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EFFECTS OF WATER CHEMISTRY ON AQUATIC PLANTS: INTERRELATIONSHIPS AMONG BIOMASS PRODUCTION, PLANT NUTRITION, AND WATER CHEMISTRY

by

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<i>Egeria</i>	Nutrient uptake	Water chemistry

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indicating that plant photosynthetic requirements were greatly in excess of the added CO₂. Depletions of solution K were attributed to foliar uptake of K.

Plant growth was shown to be limited by inorganic carbon supply in the low-cation, low-carbon solution, and by sediment nitrogen (N) availability in the higher cation, higher carbon solutions. The response of submersed aquatic plants to solution was thus affected by sediment N supply. While plant requirements of N and P (phosphorus) were provided by root uptake from sediment, K was provided by foliar uptake from solution.

Both inorganic carbon and sediment N were identified as factors potentially limiting the growth of field populations of submersed aquatic plants.

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Preface

The studies reported herein 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 Aquatic Plant Control Research Program (ARCRP). Funds were provided by DAEN-CW under Department of the Army Appropriation No. 96X3122 Construction General. Technical Monitor for OCE was Mr. E. Carl Brown. The APCRP is managed by the US Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss.

Principal Investigator for this study was Dr. R. Michael Smart, Environmental Laboratory (EL), WES. Experimental design, data analysis, and interpretation were provided by Dr. Smart and Dr. John W. Barko. The report was prepared by Dr. Smart. Technical assistance was provided by Mr. James Conley, Ms. Susie Hennington, Ms. Avis Howell, Ms. Dwilette McFarland, Mr. Don Schwartz, and Ms. Ramona Warren. Technical reviews were provided by Drs. Thomas L. Hart and Rex L. Chen. The report was edited by Ms. Jessica S. Ruff of the WES Information Technology Laboratory.

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, and under the direct supervision of Dr. Hart, Chief, Aquatic Processes and Effects Group. The APCRP was managed by Mr. J. Lewis Decell, EL.

Commander and Director of WES was COL Dwayne G. Lee, CE. Technical Director was Dr. Robert W. Whalin.

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EFFECTS OF WATER CHEMISTRY ON AQUATIC PLANTS:
INTERRELATIONSHIPS AMONG BIOMASS PRODUCTION,
PLANT NUTRITION, AND WATER CHEMISTRY

Introduction

Background

1. Previous investigations concerned with the growth and distribution of submersed aquatic plants have considered the important roles of light, temperature, and the physical and chemical composition of the sediments. These investigations have progressed from early observations regarding apparent relationships between the distribution of species and certain environmental factors (Pearsall 1920, Misra 1938) through rigorous experimental studies demonstrating the effects of these factors on plant growth (Barko and Smart 1981a, 1983, 1986). While it has long been realized that the chemical composition of the water can also affect the growth and distribution of submersed aquatic plants (West 1905, Bourn 1932, Moyle 1945, Spence 1967, Seddon 1972, Hutchinson 1975), this area has been less intensively studied. Many water chemistry parameters have been correlated with the distribution of different species of aquatic plants. However, since many of these parameters are correlated with each other, and since water chemistry is often related to sediment composition (Pearsall 1920, Moyle 1945), it is difficult to ascribe differences in growth and distribution to specific water chemistry parameters. This difficulty hinders both our ability to predict the likelihood of excessive growth of submersed aquatic vegetation and our ability to develop specific plant management options.

2. From previous investigations of plant growth in relation to water chemistry (Smart and Barko 1985, 1986), we have learned that the water chemistry parameter most likely to affect growth is dissolved inorganic carbon (C_T). This element, which accounts for more than 40 percent of the dry weight of aquatic plants (Sculthorpe 1967, Hutchinson 1975), generally occurs at levels much less than are required to support maximal photosynthesis by submersed aquatic plants (Smart and Barko 1986).

3. In a prior study of the effects of water chemistry on the growth of *Myriophyllum spicatum*, determination of the effects of solution C_T on growth were hampered by depletion of C_T from solution (Smart and Barko 1986). After

only a few weeks growth, C_T levels were reduced to less than half of their original concentration due to the effects of photosynthetic C_T uptake and $CaCO_3$ precipitation (Smart and Barko 1986). Aerating the solution with CO_2 -enriched air ameliorated the depletion of C_T and allowed the determination of the effects of C_T on plant growth.

4. Under certain rare circumstances, low concentrations of dissolved calcium (Ca), in combination with low levels of C_T , may adversely affect plant growth and distribution (Smart and Barko 1986). Low concentrations of dissolved potassium (K) can also limit the growth of submersed aquatic plants (Gerloff 1975, Barko 1982); however, considering the relatively high levels of dissolved K in most surface waters, we expect K limitation to be uncommon (Barko 1982, Smart and Barko 1986). The macronutrient elements, nitrogen (N) and phosphorus (P), are acquired primarily from sediment rather than from the water column (Smart and Barko 1985, Barko and Smart 1986); thus, low concentrations of these in the water column of lacustrine systems rarely limit the growth of rooted submersed aquatic plants.

5. Considering the importance of C_T levels in affecting photosynthesis, the relative abilities of different species to deplete C_T may be indicative of associated competitive abilities in waters of different chemical composition. The experiment reported herein examined the ability of the rooted, submersed aquatic plants *Egeria densa*, *Hydrilla verticillata*, and *Potamogeton nodosus* to deplete solution C_T and nutrient levels (Ca, magnesium (Mg), sodium (Na), and K) levels. *Egeria* and *Hydrilla* are strictly submersed species, while *Potamogeton* exhibits heterophylly, developing morphologically distinct submersed and floating leaves (Sculthorpe 1967). All of these species are capable of HCO_3^- uptake, and the floating leaves of *Potamogeton* are capable of fixing atmospheric CO_2 as well.

6. This study also determined the influence of different levels of CO_2 supply, solution C_T , and nutrients on the growth and nutrition of these species. The influence of these parameters on the growth of these species should be indicative of the relative importance of water chemistry in affecting differences in growth and distribution.

Study objectives

7. The objectives of this study were to evaluate:

a. The effects of plant growth on solution chemical composition.

- b. Interrelationships among solution chemistry, plant growth, and plant nutrition.
- c. The relative importance of solution and sediment as potential growth-limiting factors.

Materials and Methods

8. The experiment was conducted during the summer growing season (June through August), in 150- by 90- by 90-cm-deep, white fiberglass tanks in the greenhouse facility of the Environmental Laboratory, US Army Engineer Waterways Experiment Station. Solutions were maintained at $25^{\circ} \pm 1^{\circ} \text{ C}$ with thermostatically controlled liquid circulators (Remcor Corp., Chicago, Ill.). Experimental tanks were fitted with lucite covers to prevent the entry of dust and other contaminants. Neutral density shade fabric was used to reduce solar irradiance to photosynthetically active radiation levels of about $750 \mu\text{E m}^{-2} \text{ sec}^{-1}$, measured at midday.

9. Experimental solutions were formulated by additions of reagent grade chemicals to deionized (reverse osmosis) water. Gaseous CO_2 was administered to solution prior to adding required amounts of CaCO_3 to achieve solubility (Smart and Barko 1984, 1985). The chemical composition of the experimental solutions was verified by chemical analysis. Samples of each of the solutions were collected and analyzed weekly for Na, K, Ca, and Mg by atomic absorption spectrophotometry. Electrical conductivity (25° C) was determined with a Yellow Springs Instrument Model 32 conductivity meter. Dissolved inorganic carbon was determined with a Beckman Model 915A Total Organic Carbon Analyzer. Solution pH was measured with a Beckman Expandomatic IV expanded-scale pH meter. Alkalinity and acidity calculations were determined according to equations provided in Stumm and Morgan (1981).

10. Sediment used in the experiment was collected from Lake Washington, Washington, USA. This sediment was selected based on earlier investigations which indicated a high potential for supporting luxuriant submersed macrophyte growth (Barko and Smart 1981a, 1983, 1986). Physical and chemical characteristics of the sediment were similar to those provided earlier (Barko and Smart 1983, 1986). Sediment was stored at room temperature under anaerobic conditions until needed. The sediment was thoroughly mixed with a rotary mixer and allocated to 1-l sediment containers a few days prior to experimentation.

11. Apical shoots, 15 cm in length, were taken from greenhouse cultures of *Egeria* and *Hydrilla* that had been maintained at 25° C and at light levels similar to those used in the experiments. Tubers of *P. nodosus* were obtained from a commercial source (Wildlife Nurseries, Oshkosh, Wis.). Four apices or tubers were randomly selected and allocated to each container. After planting, a 2-cm layer of washed silica sand was placed over the sediment to minimize physical exchanges with the overlying water.

12. Plants were grown for a period of 7 weeks. At termination of the experiments, plant shoots were clipped at the sediment surface, rinsed briefly (30 sec) in dilute (2-percent) HCl to remove CaCO_3 encrustation (Allenby 1981), rinsed in deionized water, bagged, and dried at 80° C in a forced-draft oven to constant weight. Roots were washed over a 1-mm sieve to remove sediment and debris, and dried as for shoots. Weights of root and shoot samples were recorded to the nearest milligram. Biomass accrual (final biomass minus initial propagule biomass) was used as a measure of plant growth in all experiments. Root and shoot samples were ground in a Wiley mill to pass a 40-mesh sieve. Subsamples of the dried and ground material were combusted in a muffle furnace at 550° C to determine ash content. Additional subsamples were digested in H_2O_2 - H_2SO_4 (Allen et al. 1974) and analyzed for total Kjeldahl nitrogen and total P on a Technicon Autoanalyzer. Major cations (Na, K, Ca, Mg) were determined on the same digestate by atomic absorption spectrophotometry.

13. Three experimental solutions, representing different dilutions of the alkaline solution of Smart and Barko (1985), were used for the experiment. Major cation concentrations and C_T levels in the solutions (Table 1) were based on analyses of bicarbonate lake waters (Hutchinson 1957) and were selected to cover a broad range in water composition. Concentrations of the major cations and C_T in the high-level solution were 6X those in the low-level solution, with the midlevel solution being 3X the concentration of the low-level solution. These solutions are identical to those used in earlier work with *Myriophyllum spicatum* (Smart and Barko 1986).

14. In an attempt to determine the influence of solution C_T on the growth of these species, two aeration treatments were employed: ambient air ($350 \mu\text{l CO}_2 \text{ l}^{-1}$) and air-enriched fourfold in CO_2 concentration ($1,400 \mu\text{l CO}_2 \text{ l}^{-1}$). It was reasoned that the additional CO_2 would maintain C_T at the original levels, allowing for an evaluation of the effects of different levels of

Table 1
Chemical Composition and Characterization of Solutions Used in the Experiment

Solution Level	Chemical Composition, mg ℓ^{-1}							Alkalinity meq ℓ^{-1}	pH
	Calcium	Magnesium	Sodium	Potassium	Dissolved Inorganic Carbon	Chloride	Sulfate		
Low	10.0	1.7	2.8	1.0	3.5	7.3	13.8	0.29	7.5
Mid	30.0	5.0	8.4	3.1	10.5	22.0	41.5	0.88	8.0
High	60.0	10.1	16.9	6.1	21.0	44.0	83.0	1.75	8.3

C_T on growth (Smart and Barko 1986). Aeration was accomplished by administering humidified, compressed air (or CO_2 -enriched air) at a rate of $2.5 \ell \text{ min}^{-1}$ through each of two air lifts in each tank. This aeration rate is identical to that used in earlier work with *M. spicatum* (Smart and Barko 1986).

15. The experiment was conducted and analyzed as a $3 \times 3 \times 2$ factorial design, with three species, three solutions, and two aeration levels, for a total of 18 treatment combinations. Each treatment combination was randomly assigned one of 18 individual tanks in the greenhouse. Six replicate containers were planted in each tank. Data were subjected to one- and two-way analysis of variance procedures as appropriate (General Linear Models Procedure, Statistical Analysis System, Cary, N. C.). Mean comparisons were performed using Duncan's Multiple Range Test. Statistically significant differences referred to in the text were evaluated at the 5-percent (or less) level of statistical probability.

16. The midlevel solution-high CO_2 aeration treatment combination for *Egeria* was lost during the study due to apparent contamination of the solution followed by a massive phytoplankton bloom, resulting in greatly diminished plant growth relative to the other *Egeria* treatments. This treatment combination was subsequently eliminated from statistical analysis of the experimental results.

Results and Discussion

Effects of plant growth on solution chemistry

17. All of the species examined rapidly depleted C_T in the mid- and high-level solutions (Figure 1). The period of most rapid C_T decline, between week 2 and week 4, coincided with the period of most active plant growth. There were only slight differences in the C_T depletion curves for the three species, indicating that these species do not differ greatly in their ability to extract inorganic carbon from solution. Augmenting the airstream CO_2 concentration did not prevent the depletion of C_T from the mid- and high-level solutions by either *Hydrilla* or *Egeria*. However, addition of CO_2 to the high-level solution supporting *Potamogeton* did partially offset depletion of C_T . This suggests either that this floating-leaved species is less effective at HCO_3^- uptake than the strictly submersed species or that, with access to abundant atmospheric CO_2 supplies via floating leaves, this species may be less adapted to deplete levels of solution C_T .

18. Concurrent with the decrease in C_T from the mid- and high-level solutions, there was a decline in solution Ca (Figure 1), indicating that $CaCO_3$ precipitation may have been partially responsible for the observed C_T depletion. Augmenting the airstream CO_2 supply partially alleviated the decline in solution Ca in the high-level solution.

19. The parameters acidity and alkalinity have been previously demonstrated to be quantitatively related to photosynthetic C_T uptake and $CaCO_3$ precipitation, respectively (Smart and Barko 1986). Thus, in order to determine the relative influences of photosynthesis and $CaCO_3$ precipitation on solution C_T depletion, acidity and alkalinity were calculated from measured values of C_T and pH (Stumm and Morgan 1981). Both acidity and alkalinity declined in the mid- and high-level solutions (Figure 2), indicating that both photosynthesis and precipitation were responsible for declines in solution C_T . Declines in acidity and alkalinity were greatest in the strictly submersed species, *Hydrilla* and *Egeria*, and least in the floating-leaved species, *Potamogeton*. The addition of CO_2 slightly reduced the rates of decline of acidity and alkalinity in solutions supporting *Egeria* and *Hydrilla*, and was somewhat more effective at retarding changes in these parameters in solutions supporting *Potamogeton*.

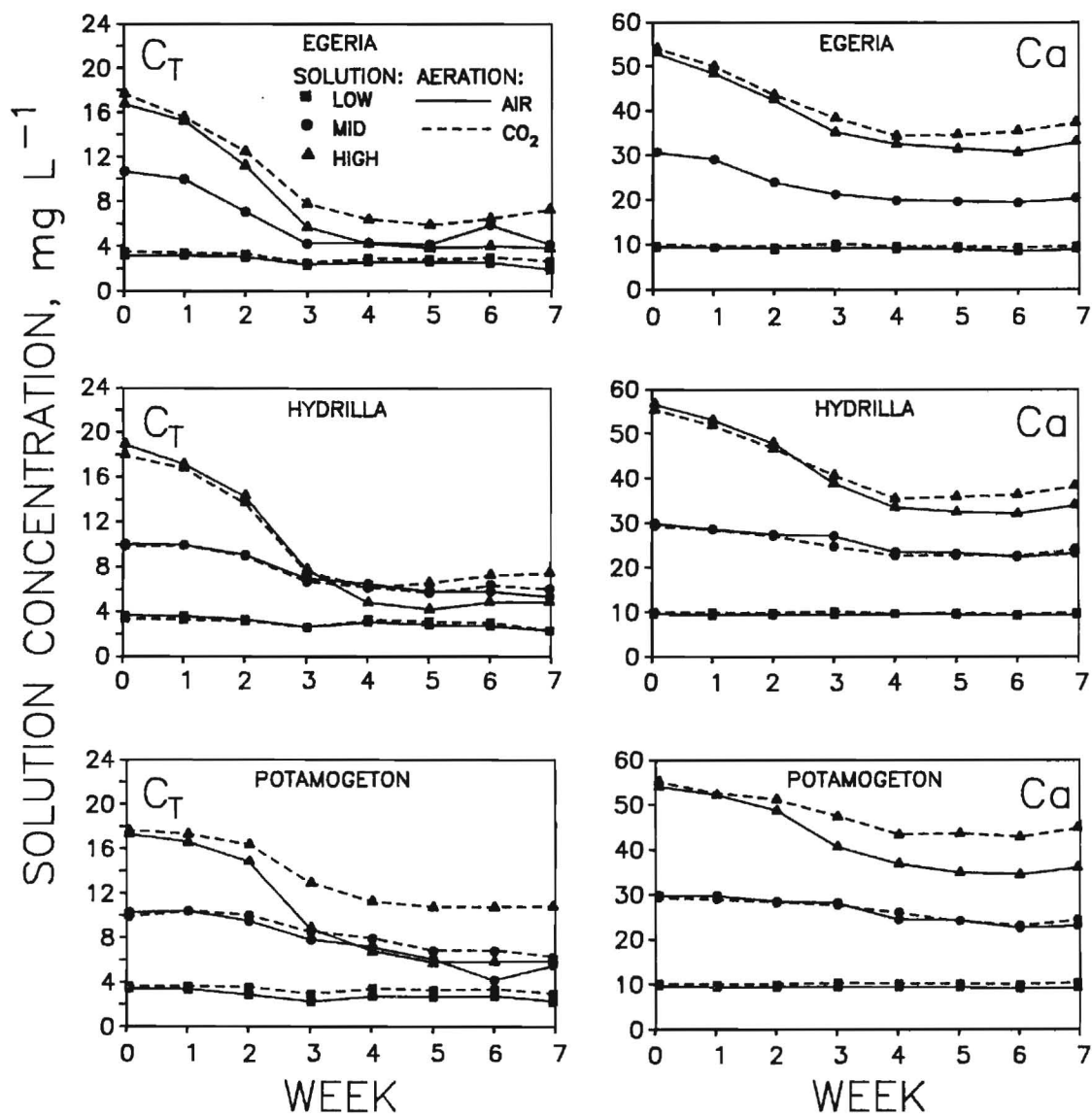


Figure 1. Temporal changes in C_T and Ca in the low-, mid-, and high-level solutions as affected by the growth of *Egeria*, *Hydrilla*, and *Potamogeton* and by aeration regime. Values are single observations

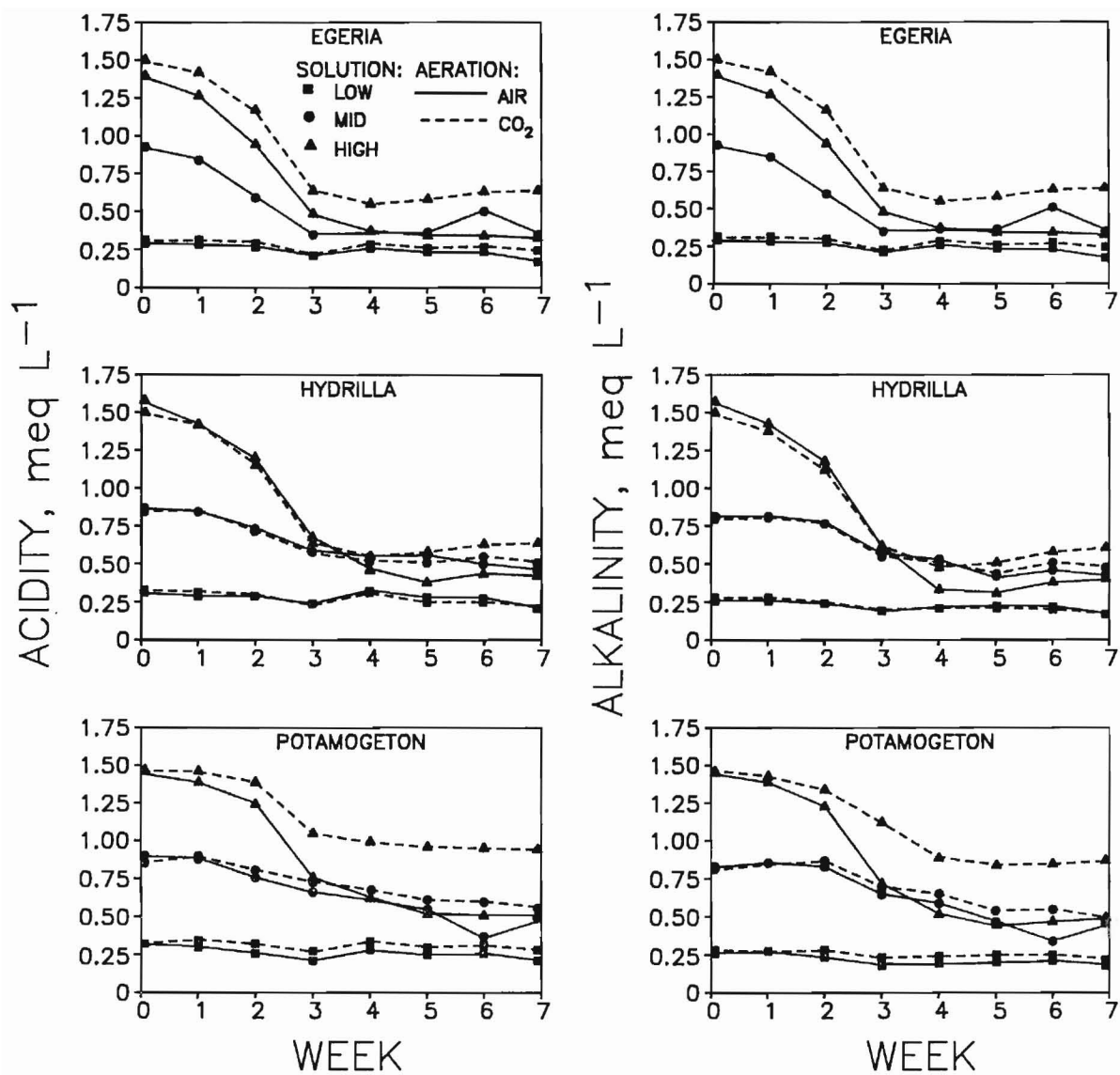


Figure 2. Temporal changes in acidity and alkalinity in the low-, mid-, and high-level solutions as affected by the growth of *Egeria*, *Hydrilla*, and *Potamogeton* and by aeration regime. Acidity and alkalinity were calculated from measured values of C_T and pH

20. The similarity in the rates of decline of Ca and alkalinity prompted an analysis of the stoichiometric relationship between these parameters (Figure 3). Within the mid- and high-level solutions, there were significant relationships between changes in solution Ca and alkalinity (Figure 3a). There were no appreciable differences in the slopes of the Ca-alkalinity relationships among the three species or between the mid- and

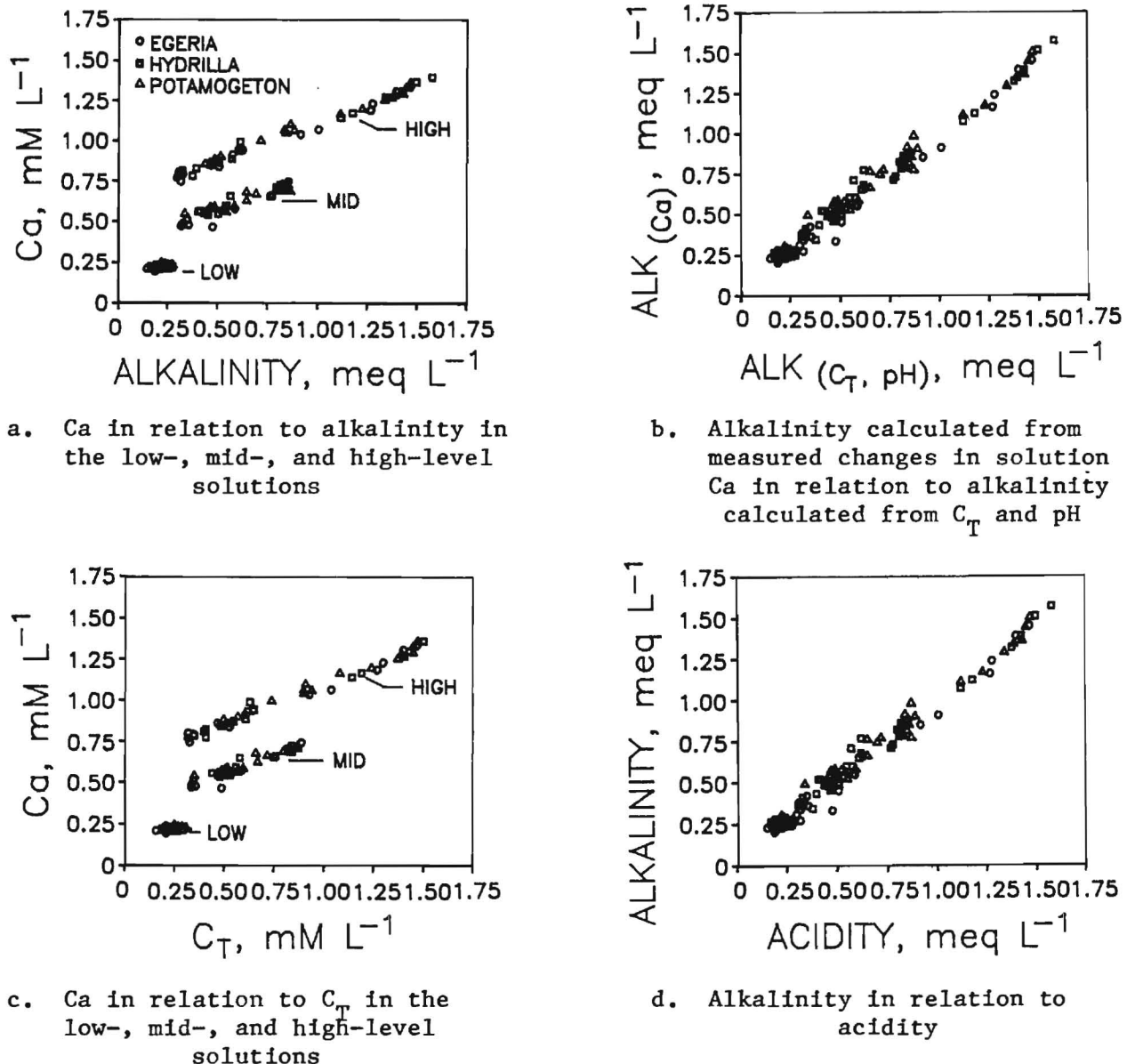


Figure 3. Relationships among water chemistry parameters as affected by the growth of *Egeria*, *Hydrilla*, and *Potamogeton* during the course of the experiment

high-level solutions (0.48 and 0.47 mM meq^{-1} , respectively). These values are very close to the expected stoichiometric relationship of 0.5 mM meq^{-1} , suggesting that most of the change in solution Ca was due to the precipitation of CaCO_3 . This indication was checked by calculating alkalinity from measured decreases in Ca and comparing these values with alkalinity calculated from C_T and pH (Figure 3b). The two alkalinity calculations are in very close agreement ($r^2 = 0.98$, slope = 0.94, intercept = 0.07). This close agreement indicates that Ca depletion was due to precipitation rather than to plant uptake of Ca and that alkalinity was not appreciably affected by processes (e.g., imbalances in cation/anion uptake) other than CaCO_3 precipitation. The similarity in the Ca-alkalinity relationships among the three species also indicates that there were no species-specific differences in CaCO_3 precipitation.

21. Changes in solution Ca were also closely related to changes in solution C_T (Figure 3c). The slope of the Ca versus C_T relationship for both the mid- and high-level solutions was 0.47 mM Ca \cdot mM C_T^{-1} . Thus, for every two carbon atoms removed from solution via photosynthesis or precipitation, approximately one Ca (and one carbon) atom was precipitated as CaCO_3 . The close relationship between CaCO_3 precipitation (change in alkalinity) and photosynthetic C_T uptake (change in acidity) indicates that precipitation is tightly coupled with photosynthesis (Figure 3d).

22. These results indicate that, once the solubility product of CaCO_3 is exceeded, continued uptake of C_T results in the loss of one carbon atom for each carbon atom fixed in photosynthesis. While CaCO_3 precipitation lessens the increase in solution pH associated with C_T uptake (Smart and Barko 1986), this process also decreases quantities of solution C_T for further photosynthesis, lessens the gradient driving the exchange between atmospheric CO_2 and the solution, and deposits CaCO_3 crystals on photosynthetic surfaces (Smart and Barko 1986). Deposition of CaCO_3 on leaf surfaces potentially impedes photosynthesis and has been associated with reduced growth of *M. spicatum* (Smart and Barko 1986).

23. Concentrations of solution K measured at the end of the experiment were significantly less in all solutions than those measured at the beginning (Figure 4). Each of the species caused similar declines in solution K. With the exception of *Hydrilla* grown under ambient air aeration, all of the species completely exhausted K supplies from the low-level solution. Slightly greater quantities were removed from the higher K solutions. Since K has been shown

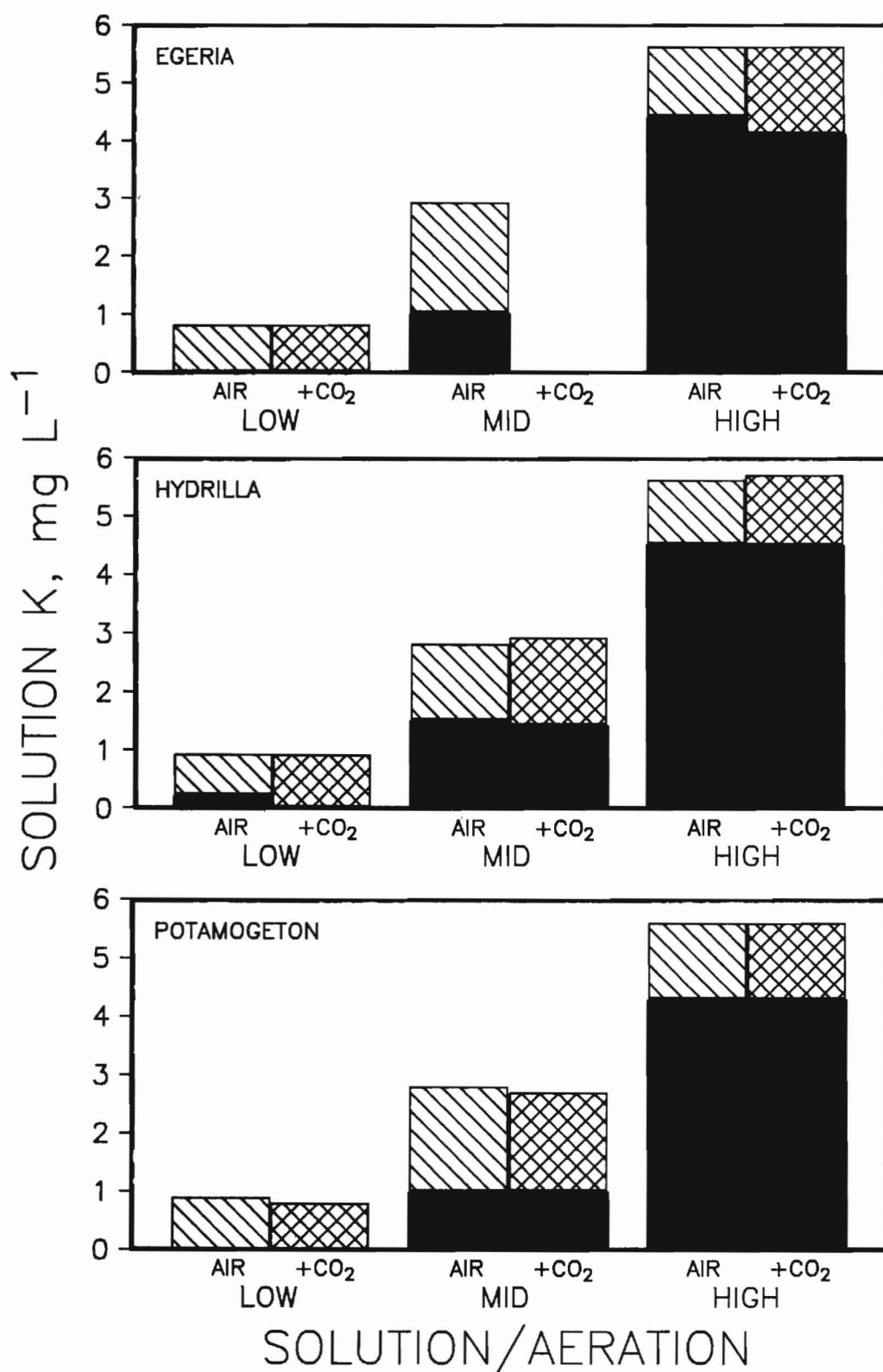


Figure 4. Solution K depletion as determined from K concentrations measured at the beginning and end of the experiment. Concentration differences (hatched portions of the bars) between initial concentrations (total bar height) and final concentrations (dark portions of the bars) were significantly greater than 0, as determined by paired-comparisons t tests

to be acquired by uptake from solution rather than from sediment (Barko 1982, Huebert and Gorham 1983), depletion of solution K probably resulted from foliar uptake.

24. Concentrations of solution Mg and Na measured at the end of the experiment were generally not appreciably different than those measured at the beginning. Solutions supporting the growth of *Hydrilla* exhibited measurable and statistically significant decreases in Mg concentration; however, the magnitude of the depletion was slight (0.2 mg l^{-1}). While Mg may be acquired from solution (Huebert and Gorham 1983), the source of Na is less certain (Smart and Barko 1985); both shoots and roots have been demonstrated to take up Na (Shepherd and Bowling 1973; Waisel, Agami, and Shapira 1982).

Effects of solution on plant growth and nutrition

25. As a result of photosynthetic carbon depletion, levels of C_T in the mid- and high-level C_T solutions were not significantly different throughout much of the study period. Aeration with CO_2 -enriched air (4X ambient) did not prevent the depletion of solution C_T . Thus, the second objective, to determine the influence of different levels of C_T on the growth of these species, could be only partially resolved. Nevertheless, growth of each of the species was responsive to increasing levels of C_T between the low and higher levels (Figure 5). A similar response was observed earlier for *M. spicatum* (Smart and Barko 1986).

26. While each of the species responded to increased C_T , none of the species consistently responded to increased airstream CO_2 concentration (Figure 5). However, as previously shown, increasing the CO_2 concentration fourfold did not prevent the depletion of C_T , and thus may not have been sufficient to promote a measurable increase in biomass production. Growth of *Egeria* and *Potamogeton* was unaffected by elevated CO_2 supply, even in the low C_T solution, in which the growth of all species is considered to have been limited by inorganic carbon availability. In contrast, the growth of *Hydrilla* was greatly stimulated by increasing the CO_2 supply in the low C_T solution. A similar response to CO_2 by *M. spicatum* was observed earlier (Smart and Barko 1986). Increasing the CO_2 supply in the higher C_T solutions did not result in significant increases in biomass production of *Hydrilla*.

27. With the exception of *Hydrilla* in the low-cation, low- C_T solution aerated with ambient air, total ash-free biomass production of all the species

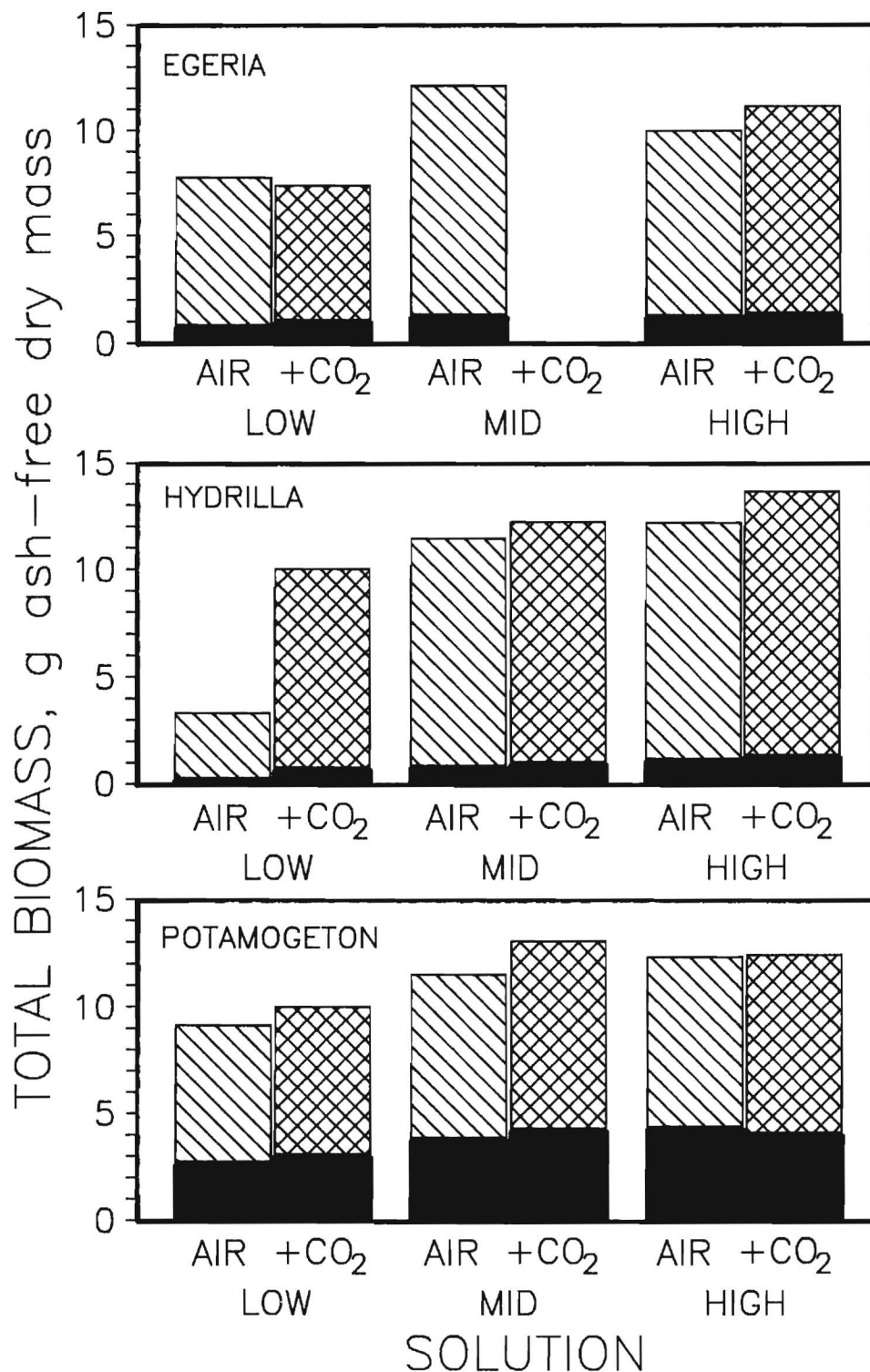


Figure 5. Total biomass responses (grams ash-free dry mass) of *Egeria*, *Hydrilla*, and *Potamogeton* in relation to solution and aeration treatments. Total biomass is the sum of ash-free shoot biomass (hatched portions of the bars) and root biomass (dark portions of the bars). Values are means of six replications

was similar (Figure 5). *Potamogeton* produced significantly higher quantities of roots in each of the solution-aeration treatments that did *Egeria* or *Hydrilla*. The similar responses of the three species to solution composition indicates that their solution requirements are not appreciably different. The diminished growth of *Hydrilla* in the low-cation, low-carbon solution suggests that *Hydrilla* may be less competitive in oligotrophic, soft waters than *Egeria* or *Potamogeton*.

28. Examination of tissue N levels (Figure 6) indicates that the growth of all three species was limited by N in the mid- and high-level solutions. In the low-level solution receiving ambient air aeration, plant growth was apparently more limited by inorganic carbon availability than by nitrogen availability. In view of the predominant nitrogen limitation observed at higher levels of inorganic carbon supply, the growth responses to increased C_T or CO_2 supply may have been much greater had adequate N been available.

29. Shoot P and K concentrations of all species were well above respective critical concentrations of these elements (Figure 6); thus, P and K were not involved in growth limitation. In spite of the sixfold difference in solution K concentration, neither *Egeria* nor *Hydrilla* responded with increased shoot K concentrations. It is surprising that, while *Egeria* and *Hydrilla* completely depleted solution K from the low-level solution, the additional K in the mid- and high-level solutions did not elicit an increase in shoot tissue K. This lack of response of shoot K in *Egeria* and *Hydrilla* to increasing solution K may have resulted from limitation by N. Barko and Smart (1986) indicated that limitation of submersed macrophyte growth by N or P resulted in diminished uptake of other elements. Nutrient uptake in these species seems to be closely coupled, and nutrient limitation by one element seems to suppress luxury consumption of other elements.

30. Internal shoot Ca concentrations ($CaCO_3$ -free) in *Egeria* and *Potamogeton* increased with increased solution Ca concentration (Figure 7). However, the levels of internal Ca measured here are minor in relation to total shoot Ca (internal plus external $CaCO_3$ encrustation) values presented elsewhere (Hutchinson 1975, Allenby 1981, Smart and Barko 1986). The quantity of $CaCO_3$ encrustation on plant shoots has been previously shown to be strongly related to levels of solution Ca and C_T (Smart and Barko 1986). The apparent relationship between internal shoot Ca and solution Ca measured here for

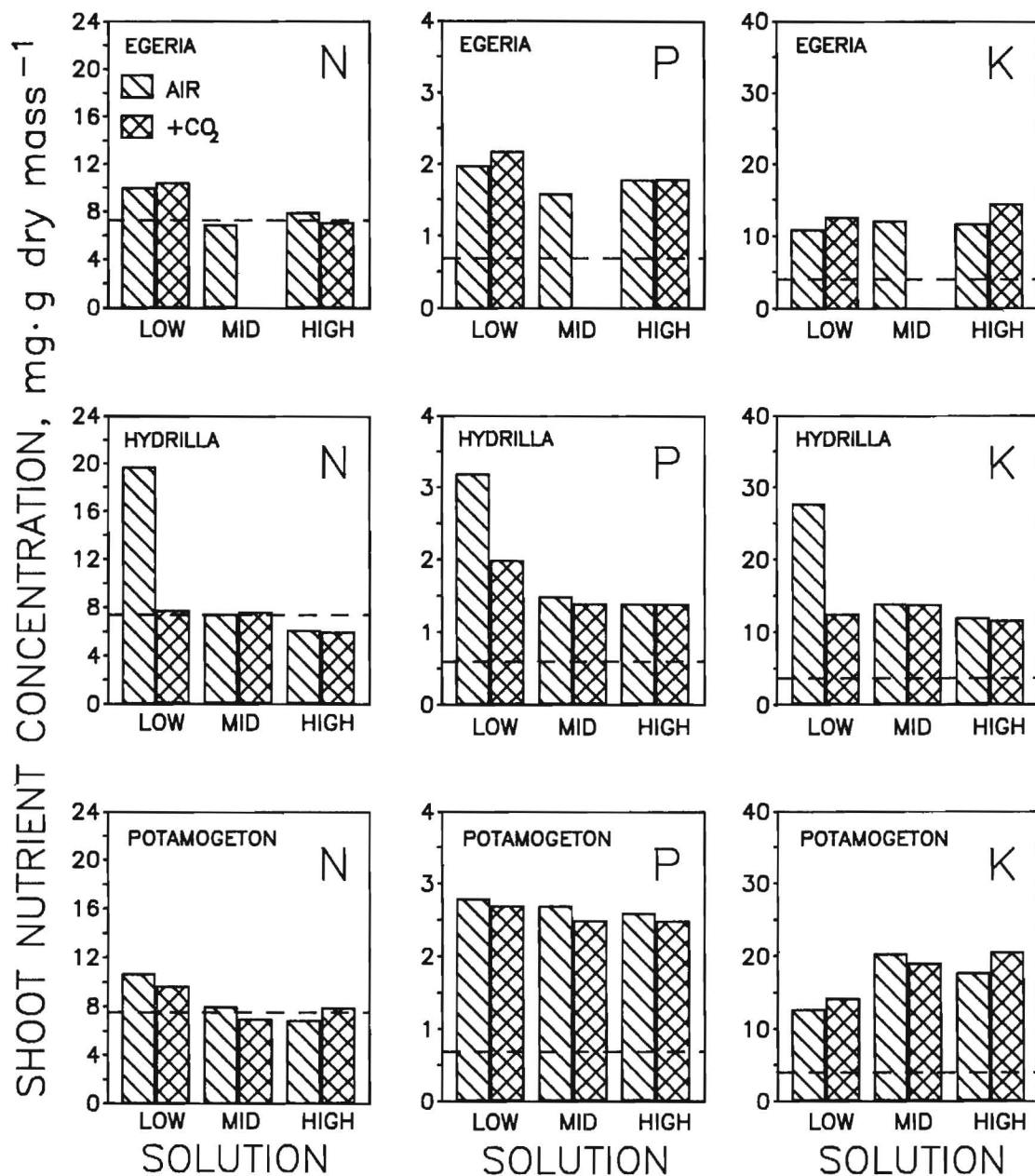


Figure 6. Shoot concentrations of N, P, and K in *Egeria*, *Hydrilla*, and *Potamogeton* in relation to solution and aeration treatments. Values are means based on three replications. Broken lines denote generalized critical nutrient concentrations (Gerloff 1975, Barko and Smart 1986)

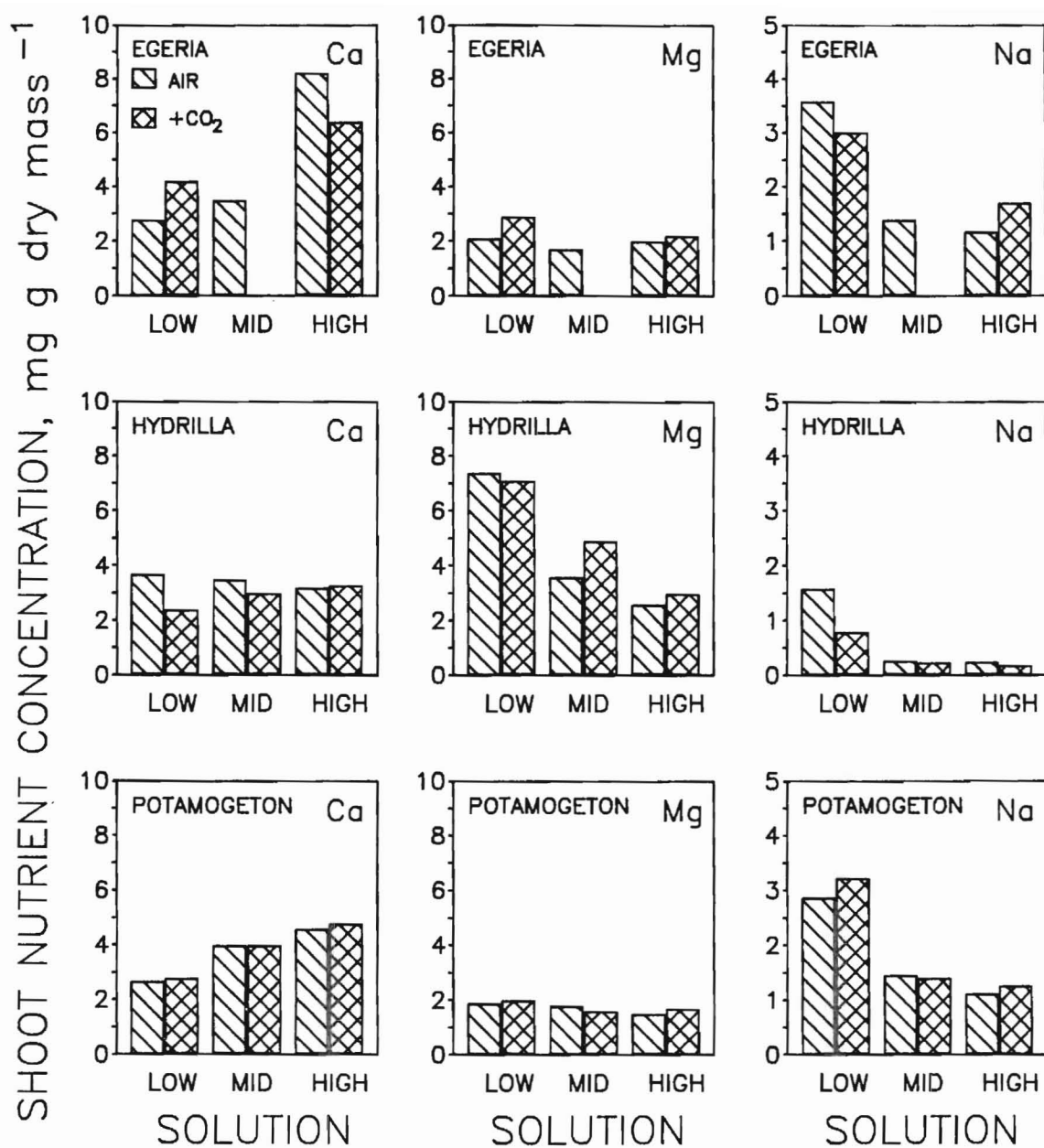


Figure 7. Shoot concentrations of Ca, Mg, and Na in *Egeria*, *Hydrilla* and *Potamogeton* in relation to solution and aeration treatments. Values are means based on three replications

Egeria and *Potamogeton* may merely reflect incomplete removal of precipitated CaCO_3 by the acid rinse.

31. None of the species responded to increased solution Mg levels by increasing shoot Mg concentration (Figure 7). Shoot Mg concentrations in

Hydrilla actually declined with increasing solution Mg. *Hydrilla* exhibited significantly higher shoot Mg concentrations than did *Egeria* or *Potamogeton*, particularly in the low-level solution. Similar high levels of shoot Mg have been previously reported for *Hydrilla* (Kulshreshtha and Gopal 1982, Barko and Smart 1986); however, the significance of this occurrence has not been demonstrated.

32. Shoot Na concentrations in all species declined with increasing solution Na (Figure 7). The high levels of shoot Na concentration under conditions of carbon limitation (low-level solution) suggest that Na may be accumulated passively, increasing under conditions of low biomass production; however, this occurrence requires verification. *Hydrilla* contained significantly lower shoot concentrations of Na than did *Egeria* or *Potamogeton*. Barko and Smart (1986) also presented data indicating that *Hydrilla* contained much lower shoot Na concentrations than did *M. spicatum* grown on the same sediments and in the same solution. Unlike *Egeria*, *Potamogeton*, and *M. spicatum*, which accumulate Na to a greater extent than Mg, *Hydrilla* appears to accumulate Mg and not Na. The nutritional significance of this occurrence remains to be investigated.

33. There have been many attempts to relate the concentration of elements in submersed aquatic plant shoots to concentrations in sediment or water (Hutchinson 1975, Casey and Downing 1976, Patterson and Brown 1979, Allenby 1981, Kimball and Baker 1982). These studies have generally failed to detect relationships between shoot nutrient concentrations and environmental nutrient concentrations for field populations of plants. In the laboratory investigation reported here, we observed no general relationships between shoot nutrient concentrations and respective concentrations in the water column. This lack of a relationship under controlled laboratory conditions of uniform sediment composition and closely defined solution concentrations suggests that there may be no simple relationship between shoot nutrient concentrations and solution concentrations. Shoot nutrient concentrations in submersed aquatic plants appear to be governed by factors affecting growth, such as sediment N availability (Barko and Smart 1986), inorganic carbon supply (Smart and Barko 1986), and light and temperature regimes (Barko and Smart 1981a), rather than by concentrations in the growth medium.

Plant growth and nutrition
effects on solution composition

34. Photosynthetic carbon uptake exerted significant demands on solution C_T and resulted in large declines in C_T and Ca due to the combined effects of photosynthetic carbon uptake and $CaCO_3$ precipitation (Figures 1, 2, and 3). Internal shoot accumulations of Ca (the product of shoot mass and Ca concentration) were insignificant in relation to losses of Ca by precipitation from the higher cation, higher carbon solutions, accounting for less than 5 percent of the measured declines in solution Ca. Thus, as indicated earlier by the close relationship between solution Ca and alkalinity (Figures 3a and 3b), Ca depletion from solution was attributable almost entirely to $CaCO_3$ precipitation rather than to plant uptake.

35. Solution K also exhibited declines associated with the growth of submersed aquatic plants (Figure 4). Unlike Ca, K is quite soluble, and losses of solution K are unlikely to have resulted from precipitation. Since several species of submersed aquatic plants have been shown to obtain K primarily from solution (Barko and Smart 1981b, Barko 1982, Huebert and Gorham 1983), we elected to compare shoot K accumulation with measured values of K depletion from solution (Figure 8). All of the species caused depletions of solution K that were significantly in excess of shoot accumulations of this element (paired-comparisons t test). While root K accumulation was not measured, roots of *Hydrilla* have been demonstrated to have significantly lower K concentrations than shoots (Barko 1982). In addition, root biomass was much lower than shoot biomass (Figure 5), comprising only 11.6 and 8.5 percent of total biomass in *Egeria* and *Hydrilla*, respectively. Even if roots of these species contained K concentrations similar to shoots, root K accumulation would be far less than that needed to account for measured values of solution K depletion. In contrast, root biomass to *Potamogeton* (Figure 5) comprised a larger portion of total biomass (32.7 percent) and may have constituted a sizable sink for solution K.

36. In this relatively short-term experiment, there was very little senescence of plant material; thus, nutrient losses to litter were insignificant. Moreover, since K is extremely mobile and is rapidly leached from senescing or decomposing plant material (Boyd 1970, 1971), K accumulations in litter would be expected to be very low. The fate of the K lost from solution in this experiment is unknown. It has recently been suggested that, under

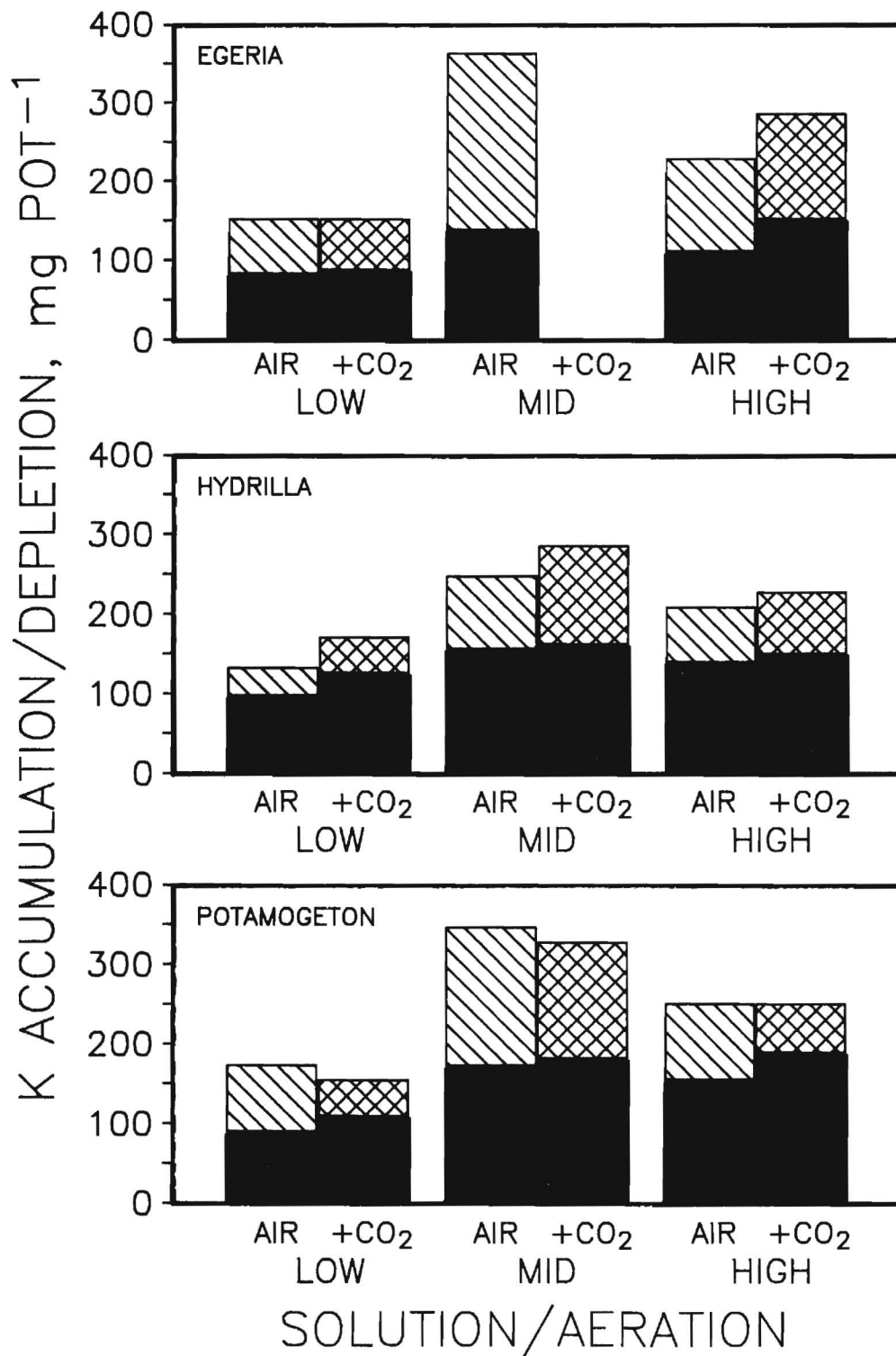


Figure 8. Comparisons of shoot K accumulation by *Egeria*, *Hydrilla*, and *Potamogeton* in relation to solution and aeration treatments with respective values for solution K depletion. Values for shoot K accumulation (dark portions of the bars) are means ($n = 3$) of the product of shoot mass and shoot K concentration. Values for solution K depletion (represented by the total height of the bars) were determined from differences in initial and final solution K concentrations expressed on a per-container basis

N-limiting conditions, *Hydrilla* transports K obtained by foliar uptake from the water to the roots where it is exchanged for sediment NH_4 (Barko et al., in press). In view of the N-limiting conditions observed in this experiment, transport of shoot K to sediments may explain the excess depletion of solution K by *Egeria* and *Hydrilla*.

37. While neither Na nor Mg exhibited marked depletions in solution concentration, shoot accumulations of these elements were generally low, making it difficult to detect statistically significant differences in solution concentration. In isolated cases (e.g., Mg accumulation in *Hydrilla* grown in the low-level solution aerated with CO_2 -enriched air), shoot accumulations were sufficiently large to produce measurable decreases in solution concentration. While this observation suggests that Mg was acquired by foliar uptake from the water column, it was not possible to test the statistical significance of this occurrence. The lack of overall significant depletions in solution concentrations of Mg and Na in this investigation should not, therefore, be taken as evidence that these elements are acquired from sediment rather than solution.

Relative importance of carbon and nitrogen limitation

38. The rapid depletion of C_T by photosynthetic carbon uptake and precipitation of CaCO_3 requires that these studies be conducted under conditions where the volume of solution is high relative to the level of plant biomass produced (Smart and Barko 1985). The atmospheric exchange of CO_2 was also facilitated by aerating the solutions with compressed air (Smart and Barko 1985). While these practices partially alleviate C_T depletion, they also tend to minimize carbon limitation and may result in growth limitation by other environmental resources. This practice results in overly conservative estimates of the importance of solution parameters and may overemphasize the importance of sediment parameters.

39. While the growth of all of these species was limited by N availability in the mid- and high-level solutions, limitation occurred only at very high areal biomass levels (sediment surface area basis). Shoot biomass levels attained in this experiment were equivalent to between 700 and 900 g dry mass $\cdot \text{m}^{-2}$ sediment surface area. These levels of biomass are rarely attained under field conditions. Thus, N limitation observed here cannot be directly extrapolated to field conditions and merely represents a potential limitation to

submersed aquatic plant growth. In contrast, evidence of carbon limitation under the relatively uncrowded conditions and high aeration regimes employed in this study indicates a high potential for carbon limitation in natural populations of submersed aquatic plants.

40. The results presented here suggest that the growth of rooted submersed aquatic plants in eutrophic systems may be limited by the availability of inorganic carbon. Given adequate temperature and irradiance regimes, the most likely limiting factors are inorganic carbon and sediment N. While sediment N is potentially growth-limiting, fine-textured, inorganic sediments may contain sufficient N to support nuisance levels of submersed plant biomass for several years. The extent to which N replenishment in sediment balances losses of N due to plant uptake will ultimately determine the length of the period prior to the onset of N limitation (Barko et al., in press). It is suggested then that, over the short term, aquatic plant problems will depend on the availability of inorganic carbon for photosynthesis, and over the long term, on the availability of sediment N.

41. In spite of the potential importance of inorganic carbon as a growth-limiting factor, there is not likely to be a simple relationship between solution carbon level and biomass production or species distribution. The reason for this is that inorganic carbon availability is only indirectly related to water chemistry. While waters of higher alkalinity generally contain a greater quantity of readily available carbon, it is the rate of regeneration of this carbon that is of primary importance. Actively growing submersed macrophyte populations are capable of depleting the C_T available in the water column in a matter of days or weeks. Continued growth of these populations will depend on the carbon regenerating capacity of the system. The potential of a water body for supporting problem-level populations is thus more dependent on the recycling of carbon than on water chemistry per se. While biomass production may be proportional to inorganic carbon supply, the supply of carbon is dependent on rates of water column respiration, sediment respiration, atmospheric exchange, dissolution of precipitated carbonates, and advection, in addition to the chemical composition of the water.

Conclusions and Recommendations

42. The photosynthesis of submersed aquatic plants exerts a high demand on solution C_T . As photosynthetic uptake of C_T proceeds, there is a shift in the carbonate equilibrium toward the formation of CO_3^{--} and subsequent $CaCO_3$ precipitation. The combined effects of photosynthetic uptake and precipitation result in large depletions of solution C_T and Ca. Rapid aeration, even at 4X ambient CO_2 concentrations, does not prevent depletion of C_T . Submersed aquatic plants are thus dependent on a continuous supply of inorganic carbon. Sources of this carbon include: atmospheric exchange, advection, sediment and water column respiration, and dissolution of precipitated carbonates. We recommend that these sources be quantified to ascertain the important processes governing inorganic carbon supply to submersed aquatic plants.

43. The uptake of nutrient elements from solution can also result in significant depletions of these elements from the water column. Of the major cations, K is most likely to exhibit depletion due to relatively high plant requirements for K, the limited ability of many submersed aquatic plants to acquire sediment K, and the apparent involvement of K in root-sediment exchange processes. It is recommended that future investigations consider the role of K derived from solution in mediating root-sediment exchange processes.

44. Plant requirements of Na, Ca, and Mg are apparently low, and in the absence of $CaCO_3$ precipitation, these elements are unlikely to become depleted from solution. One possible exception to this generalization is the apparent high requirement of *Hydrilla* for solution Mg. While Mg is unlikely to limit the growth of *Hydrilla*, it is recommended that future investigations consider the possibly different metabolic role of this element in species that accumulate Mg (e.g., *Hydrilla*) and in those that do not (e.g., *Egeria* and *Myriophyllum*).

45. Photosynthesis and growth are strongly dependent on the supply of inorganic carbon, and under conditions of adequate light, temperature, and sediment nutrient availability, carbon limitation of submersed aquatic plant populations is likely. Under natural environmental conditions, biomass production of submersed plant populations is likely to be limited by the rate of supply of either inorganic carbon or N. The difference between the occurrence of innocuous submersed aquatic plant populations and the development of noxious aquatic "weed" infestations may depend on the relative rates of supply

of carbon and/or N to field populations. It is recommended that future investigations consider the interactive roles of inorganic carbon supply and N availability in controlling biomass production of submersed aquatic plant populations.

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