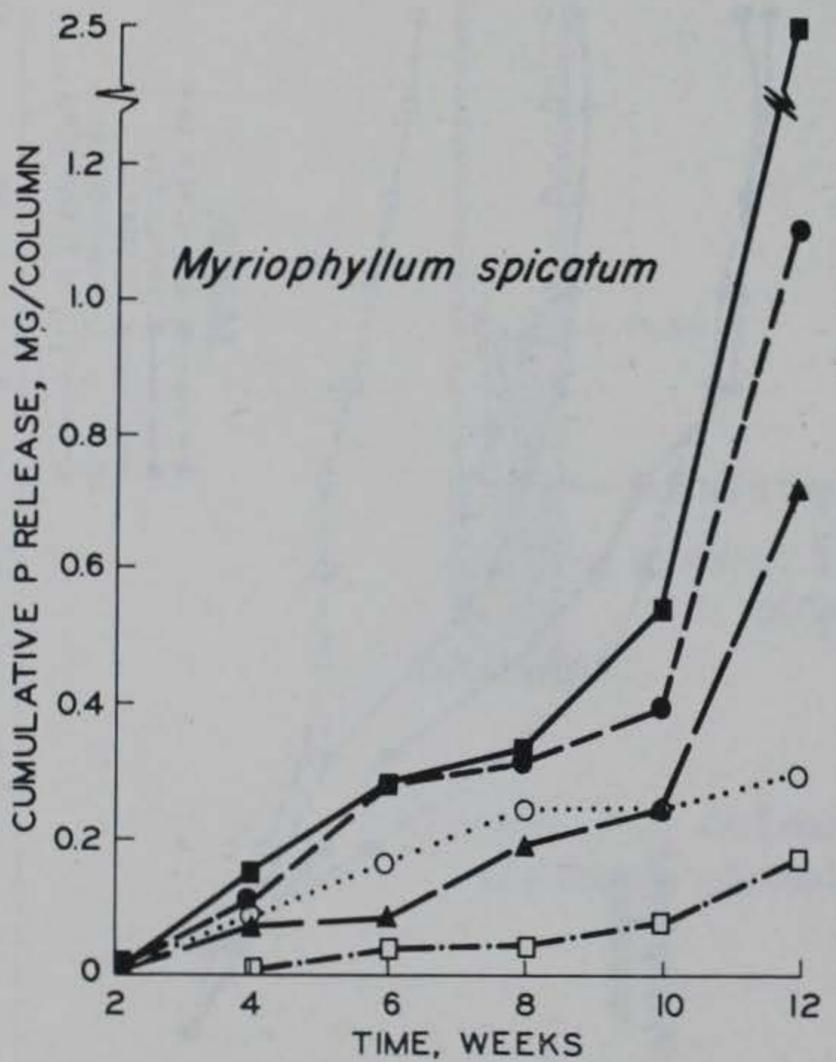
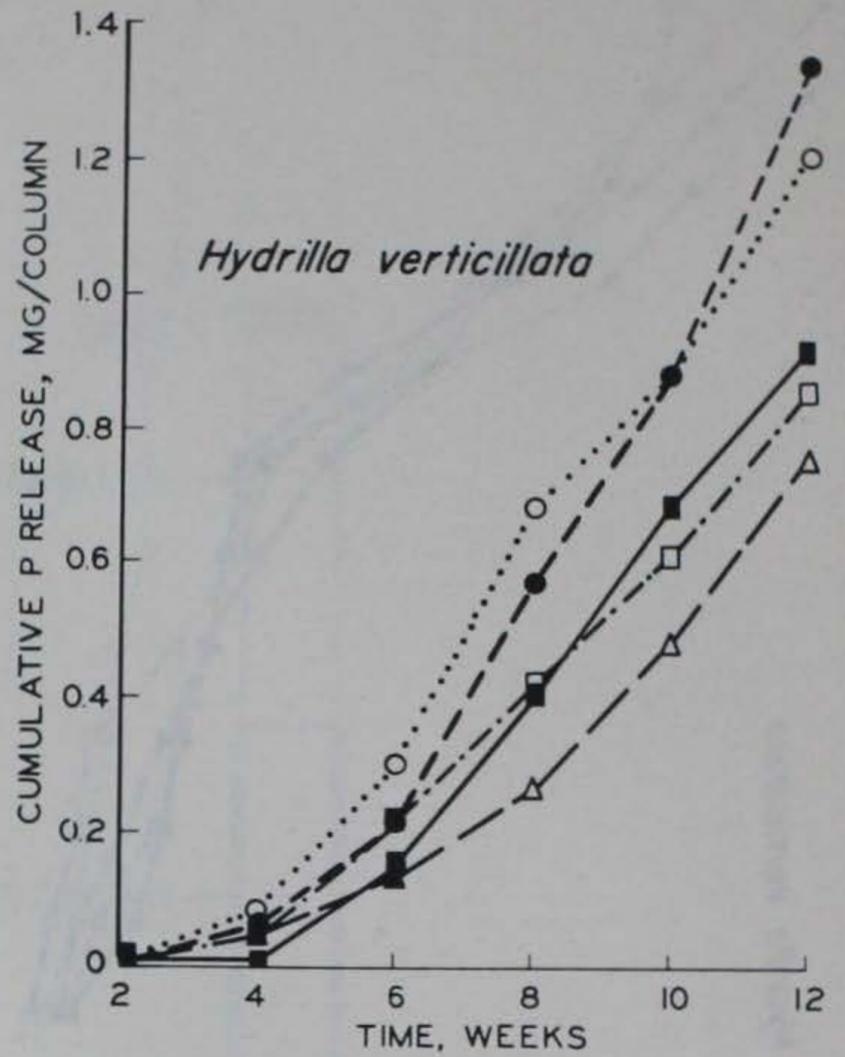
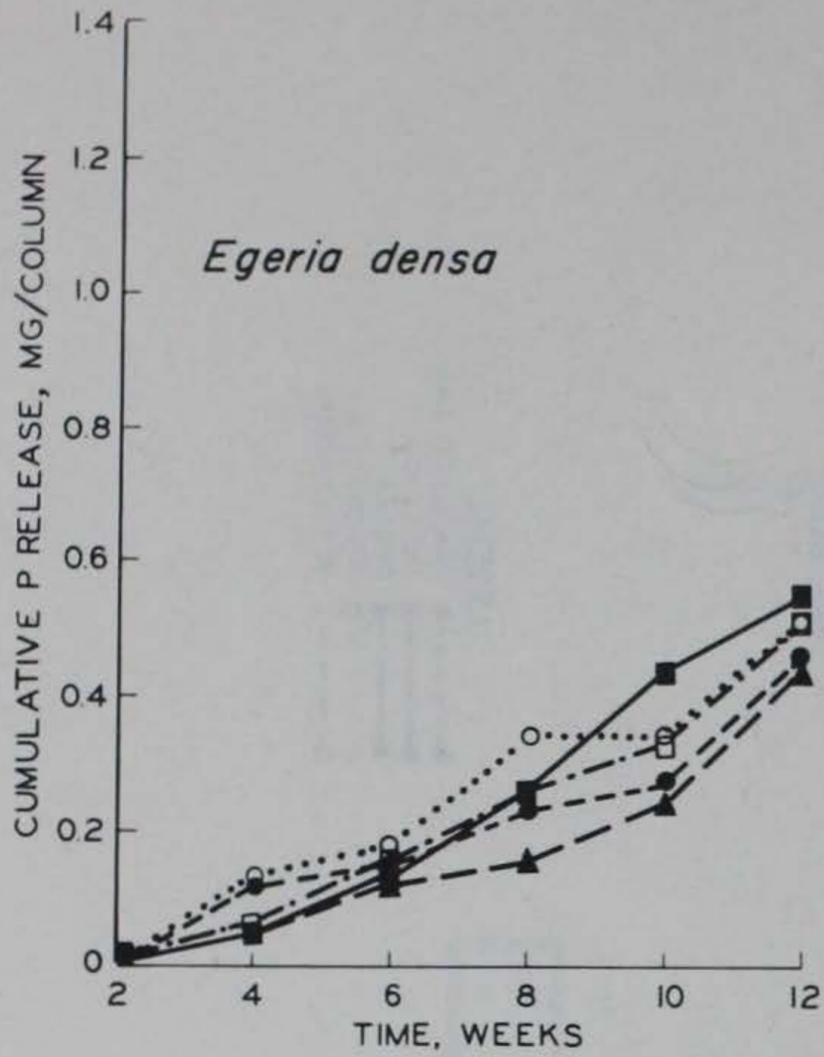


Figure 3. Cumulative phosphorus release. Data points are means of four replications