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Growth and Rooting Depth Characteristics of *Hydrilla verticillata* (L.f.) Royle and *Myriophyllum spicatum* L. on Fertilized and Unfertilized Sediments

by Dwilette G. McFarland, John W. Barko

WES

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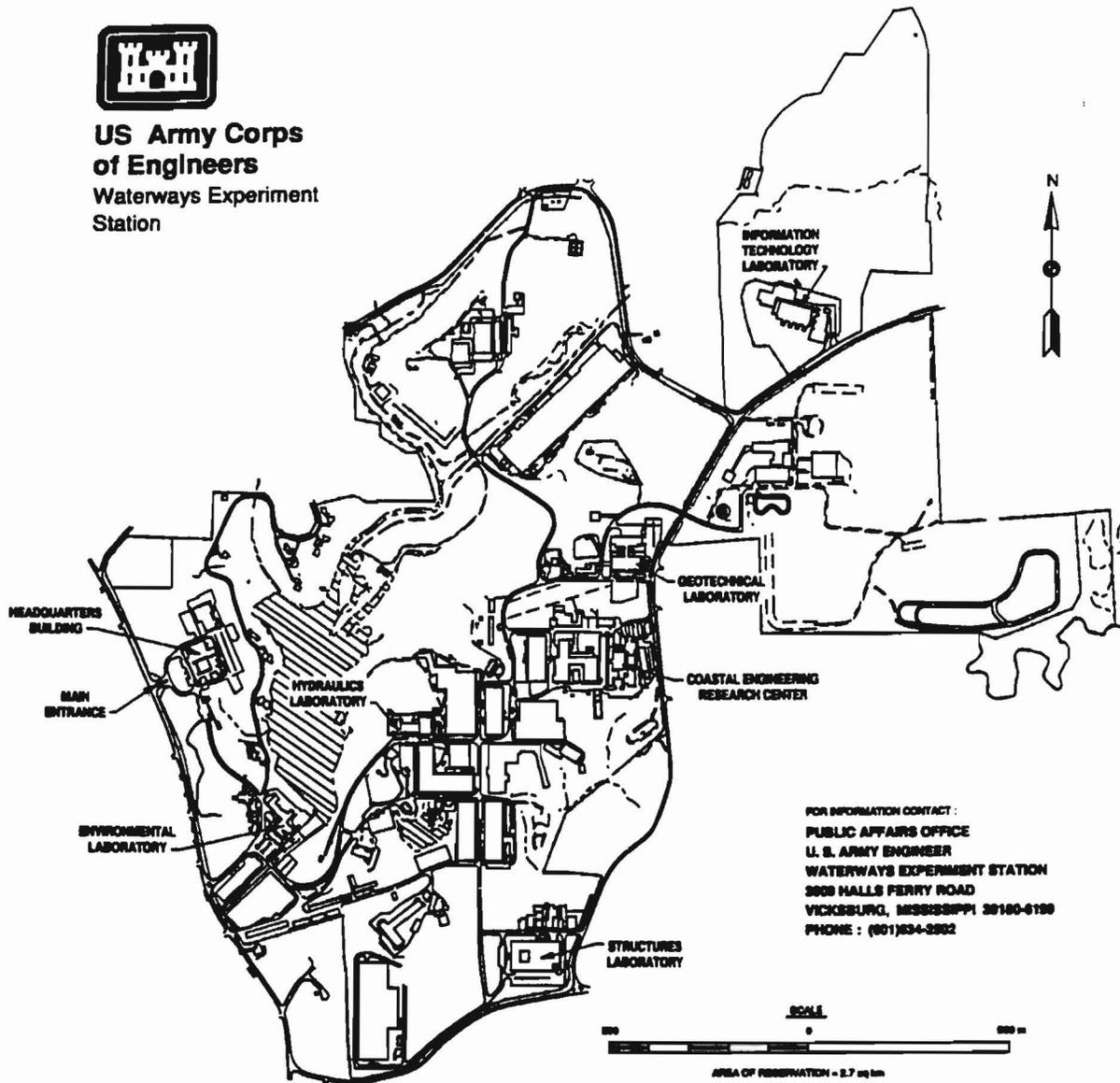
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Preface

The work reported herein was conducted as part of the Aquatic Plant Control Research Program (APCRP), Work Unit 32351. The APCRP is sponsored by the Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Waterways Experiment Station (WES) under the purview of the Environmental Laboratory (EL). Funding was provided under Department of the Army Appropriation No. 96X3122, Construction General. The APCRP is managed under the Environmental Resources Research and Assistance Programs (ERRAP), Mr. J. L. Decell, Manager. Mr. Robert C. Gunkel was Assistant Manager, ERRAP, for the APCRP. Technical Monitor during this study was Ms. Denise White, HQUSACE.

Principal Investigator was Dr. John W. Barko, Ecosystems Processes and Effects Branch (EPEB), Environmental Processes and Effects Division (EPED), EL, WES. Experimental design, data analysis, and interpretation were provided by Dr. Barko and Ms. Dwilette G. McFarland. Technical assistance was provided by Meses. Gail A. Bird, Wanda A. Dee, and Monica N. Humphrey and Messrs. Harry L. Eakin, Kevin Pigott, and F. Ashley Boyd. The report was reviewed within EL by Dr. Craig Smith and Mr. Thomas Sturgis and prepared by Ms. McFarland and Dr. Barko.

This investigation was performed under the general supervision of Dr. Richard E. Price, Chief, EPEB, Mr. Donald L. Robey, Chief, EPED, and Dr. John Harrison, Director, EL.

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1 Introduction

For nearly a century, the relative importance of roots versus shoots in the mineral nutrition of submersed aquatic macrophytes has been a subject of considerable controversy (Pond 1905 and literature therein; Arbor 1920; King 1943; Denny 1972; Bristow 1975; Barko and Smart 1980; Agami and Waisel 1986; Barko and Smart 1986). Today, however, a substantial body of evidence indicates that roots of submersed macrophytes function effectively in obtaining major nutrients, especially nitrogen (N) and phosphorus (P), that are usually available in greater quantities in sediment than in the water column (Barko and Smart 1980; Barko and Smart 1981a; Barko, Gunnison, and Carpenter 1991). Both laboratory and field studies have shown that rooted submersed species can significantly diminish N and P pools in sediment to levels that are potentially growth limiting (Prentki 1979; Short 1983; Carignan 1985; Barko et al. 1988). It has been further demonstrated that in response to poor sediment conditions, root growth of submersed macrophytes may dramatically increase relative to shoot production (Denny 1972; Sand-Jensen and S ndergaard 1979; Mantai and Newton 1982; Barko and Smart 1986). Such adjustments in root-to-shoot ratio suggest that these macrophytes may be able to overcome the effects of nutrient deficiency by increasing access to sediment nutrient supplies.

The present investigation focuses on two submersed macrophyte species, *Myriophyllum spicatum* L. and *Hydrilla verticillata* (L.f.) Royle. Both are highly prolific exotic species in North America, capable of forming dense plant stands that impede water flow and cause a variety of water-use problems (Grace and Wetzel 1978; Anderson and Dechoretz 1982; Swarbrick, Finlayson, and Cauldwell 1982; Environmental Laboratory 1985; Smith, Barko, and McFarland 1991). At present, the distribution of *M. spicatum* covers a much wider range in North America (from Florida to Alaska) than does the monoecious *Hydrilla* biotype used in this study (Holmquist 1971; Couch and Nelson 1985; Smith, Barko, and McFarland 1991). However, since 1982, when monoecious *Hydrilla* was first reported in the Potomac River, Virginia, it has rapidly spread to at least four states in the Northeast, United States, i.e., Maryland, Delaware, North Carolina, and Pennsylvania, and to the District of Columbia as well (Environmental Laboratory 1985; Langeland and Smith 1984; Rybicki et al. 1987).

Problems associated with the nuisance growth of *M. spicatum* and *H. verticillata* have prompted numerous studies of the ecology of these species. The majority of these studies have examined effects of limnological factors including light, temperature, sediment, and water chemistry (Steward and Van 1978; Barko and Smart 1981a, 1981b; Barko 1982; Barko and Smart 1986; Smart and Barko 1986; Spencer and Anderson 1986; McFarland and Barko 1987; Steward 1991). Notably, sediment composition has been shown to greatly affect the growth of *Hydrilla* and *Myriophyllum* through influences on nutrient availability (Barko and Smart 1986). Yet to date, there have been no studies to ascertain specific rooting depth responses of these macrophytes to levels of sediment nutrient supply. From an ecological standpoint, spatial aspects of root development are of particular importance because of their possible impacts on macrophyte production and interspecific interactions in littoral communities.

Reported here are results of a three-part investigation designed to examine the rooting capabilities of monoecious *Hydrilla verticillata* (L.f.) Royle and *Myriophyllum spicatum* L. Specific objectives of this study were to (a) assess growth and rooting depth responses to nutrient-rich and nutrient-poor sediments, and (b) determine changes in sediment nutrient pools because of uptake within the root zones of these species.

2 Methods and Materials

Experimental Environment

The investigation was conducted in 1,200-L, white fiberglass tanks (150-cm length by 90-cm width by 90-cm depth) housed in a greenhouse facility at the U.S. Army Engineer Waterways Experiment Station (WES), Vicksburg, Mississippi. The tanks were filled approximately 85 cm deep with the low alkalinity culture solution described in Smart and Barko (1985). This solution (prepared with reagent-grade salts and deionized/distilled water) contained major cations ($\text{Na}^+ = 16.0$, $\text{K}^+ = 6.0$, $\text{Ca}^{+2} = 25.0$, and $\text{Mg}^{+2} = 6.8$ mg/L) and anions ($\text{Cl}^- = 44.2$, $\text{HCO}_3^- = 51.8$, and $\text{SO}_4^{-2} = 26.9$ mg/L) but lacked N and P, specifically omitted to minimize algal growth in the tanks and to allow sediment to be the only source of these nutrients for macrophyte uptake (Smart and Barko 1985). Initial pH and conductivity of the solution were approximately 8.0 and 280 $\mu\text{S}/\text{cm}$, respectively. Liquid circulators affixed to each tank provided continuous water circulation and temperature control at 25 ± 1 °C. The solution was aerated with humidified air to enhance mixing and air/water CO_2 exchange. Maximum midday photosynthetically active radiation inside the tanks averaged 450 $\mu\text{E}/\text{m}^2/\text{sec}$ beneath a neutral-density shade fabric that reduced natural irradiance by approximately 75 percent.

Experimental Design

The study included three separate experiments conducted over consecutive summers (July to September) between 1989 and 1991. In Experiment 1, which ran approximately 6 weeks, responses of *Hydrilla* were examined at two levels of sediment-N fertility and four sediment depths (i.e., 10, 20, 30, and 40 cm). One tank was prepared for each fertility/sediment-depth treatment combination, replicated six times. Replicates consisted of tubular planting containers described below. In addition, non-planted control tanks were prepared for each fertility level, at the maximum (40-cm) sediment depth, replicated three times. In Experiment 2, responses of *Myriophyllum* were assessed using basically the same design and time frame described for *Hydrilla* in Experiment 1. To obtain a simultaneous comparison of rooting capabilities of both species, a third experiment was conducted. In Experiment 3, which ran approximately 8 weeks, responses of *Hydrilla* and *Myriophyllum* were

examined individually on low-N sediment, at depths of 20, 40, and 60 cm. Each species/sediment-depth treatment combination was established in a separate tank and replicated six times. Six non-planted containers of the same sediment (60 cm deep) were placed in a single tank as replicate controls.

Sediment and Plant Preparation

Fine-textured sediment from Brown's Lake, WES (characterized in Barko and Smart 1986), was used to obtain different levels of sediment-N fertility. The high N level was provided as "fresh" N-amended sediment, prepared by fertilizing with NH_4Cl (0.8 g/L wet sediment), and the low N level, as unfertilized "used" sediment rendered N-poor due to previous support of submersed macrophyte growth (see McCreary, McFarland, and Barko (1991) and McFarland, Barko, and McCreary (1991) for details).

Different sediment depths were achieved by using polyvinyl chloride (PVC) sediment tube assemblies, each consisting of an outer supporting tube (15 cm diam, 43 cm deep in Experiments 1 and 2, and 63 cm deep in Experiment 3) and an inner insert tube (10 cm diam). Insert tubes were cut to different lengths to obtain the desired sediment depth. These were subsequently capped at the base, filled with sediment, and placed inside the supporting tubes. Sufficient coarse silica sand was placed into each of the supporting tubes to position all insert tubes so that the sediment surface was at the same depth in the tanks.

Myriophyllum spicatum L. and monoecious *Hydrilla verticillata* (L.f.) Royle were obtained from 5-week-old cultures established from the WES continuous greenhouse stock. Both species were originally collected from natural populations—*Myriophyllum*, from Lake Wingra, Wisconsin, and *Hydrilla*, from the Potomac River, Virginia. The two species were planted separately, six apices (15 cm in length) per container, with basal ends buried about 3 cm in the sediment. A thin layer of washed silica sand was placed over the sediment surface, and the containers were submersed in experimental tanks immediately after planting.

At the end of each experiment, aboveground plant material was clipped at the sediment surface and processed according to procedures described below. Sediment inside the planting tubes was then extruded upward from the base and sectioned horizontally every 5 cm from top to bottom. These sections were laid flat and cross-sectioned vertically into two (≈ 202 ml) halves. One-half was used for determinations of belowground biomass retrieved by rinsing through a 1-mm mesh sieve. The remaining half was analyzed for sediment-nutrient concentrations. Evaluations of growth involving belowground responses (e.g., belowground biomass, tuber number, and tuber mass) incorporated minor corrections for sediment volume after sectioning.

Analytical Procedures

Subsamples of prepared sediments were analyzed for moisture content and density after oven-drying measured volumes of sediment at 105 °C. Concentrations of extractable nutrients (i.e., exchangeable $\text{NH}_4\text{-N}$ in all experiments, with additional determinations of extractable $\text{PO}_4\text{-P}$ in Experiment 3) were corrected for moisture content and are expressed here on the basis of dry sediment mass. Exchangeable N was obtained by extraction with 1 M NaCl in a cation exchange procedure modified from Bremner (1965). Extractable P was obtained using 0.03 N NH_4F and 0.025 N HCl (after Olsen and Sommers 1982). Both N and P concentrations were analyzed colorimetrically with a Technicon Autoanalyzer II, employing a molybdate method for P and a salicylate method for N (American Public Health Association, American Water Works Association, Water Pollution Control Federation 1989).

Plant materials were oven-dried at 80 °C for dry mass determinations and ground to a particle size <0.7 mm prior to digestion according to Allen et al. (1974). N and P concentrations in the resulting digestates were determined using the same autoanalyzer procedures described above. The accuracy of analytical procedures used to obtain tissue nutrient concentrations was checked by including reference tissues of the National Bureau of Standards in all experimental sample sets.

Experimental data were evaluated using analysis of variance (ANOVA) and post-ANOVA procedures of the Statistical Analysis System (SAS Institute, Inc. 1991). Comparisons of means were performed using Duncan's Multiple Range Test and Student's *t*-test. In this report, statements of statistical significance without specific indication of probability level refer to $P < 0.05$.

3 Results

Experiment 1

Sediment fertility had the greatest overall effect on aboveground biomass in *Hydrilla*, resulting in reductions as great as 66 percent on unfertilized versus fertilized sediment (Figure 1). Aboveground production was similar among depth treatments of fertilized sediment. However, increased depth of unfertilized sediment (from 10 to 40 cm) promoted a significant (near two-fold) increase in aboveground biomass response. Most of this biomass increase occurred with the increase in sediment depth from 10 to 20 cm.

Maximum belowground biomass in *Hydrilla* was obtained in the 10-cm tubes of fertilized sediment (Figure 1). With increases in the depth of that sediment (to 40 cm), belowground production diminished significantly by approximately one-third. Variations in the depth of unfertilized sediment essentially had no effect on belowground production.

At both fertility levels, belowground biomass was closely correlated with tuber number ($r = 0.80$, $P = 0.0001$) and tuber mass ($r = 0.92$, $P = 0.0001$), as indicated by similar patterns of response to treatment (Figures 1 and 2). Overall, the contribution of tuber mass to belowground biomass ranged from approximately 47 to 66 percent and 50 to 74 percent for fertilized and unfertilized sediments, respectively.

Although sediment fertility effected relatively minor differences in belowground biomass (two-way ANOVA; $F = 9.35$, $P = 0.04$), its influence on the vertical distribution of biomass over 40 cm was rather striking. Profiles presented in Figure 3 show that roots of *Hydrilla* extended at least 15 cm deeper in unfertilized than in fertilized sediment. There were no significant differences in the belowground biomass between corresponding sections down to 20 cm; but beyond 20 cm, the biomass in corresponding sections was consistently greater ($P < 0.01$) in the low fertility treatment.

Tuber formation was largely concentrated in the upper 15 cm of the sediment column, resulting in a sharp reduction in belowground biomass at 20 cm and beyond (Figures 3 and 4). Comparisons between corresponding 5-, 10-,

and 15-cm sections indicated no significant difference in the distribution of tubers (i.e., both in number and mass) relative to fertility treatment (Figure 4).

For both fertilized and unfertilized control (i.e., non-planted) sediments, exchangeable N concentrations showed minimal variation at depths below 5 cm (Figures 5 and 6). In both cases, N concentrations within the top 5 cm were reduced somewhat, presumably due to diffusional losses of this nutrient into the water column. (Note: These same losses were also observed in Experiments 2 and 3. See below.)

Depth profiles of planted sediments demonstrated marked reductions in exchangeable N concentrations down to 25 cm in fertilized and to 40 cm in unfertilized sediment (Figures 5 and 6). Regions of significant N reduction over depth coincided precisely with regions of root formation in *Hydrilla*. In fertilized sediment, exchangeable N depletion because of *Hydrilla* planting was greatest (about 95 percent) near the top of the column and decreased (to about 10 percent) in the 25-cm section. In contrast, exchangeable N was depleted almost entirely throughout the 40-cm depth of planted, unfertilized sediment.

Experiment 2

Low N availability in unfertilized sediment strongly inhibited production of aboveground biomass in *Myriophyllum* (Figure 7). On fertilized sediment, aboveground biomass was about the same regardless of sediment depth treatment. However, consecutive increases in the depth of unfertilized sediment promoted an approximately linear increase in aboveground biomass response.

Belowground biomass in *Myriophyllum* responded primarily to combined effects of sediment depth and fertility treatments (Figure 7). Belowground biomass did not differ significantly among depth treatments in fertilized sediment; but with an increase in the depth of unfertilized sediment from 10 to 40 cm, belowground production increased nearly two-fold.

Sediment depth profiles down to 40 cm showed that the belowground biomass in *Myriophyllum* was concentrated mainly in the top 10 cm of the sediment column (Figure 8). Diminishing amounts of biomass were measured to a depth of 30 cm in fertilized sediment and to the maximum depth of 40 cm in unfertilized sediment.

Depth profiles of exchangeable N concentration showed extensive N removal in planted sediments relative to their control counterparts (Figures 9 and 10). Significant reductions in exchangeable N concentrations occurred in planted, fertilized sediment down to 25 cm—just 5 cm short of the maximum (30-cm) rooting depth achieved in this treatment (Figure 8). Here, exchangeable N reductions were greatest in the top 10 cm and generally diminished with decreasing belowground biomass as a function of increased sediment depth (Figures 8 and 9). Unlike fertilized sediment, exchangeable N in the

planted, unfertilized sediment was quite evenly and almost completely removed along the entire 40-cm rooting depth achieved by *Myriophyllum* (Figure 10).

Experiment 3

Both in *Hydrilla* and *Myriophyllum*, production of aboveground biomass was least in the 20-cm sediment columns (Figure 11). Increasing sediment depth resulted in significantly increased aboveground production, although to an appreciable extent only in *Hydrilla*. Whereas on 20-cm-deep sediment, *Hydrilla* produced approximately 16 percent less aboveground biomass than did *Myriophyllum* ($P < 0.01$, $t = 4.0528$), its aboveground production on 60-cm-deep sediment exceeded that in *Myriophyllum* by about 25 percent ($P < 0.0001$, $t = 7.5509$).

For both species, changes in belowground biomass due to sediment depth treatment were not statistically significant (Figure 11). On the whole, belowground biomass was strongly dependent upon species—in *Myriophyllum*, ranging 1.4 to 2.5 times greater than in *Hydrilla* on 20- to 60-cm-deep columns, respectively.

Differences between rooting characteristics of *Hydrilla* and *Myriophyllum* were most clearly demonstrated in depth profiles of belowground biomass over 60 cm (Figure 12). For both species, at least three-quarters of the belowground biomass was contained within the upper 20 cm of the sediment column. At depths beyond 20 cm, the biomass of root structures gradually declined to minima occurring between 45 and 60 cm. In nearly all sections, belowground biomass in *Hydrilla* was less than in *Myriophyllum*. The most noticeable exception to this occurred because of tuber production which peaked in the 15-cm section. Essentially no tubers were formed by *Hydrilla* at depths below 15 cm.

To further identify differences between *Hydrilla* and *Myriophyllum* in obtaining nutrients under poor sediment conditions, assessments of P concentrations in sediment and in plant tissues were included with analyses for N.

Comparisons of nutrient concentrations in planted versus non-planted (control) sediments indicate that the removal of exchangeable N and extractable P was more extensive in sediment planted with *Hydrilla* than with *Myriophyllum* (Figures 13 and 14). This occurred despite the fact that both species rooted to 60 cm and that *Hydrilla* produced less than one-half the belowground biomass produced by *Myriophyllum* in the 60-cm columns. Sediment planted with *Hydrilla* showed reductions of 81.1 percent in exchangeable N and 33.0 percent in extractable P relative to control levels of these nutrients (Figures 13 and 14). Respective reductions in N and P in *Myriophyllum*-planted sediment were 69.4 and 6.0 percent relative to the controls.

Marked differences in the nutrient demands of *Myriophyllum* and *Hydrilla* were reflected in patterns of N and P removal from low-N sediment (Figures 13 and 14). Depressed concentrations of exchangeable N developed down to approximately 55 cm in sediment supporting growth of each species. From depths of 40 to 55 cm, however, reductions in this nutrient were substantially greater in sediment planted with *Hydrilla*. In *Myriophyllum*-planted sediment, reductions in extractable P lessened gradually—reaching control levels at depths of 25 cm and beyond. In contrast, reductions in sediment P due to growth of *Hydrilla* were nearly uniform, and in all sections significantly greater than in *Myriophyllum*-planted sediment.

Table 1 lists concentrations of N and P in aboveground tissues of both species in relation to sediment depth. To the knowledge of these authors, critical (i.e., growth-limiting) concentrations of N and P have not been determined specifically for monoecious *Hydrilla*; but for the dioecious biotype, these values are estimated to be 9.2 (\pm 0.4) mg N (Smart, Barko, and McFarland, in preparation) and 0.7 mg P per gram dry plant tissue (Steward 1972). In *M. spicatum*, 7.5 mg N and 0.7 mg P per gram dry plant tissue are estimated as critical (Gerloff 1975). Based on the above values, N concentrations in the present study reached critically low levels in *Hydrilla* in the 20- and 40-cm depth treatments, and in *Myriophyllum* in the 20-cm depth treatment. Tissue P concentrations, though diluted in the shallower (20- and 40-cm) depth treatments, were in no instance below critical levels.

4 Discussion

Results obtained in this investigation and elsewhere (Best and Mantai 1978; Mantai and Newton 1982; Anderson and Kalff 1986; Barko and Smart 1986; Barko, Gunnison, and Carpenter 1991) show that N availability in sediment can strongly affect growth and rooting characteristics of submersed aquatic macrophytes. Diminished biomass production and increased rooting depths observed here in both species on unfertilized sediment are responses indicative of nutrient-poor environments (Denny 1972; Mantai and Newton 1982; Barko and Smart 1986). Ratios of root-to-shoot biomass (calculated from results of Experiments 1 and 2) increased in both species because of decreased sediment fertility, although in *Hydrilla*, the range of response (from 0.06 to 0.09) was somewhat less than in *Myriophyllum* (0.11 to 0.23). Increased root-to-shoot ratios associated with greater rooting depths, as observed here, have been speculated to enhance macrophyte nutrition by maximizing root surface area in contact with sediment (Barko and Smart 1986; Barko, Gunnison, and Carpenter 1991).

Although *Hydrilla* and *Myriophyllum* were most responsive to sediment fertility, their responses to sediment depth were also quite apparent. The data, particularly from Experiment 3, clearly demonstrate that under N-poor sediment conditions, N-deficiency in plant tissues and associated reductions in growth may be overcome by increases in sediment depth. These results suggest that sediment volume as a function of depth regulated production and nutritional responses in both species by influencing the mass of sediment nutrients available for growth. Notably, the high production levels in *Myriophyllum* and *Hydrilla* on N-rich sediment (in Experiments 1 and 2) were essentially unaffected by sediment depth, strongly suggesting that the availability of N under those conditions was nonlimiting. This was supported by tissue N concentrations obtained under fertilized sediment conditions (unpublished data) that were above critical levels estimated for these species (Gerloff 1975; Gerloff and Krombholz 1978; Smart, Barko, and McFarland, in preparation; Steward 1972).

In nature, the availability of sediments is potentially determined by various limnological and anthropogenic processes (e.g., erosional wave action, dredging operations, and sedimentation). From our collective findings, it appears that variations in sediment depth imposed by such processes are more

likely to affect growth of submersed macrophytes when nutrient concentrations in sediment are low.

Tuber formation in *Hydrilla* was restricted mainly to the upper 15 cm of the sediment column; thus, whether these propagules are able to emerge from greater sediment depths is questionable. Planting depth has long been shown to be an important determinant of the growth and survival of the propagules of terrestrial plants (Black 1956; Harper and Obeid 1967; Barkham 1980; Bourdot 1984). Only recently have similar studies been conducted with submersed aquatic vegetation. In experiments of Rybicki and Carter (1986) and Spencer (1987), the emergence of young *Vallisneria americana* Michx. and *Potamogeton pectinatus* L. decreased with increased tuber depth in sediment. Furthermore, initial plant mass, length, and number of ramets of *P. pectinatus* were also found to be inversely related to tuber depth (Spencer 1987). While it is likely that the initial growth of *Hydrilla* tubers would be similarly affected by depth in sediment, the range of *Hydrilla*'s responsiveness to this variable is unknown.

Depth profiles of nutrients in planted and non-planted sediments made it possible to examine the relative efficiency of each species in acquiring sediment nutrients. Here, under both conditions of sediment fertility, decreases in exchangeable N and extractable P due to growth of *Hydrilla* were generally as great if not greater than those attributable to *Myriophyllum* growth. This occurred despite considerably less belowground biomass in *Hydrilla* than in *Myriophyllum*. Interestingly, maximum rooting depths were nearly identical for both species under similar growth conditions. Yet, based on the extent of sediment nutrient removal, roots of *Hydrilla* appear more efficient (i.e., on a per gram root mass basis) than those of *Myriophyllum* in obtaining sediment nutrients. Past studies have suggested adaptive advantages in submersed macrophytes under low nutrient conditions related to different propensities for root production (Barko and Smart 1986; McCreary, McFarland, and Barko 1991; McFarland, Barko, and McCreary 1991; Smart, Barko, and McFarland, in preparation). In view of the present findings, the efficiency of nutrient uptake by these macrophytes may be an important consideration as well.

As demonstrated by the findings of these authors and those of others (see below), growth of *Hydrilla* and *Myriophyllum* can result in marked reductions in sediment nutrient pools. Laboratory studies by Barko et al. (1988) demonstrated >90-percent reductions in exchangeable N and >30-percent reductions in extractable P over two 6-week periods of *Hydrilla* growth. Thus far, field investigations of N uptake by rooted submersed macrophytes have generally been quite limited (cf. Barko, Gunnison, and Carpenter 1991). However, the in situ studies of Prentki (1979) and Smith and Adams (1986) have shown substantial P depletion in excess of replenishment rates in sediment supporting beds of *Myriophyllum spicatum*. Considering the potential significance of sediment nutrient depletion on littoral community dynamics, processes affecting nutrient replenishment need to be better understood.

5 Conclusions and Recommendations

Results of the studies reported here and in previous research (Mantai and Newton 1982; Barko and Smart 1986) demonstrate inherent abilities of submersed macrophytes to access sediment nutrients by means of root elongation and adjustments in root-to-shoot biomass ratio. These capabilities, in addition to variations in the availability of sediment nutrients (based on sediment composition), can greatly influence submersed macrophyte growth. It is now apparent that, under infertile sediment conditions, both *Hydrilla* and *Myriophyllum* can potentially offset nutrient limitation, at least over the short term, by exploiting available nutrients at greater sediment depths. This capacity, which may vary among species, might affect competitive relationships under nutrient-limiting conditions. Accordingly, future studies should compare responses obtained from *Hydrilla* and *Myriophyllum* to those of other macrophyte taxa. These comparative evaluations could be useful in predicting growth and species composition of submersed macrophyte communities, particularly in areas where sediment nutrient concentrations are low.

Hydrilla is well-known to rely on tubers as a means of perennation and regrowth (Bowes, Holaday, and Haller 1979; Yeo, Falk, and Thurston 1984; Van, Haller, and Garrard 1978; McFarland and Barko 1991). From experiments in this report, these propagules in *Hydrilla* might be expected to form mainly within the upper 15 cm of the sediment column. Although data are rather limited, previous laboratory and field studies have shown tuber depth to play a prominent role in determining plant emergence and initial plant mass (Rybicki and Carter 1986; Spencer 1987). Under field conditions, various processes (e.g., sediment deposition and accretion and wave action) may affect the depth of tubers in sediment. Studies to elucidate potential impacts of these processes on the growth of *Hydrilla* would allow greater understanding of the dynamics of its populations in nature. Such understanding is considered prerequisite to predicting changes in population density and vigor in relation to gains and losses in littoral sediments.

Results reported here show significant sediment nutrient depletion within the root zones of the two studied species. In nature, replenishment of nutrients via sedimentation provides a means of counterbalancing nutrient losses from sediment because of macrophyte uptake (Barko et al. 1988). Factors affecting

sedimentation have been extensively studied in open-water environments (e.g., Hakanson 1977; Patterson and Brown 1979; Carpenter 1981) but have received far less investigative attention with respect to the littoral zone (cf. Barko, Gunnison, and Carpenter 1991). Field investigations are needed to examine long-term nutrient replenishment (through sedimentation) in relation to uptake and other forms of nutrient loss in sediments supporting submersed macrophyte beds. This information could greatly advance understanding of nutritional factors affecting macrophyte succession, especially during periods of dominance by different aquatic macrophyte species.

Findings of the work herein contrast with the assertion by Sculthorpe (1967) that the principal influence of sediments on the distribution of submersed macrophytes is due to physical texture rather than chemical composition. Additionally, other researchers have suggested that sediment texture may determine rooting depth of submersed macrophytes (Denny 1980) and may also influence rooting success in flowing water systems (Haslam 1978). With these considerations, these authors recommend that future studies examine effects of interactions between sediment texture and nutrient availability on rooting responses of native and invasive macrophytes species. Variations in the capacity of different species to penetrate sediment and take up sediment nutrients may affect the outcome of interspecific interactions. Information on this aspect of submersed macrophyte ecology could be helpful in planting programs to establish nonadventive species in areas susceptible to invasion by nuisance species such as *Myriophyllum* and *Hydrilla*.

The results of this study demonstrate the flexibility of both *Hydrilla* and *Myriophyllum* in adjusting to different sediment conditions. It is recommended that additional studies of the nutrition of submersed macrophytes be conducted to further understanding of the complex mechanisms governing growth. From a management perspective, better understanding of these mechanisms could ultimately promote the development of strategies that exploit natural or manipulated changes in sediment nutrient availability as a means of regulating species composition of submersed macrophyte communities.

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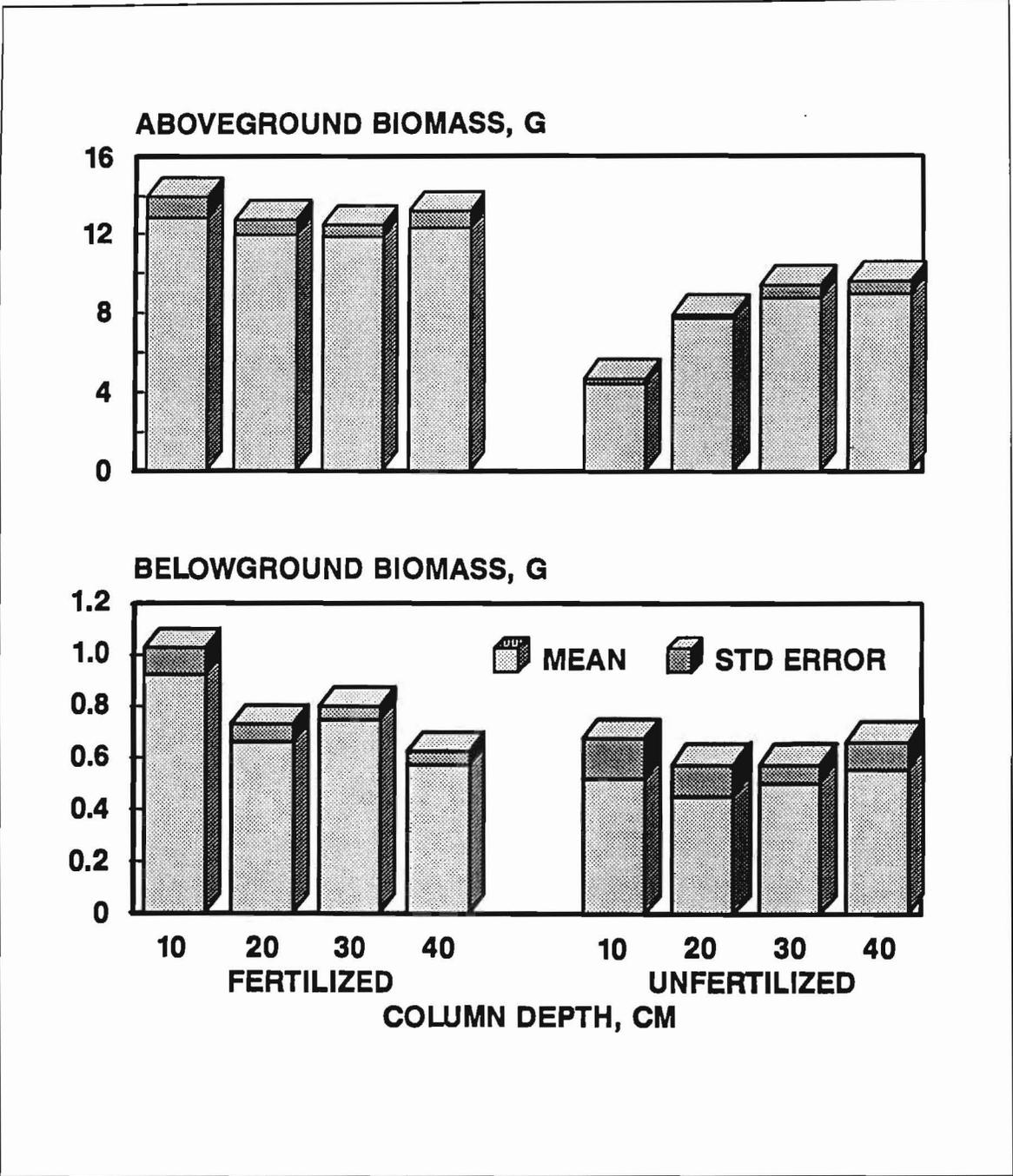


Figure 1. Aboveground and belowground biomass of monoecious *Hydrilla verticillata* (L.f.) Royle planted in fertilized and unfertilized sediments of different depths. Values are means ($n = 6$) with their associated standard errors

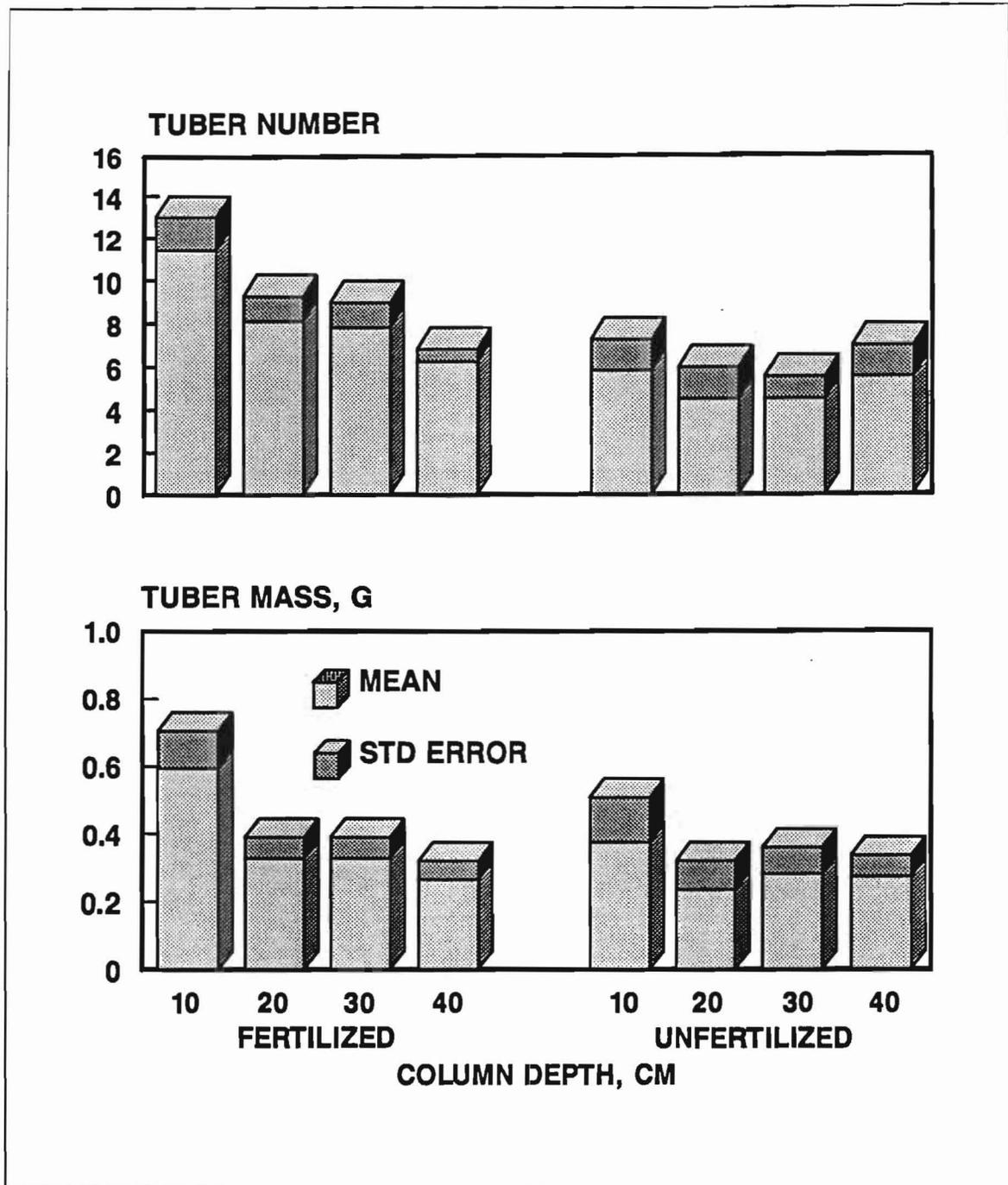


Figure 2. Tuber number and tuber mass of monoecious *Hydrilla verticillata* (L.f.) Royle planted in fertilized and unfertilized sediments of different depths. Values are means ($n = 6$) with their associated standard errors

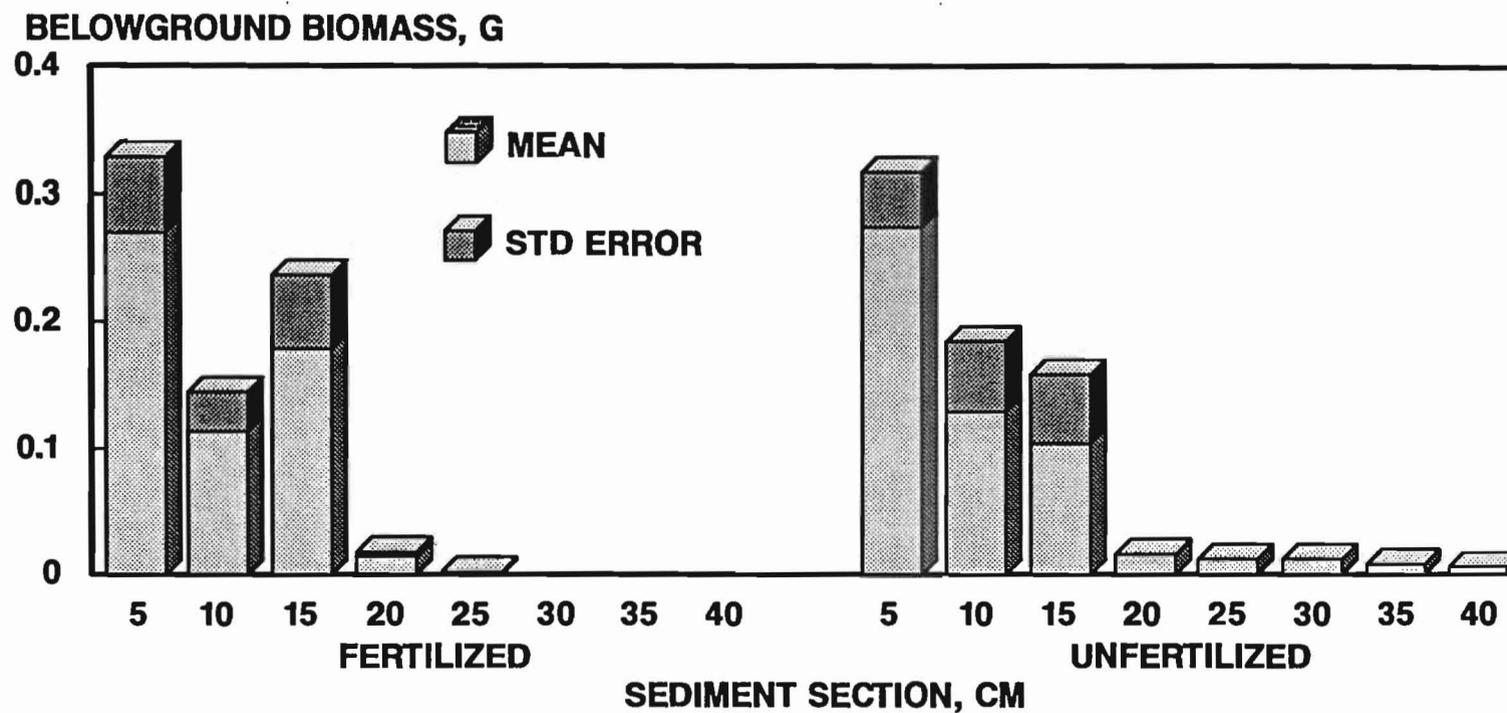


Figure 3. Belowground biomass of monoecious *Hydrilla verticillata* (L.f.) Royle in consecutive 5-cm (404-ml) sections of sediment (i.e., fertilized and unfertilized), from top to bottom of 40-cm-deep sediment tubes. Values are means ($n = 6$) with their associated standard errors

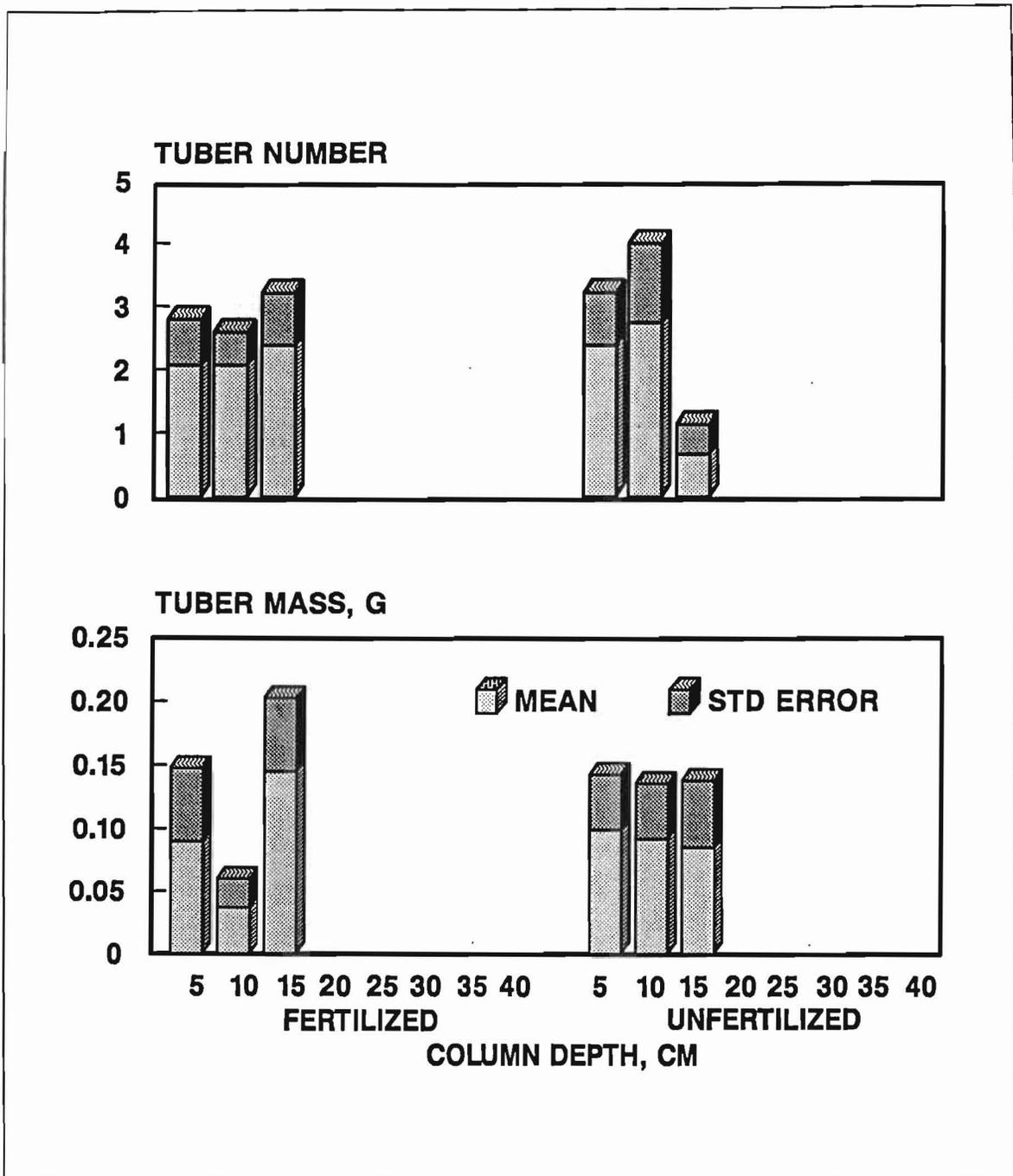


Figure 4. Tuber number and tuber mass of monoecious *Hydrilla verticillata* (L.f.) Royle in consecutive 5-cm (404-ml) sections of sediment (i.e., fertilized and unfertilized), from top to bottom of 40-cm-deep sediment tubes. Values are means ($n = 6$) with their associated standard errors

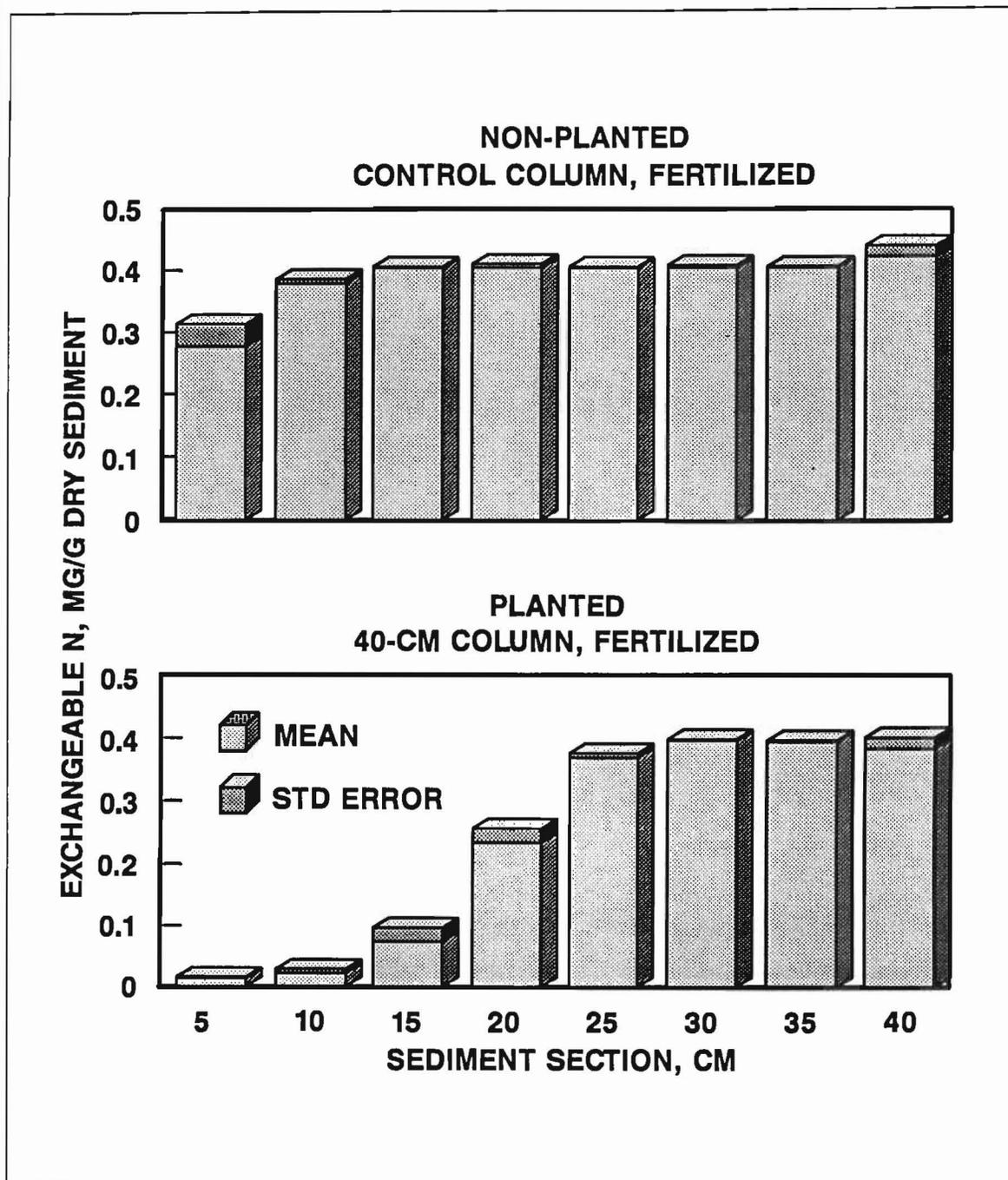


Figure 5. Concentrations of exchangeable N determined at the end of Experiment 1. Determinations are based on analyses of consecutive 5-cm sections (from top to bottom) of fertilized sediment, in 40-cm-deep sediment tubes. Means, both for non-planted control sediment ($n = 3$) and planted sediment ($n = 6$), are presented in top and bottom panels, respectively, with their associated standard errors

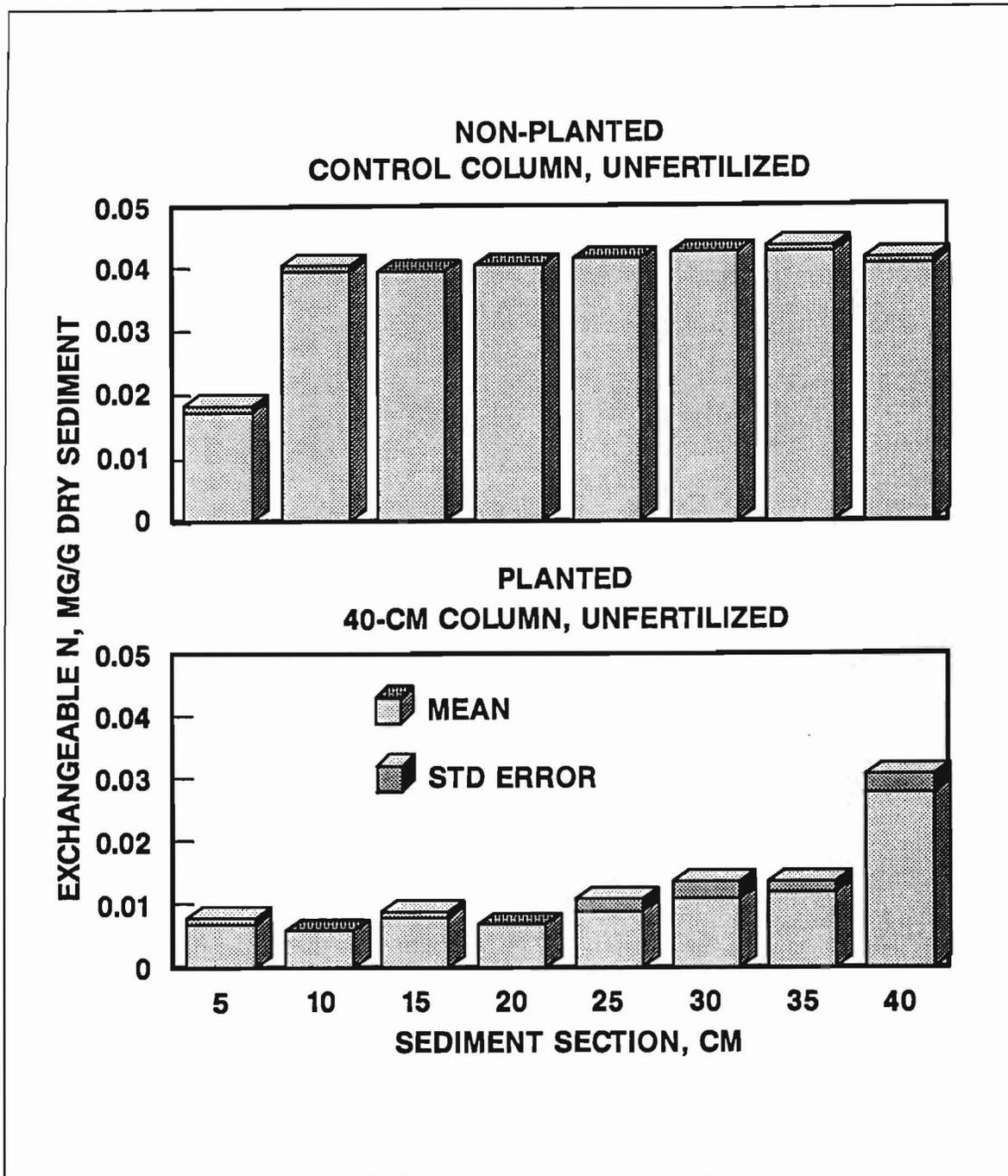


Figure 6. Concentrations of exchangeable N determined at the end of Experiment 1. Determinations are based on analyses of consecutive 5-cm sections (from top to bottom) of unfertilized sediment, in 40-cm-deep sediment tubes. Means, both for non-planted control sediment ($n = 3$) and planted sediment ($n = 6$), are presented in top and bottom panels, respectively, with their associated standard errors

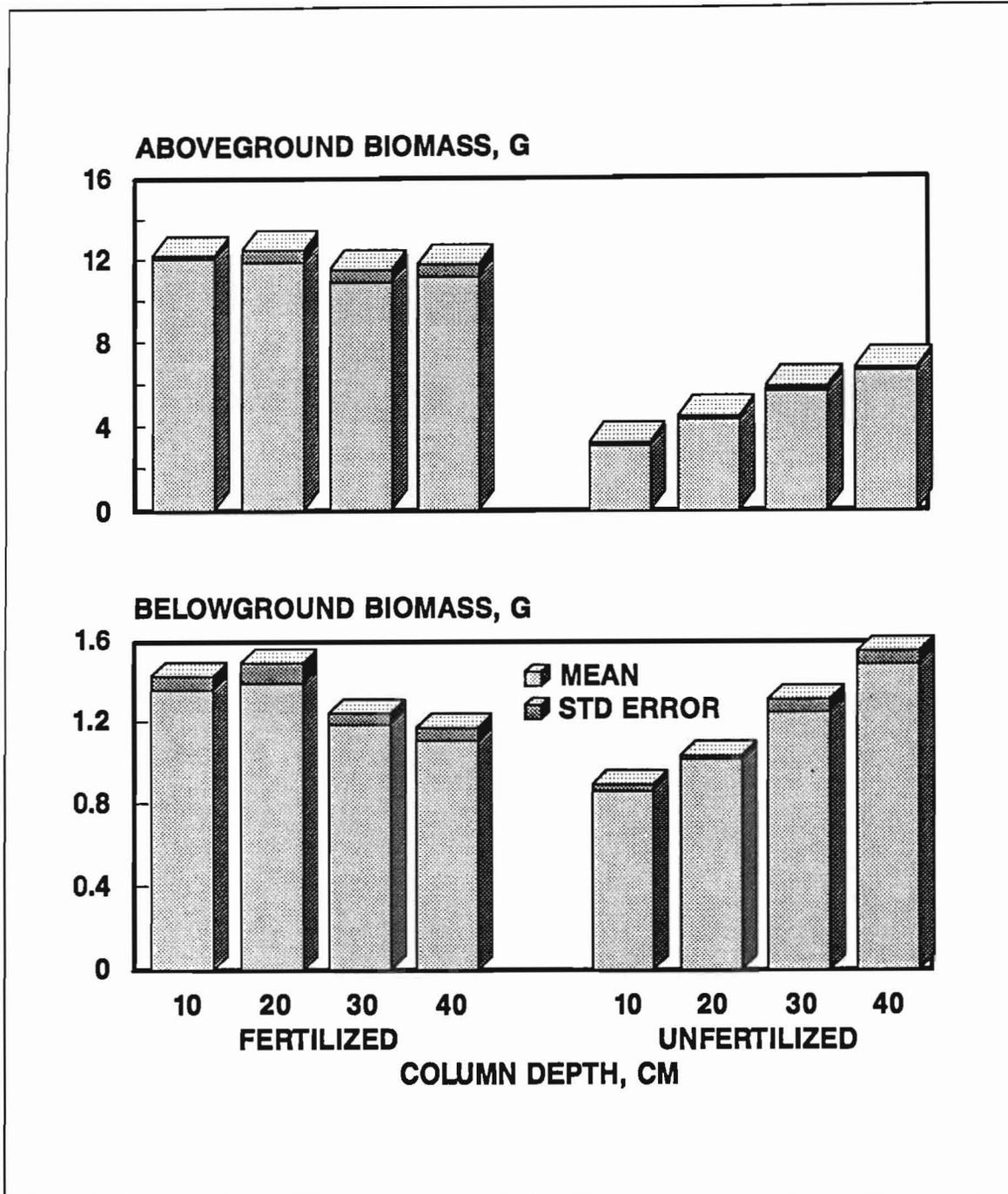


Figure 7. Aboveground and belowground biomass of *Myriophyllum spicatum* L. planted in fertilized and unfertilized sediments of different depths. Values are means ($n = 6$) with their associated standard errors

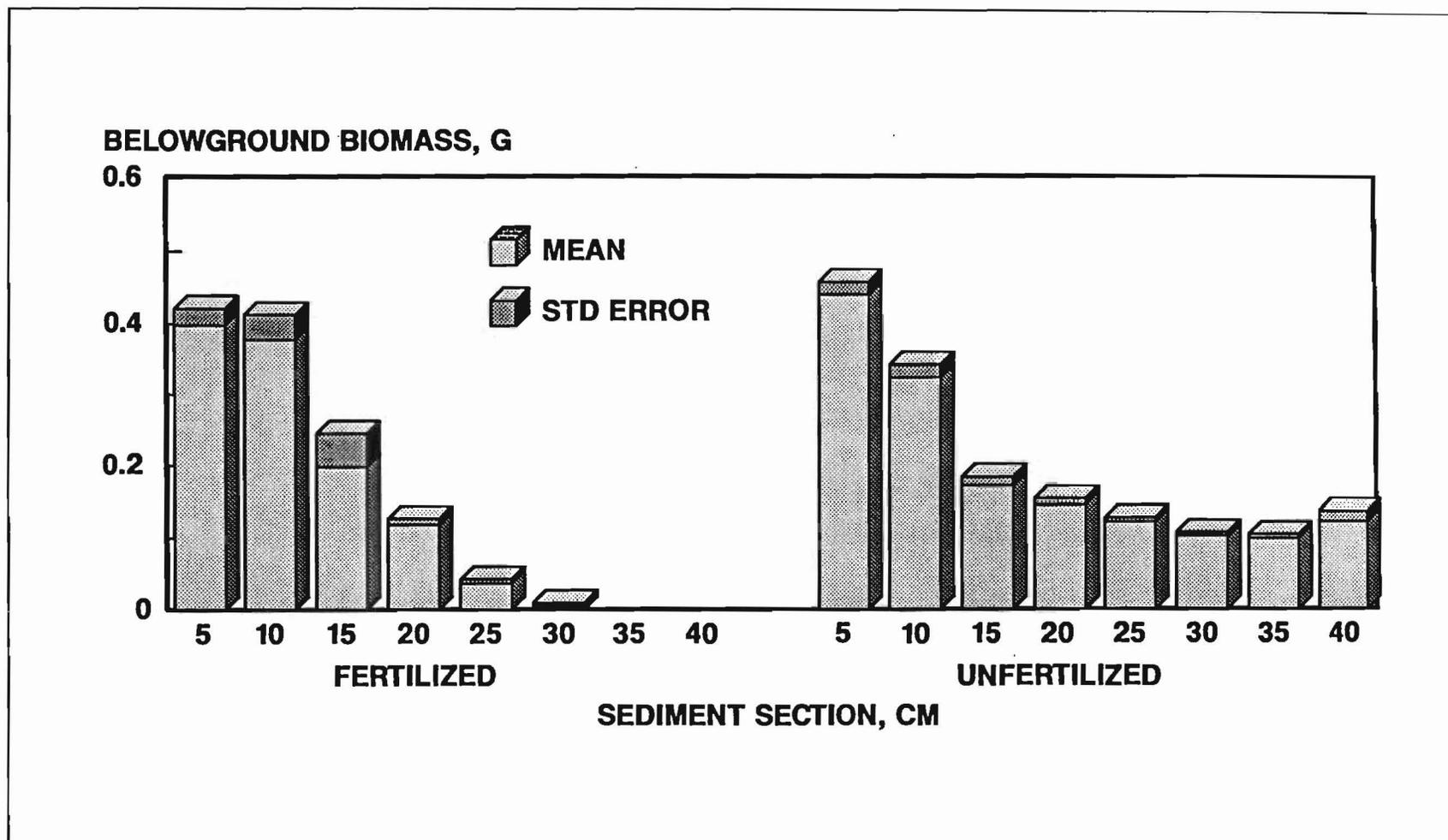


Figure 8. Belowground biomass of *Myriophyllum spicatum* L. in consecutive 5-cm (404-ml) sections of sediment (i.e., fertilized and unfertilized), from top to bottom of 40-cm-deep sediment tubes. Values are means ($n = 6$) with their associated standard errors

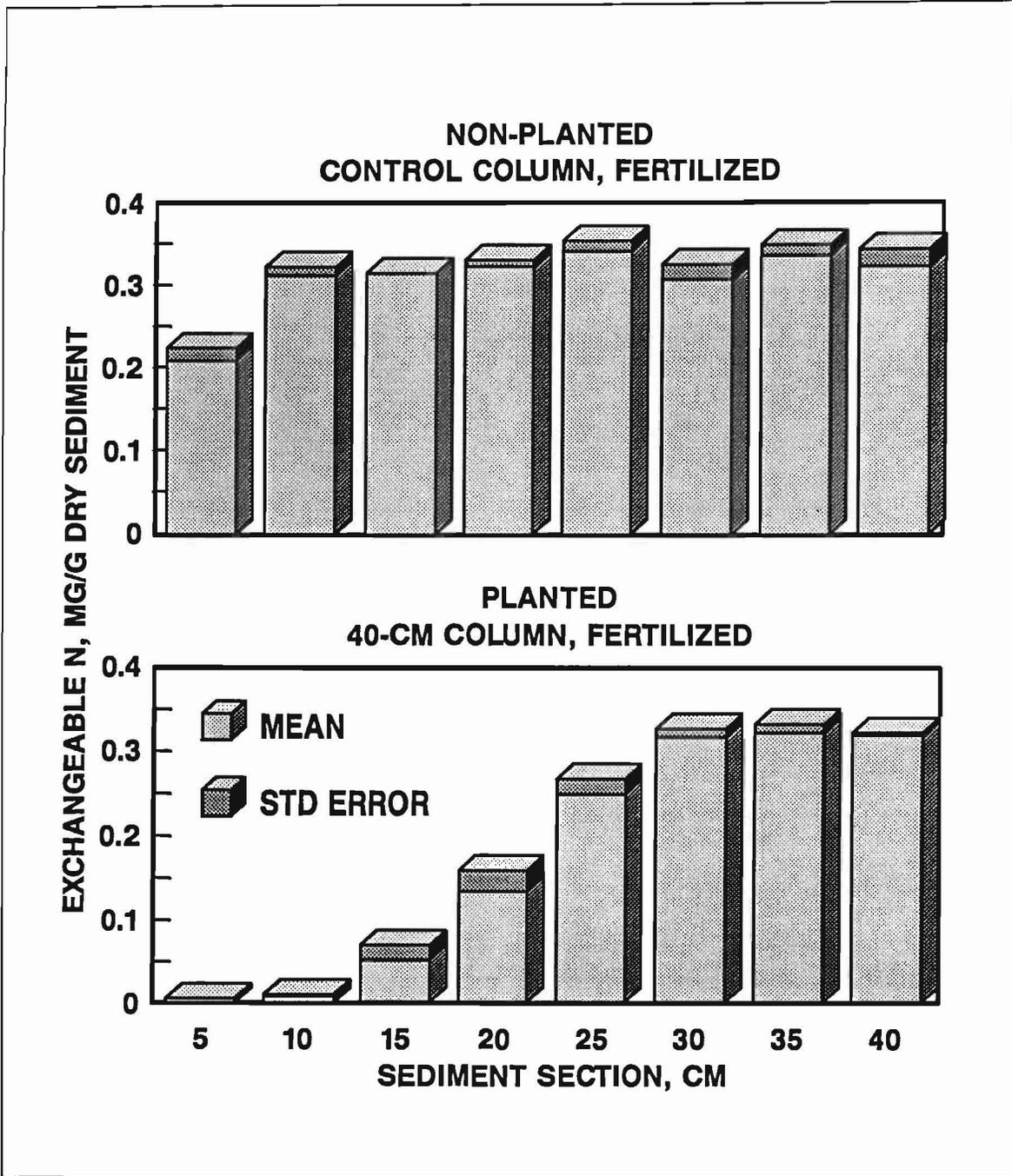


Figure 9. Concentrations of exchangeable N determined at the end of Experiment 2. Determinations are based on analyses of consecutive 5-cm sections (from top to bottom) of fertilized sediment, in 40-cm-deep sediment tubes. Means, both for non-planted control sediment ($n = 3$) and planted sediment ($n = 6$), are presented in top and bottom panels, respectively, with their associated standard errors

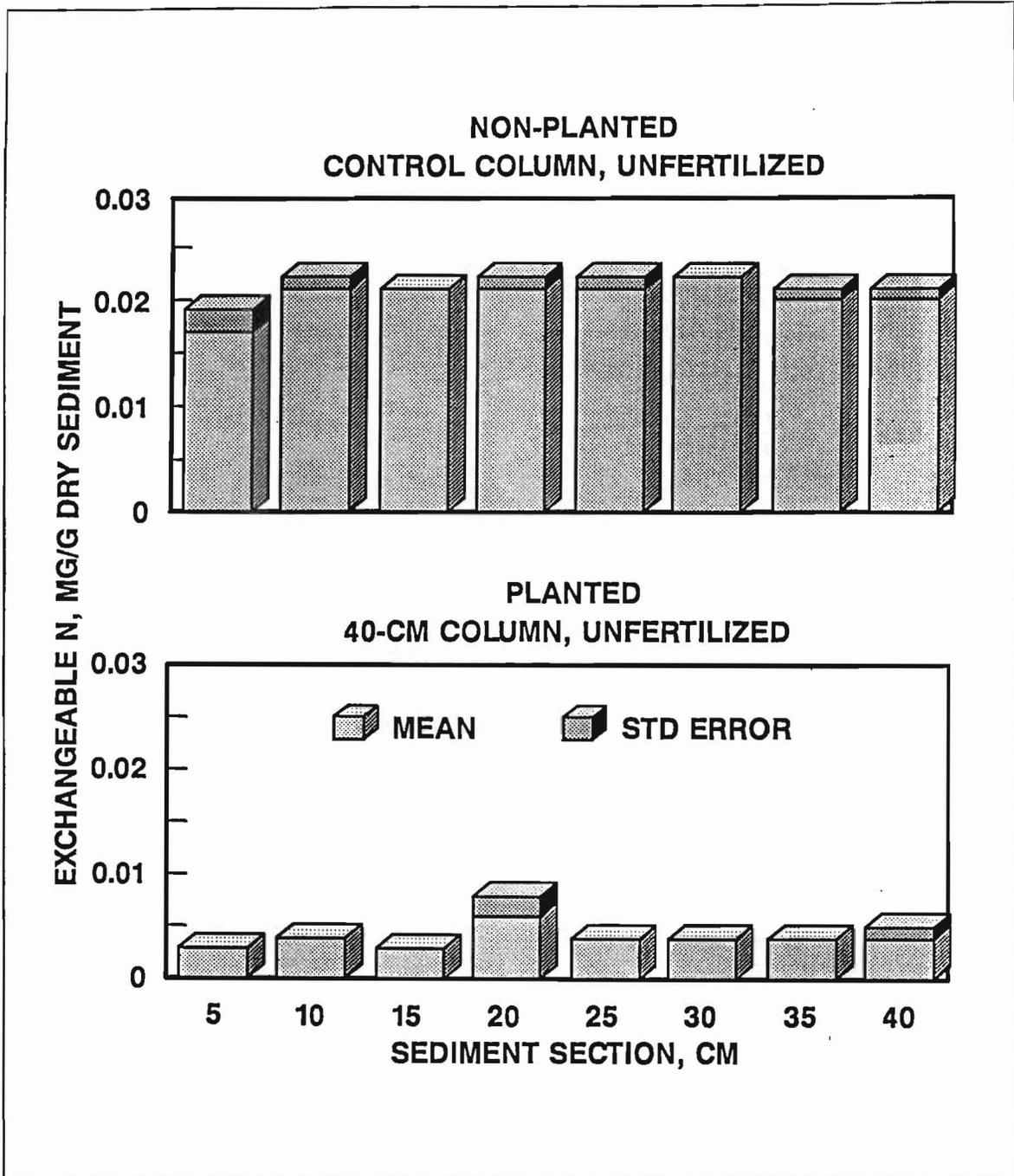


Figure 10. Concentrations of exchangeable N determined at the end of Experiment 2. Determinations are based on analyses of consecutive 5-cm sections (from top to bottom) of unfertilized sediment, in 40-cm-deep sediment tubes. Means, both for non-planted control sediment ($n = 3$) and planted sediment ($n = 6$), are presented in top and bottom panels, respectively, with their associated standard errors

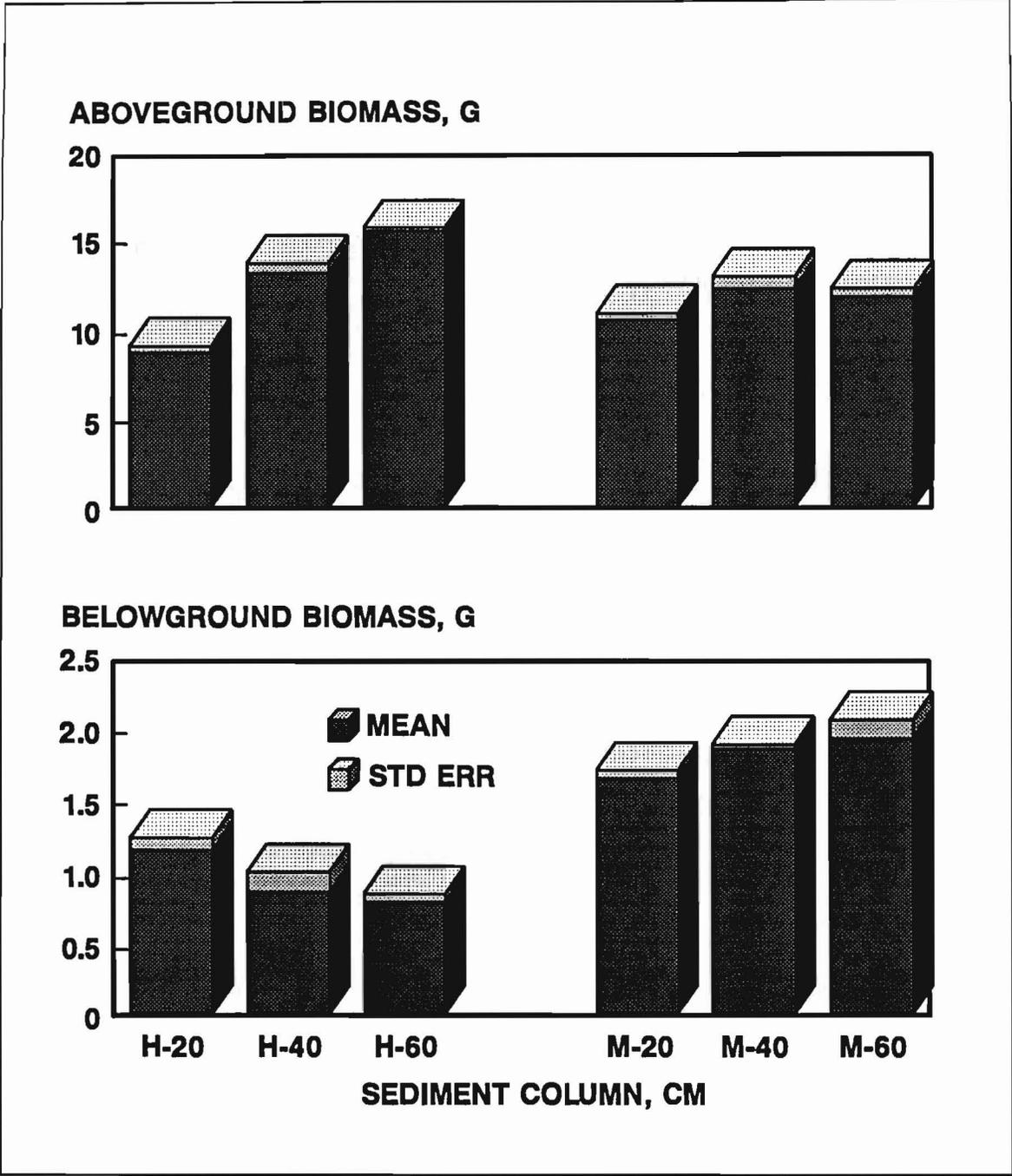


Figure 11. Aboveground and belowground biomass of monoecious *Hydrilla verticillata* (L.f.) Royle (H) and *Myriophyllum spicatum* L. (M) planted in fertilized and unfertilized sediments of different depths (i.e., 20, 40, and 60 cm). Values are means ($n = 6$) with their associated standard errors

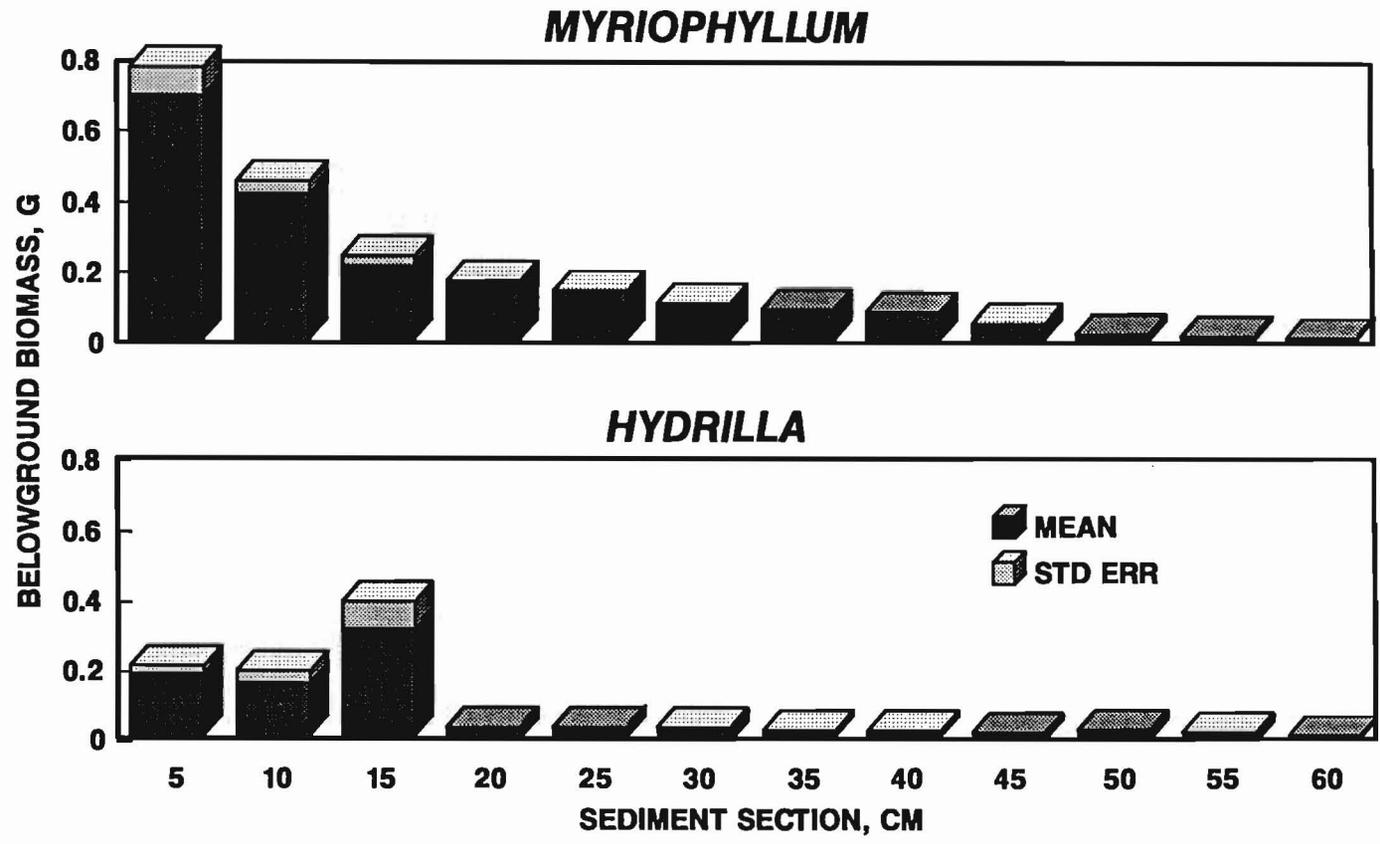


Figure 12. Belowground biomass of monoecious *Hydrilla verticillata* (L.f.) Royle and *Myriophyllum spicatum* L. in consecutive 5-cm (404-ml) sections of sediment (i.e., fertilized and unfertilized), from top to bottom of 60-cm-deep sediment tubes. Values are means ($n = 6$) with their associated standard errors

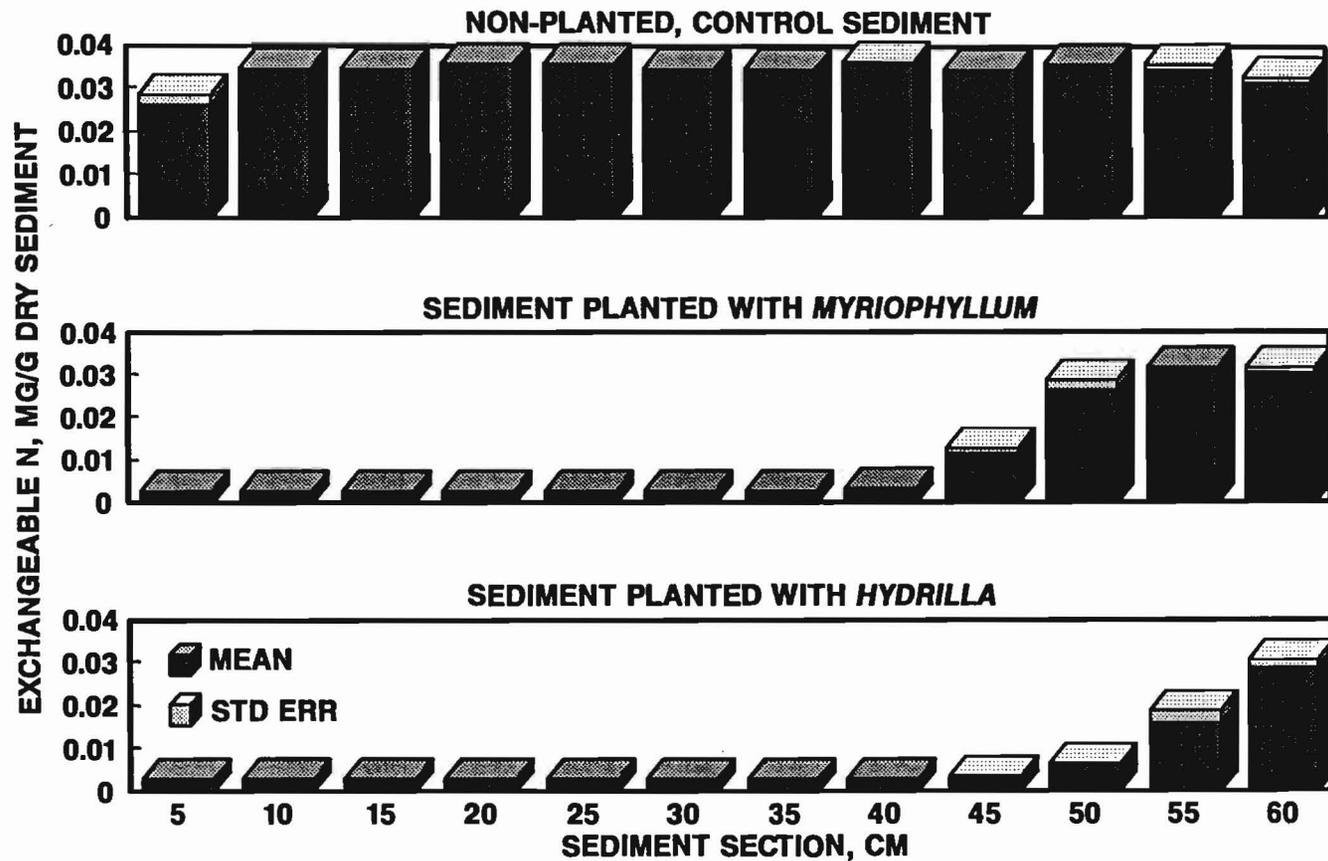


Figure 13. Concentrations of exchangeable N determined at the end of Experiment 3. Determinations are based on analyses of consecutive 5-cm sections (from top to bottom) of unfertilized sediment, in 60-cm-deep sediment tubes. Values are means ($n = 6$) with associated standard errors for non-planted control sediment (top panel), and sediment planted with *Myriophyllum spicatum* (middle panel) and monoecious *Hydrilla verticillata* (bottom panel)

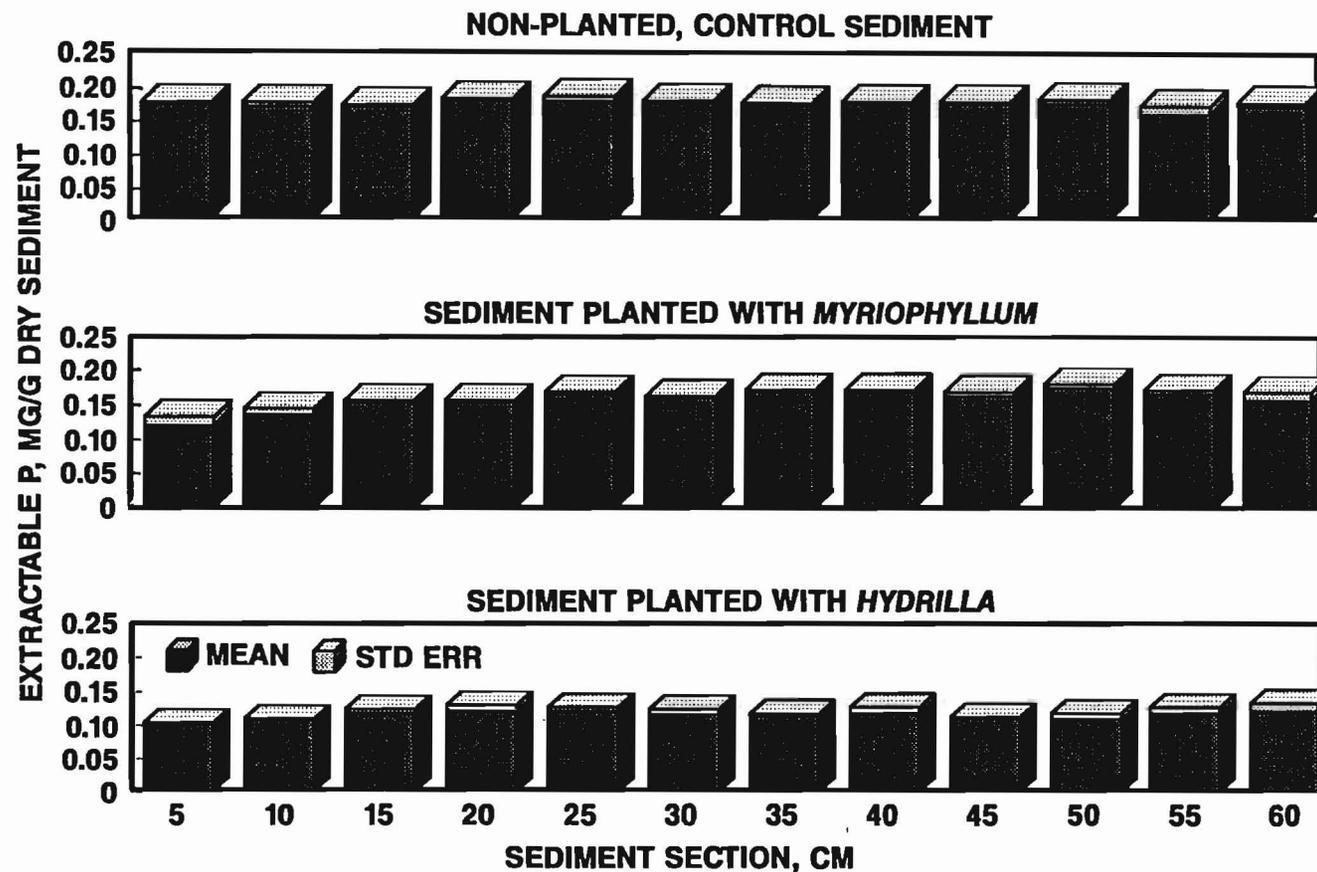


Figure 14. Concentrations of extractable P determined at the end of Experiment 3. Determinations are based on analyses of consecutive 5-cm sections (from top to bottom) of unfertilized sediment, in 60-cm-deep sediment tubes. Values are means ($n = 6$) with associated standard errors for non-planted control sediment (top panel), and sediment planted with *Myriophyllum spicatum* (middle panel) and monoecious *Hydrilla verticillata* (bottom panel)

Table 1
Nutrient Concentrations in Aboveground Tissues of *Hydrilla* and *Myriophyllum* on Unfertilized Sediment of Different Depths

Sediment Depth, cm	Nitrogen mg/g dry tissue		Phosphorus mg/g dry tissue	
	<i>Hydrilla</i>	<i>Myriophyllum</i>	<i>Hydrilla</i>	<i>Myriophyllum</i>
20	7.326 A*	5.586 a	2.209 A	2.114 a
40	9.987 B	9.886 b	2.594 B	2.709 b
60	10.715 C	10.941 c	2.830 C	2.738 b

Note: Within each column, values sharing the same letter (upper case for *Hydrilla* and lower case for *Myriophyllum*) do not differ significantly. Asterisk denotes values that are significantly greater for one species compared with the other. Duncan's Multiple Range Test and Student's t-test were used to determine statistical significance at $P < 0.05$.

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13. ABSTRACT (Maximum 200 words)

In a series of controlled greenhouse experiments, growth and rooting depth characteristics of *Hydrilla verticillata* (L.f.) Royle and *Myriophyllum spicatum* L. were examined relative to sediment-N availability, over a range of sediment depths from 10 to 60 cm. Each species was grown separately on fine-textured, inorganic sediment, either amended with ammonium chloride (N-amended) or rendered N-poor due to previous support of submersed macrophyte growth (nonamended). For both species, diminished biomass production was accompanied by increased root-to-shoot ratios and increased rooting depth (to 60 cm) on nonamended sediment. High production levels in *Myriophyllum* and *Hydrilla* on N-amended sediment were unaffected by sediment depth, indicating (along with high tissue N concentrations) that the availability of N under those conditions was nonlimiting. With increased depth of nonamended sediment, both *Hydrilla* and *Myriophyllum* increased production and mitigated N-deficiency in plant tissues by increasing root accession of this nutrient from greater sediment depths. This ability, speculated here to be more or less developed in other macrophyte species, may affect the outcome of interspecific interactions, particularly when N concentrations in sediment are low.

14. SUBJECT TERMS Aquatic plants Nitrogen Sediment composition <i>Hydrilla</i> Nutrient limitation Sediment nutrient availability <i>Myriophyllum</i> Nutrient uptake Submersed macrophytes	15. NUMBER OF PAGES 39
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