



US Army Corps
of Engineers

AD-A226 124

INTERACTIVE INFLUENCES OF SELECTED ENVIRONMENTAL VARIABLES ON GROWTH AND TUBER FORMATION IN *HYDRILLA*

by

Dwilette G. McFarland, John W. Barko

Environmental Laboratory

DEPARTMENT OF THE ARMY

Waterways Experiment Station, Corps of Engineers
3909 Halls Ferry Road, Vicksburg, Mississippi 39180-6199



July 1990

Final Report

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SECURITY CLASSIFICATION OF THIS PAGE

REPORT DOCUMENTATION PAGE				Form Approved OMB No. 0704-0188	
1a. REPORT SECURITY CLASSIFICATION Unclassified			1b. RESTRICTIVE MARKINGS		
2a. SECURITY CLASSIFICATION AUTHORITY			3. DISTRIBUTION/AVAILABILITY OF REPORT Approved for public release; distribution unlimited.		
2b. DECLASSIFICATION/DOWNGRADING SCHEDULE					
4. PERFORMING ORGANIZATION REPORT NUMBER(S) Technical Report A-90-6			5. MONITORING ORGANIZATION REPORT NUMBER(S)		
6a. NAME OF PERFORMING ORGANIZATION USAEWES Environmental Laboratory		6b. OFFICE SYMBOL (If applicable)	7a. NAME OF MONITORING ORGANIZATION		
6c. ADDRESS (City, State, and ZIP Code) 3909 Halls Ferry Road Vicksburg, MS 39180-6199			7b. ADDRESS (City, State, and ZIP Code)		
8a. NAME OF FUNDING/SPONSORING ORGANIZATION US Army Corps of Engineers		8b. OFFICE SYMBOL (If applicable)	9. PROCUREMENT INSTRUMENT IDENTIFICATION NUMBER		
8c. ADDRESS (City, State, and ZIP Code) Washington, DC 20314-1000			10. SOURCE OF FUNDING NUMBERS		
			PROGRAM ELEMENT NO.	PROJECT NO.	TASK NO.
					WORK UNIT ACCESSION NO.
11. TITLE (Include Security Classification) Interactive Influences of Selected Environmental Variables on Growth and Tuber Formation in <i>Hydrilla</i>					
12. PERSONAL AUTHOR(S) McFarland, D. G., Barko, J. W.					
13a. TYPE OF REPORT Final report		13b. TIME COVERED FROM _____ TO _____		14. DATE OF REPORT (Year, Month, Day) July 1990	
				15. PAGE COUNT 26	
16. SUPPLEMENTARY NOTATION Available from National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161					
17. COSATI CODES			18. SUBJECT TERMS (Continue on reverse if necessary and identify by block number)		
FIELD	GROUP	SUB-GROUP	Biomass <i>Hydrilla</i> Sediment composition		
			Biotypes Interaction Tuber production		
			Day length Photoperiod Water temperature		
19. ABSTRACT (Continue on reverse if necessary and identify by block number)					
△ In a 5-week greenhouse investigation, variations in the growth of both monoecious and dioecious <i>Hydrilla</i> [<i>Hydrilla verticillata</i> (L. f.) Royle] were compared over a range of temperatures (12°C to 32°C) on a fertile inorganic sediment and on an infertile organic sediment. For these biotypes, total biomass production was severely restricted at 16°C and below, with thermal optima for growth occurring between 28°C and 32°C. Total biomass, shoot number, and shoot length for each biotype were greater on the inorganic sediment than on the organic sediment. At higher temperatures, dioecious <i>Hydrilla</i> lengthened more extensively than monoecious <i>Hydrilla</i>; however, the latter produced higher shoot densities and tuber numbers under most experimental conditions. Monoecious <i>Hydrilla</i> appears to be better adapted to moderate temperatures than dioecious <i>Hydrilla</i>, and its potential distribution may include sediments less favorable for growth of the dioecious biotype.					
(Continued)					
20. DISTRIBUTION/AVAILABILITY OF ABSTRACT ☒ UNCLASSIFIED/UNLIMITED ☐ SAME AS RPT ☐ DTIC USERS			21. ABSTRACT SECURITY CLASSIFICATION Unclassified		
22a. NAME OF RESPONSIBLE INDIVIDUAL			22b. TELEPHONE (Include Area Code)		22c. OFFICE SYMBOL

19. ABSTRACT (Continued).

In a separate investigation conducted in two 10-week phases, biomass and tuber production in dioecious *Hydrilla* were examined under controlled environmental conditions, over a range of temperatures (20° to 30° C), under contrasting 10-hr (short) and 14-hr (long) photoperiods. *Hydrilla* was grown on fine-textured inorganic sediment amended either with ammonium chloride (fertile), or with washed builder's sand (infertile). Long photoperiod and higher temperatures generally increased total biomass production. Growth was diminished on the sand-amended sediment as compared with the nutrient-amended sediment; however, tuber formation was unaffected by sediment type. Although greater numbers of tubers were produced under short days, the mass of individual tubers was greater under long days. Tuber formation was stimulated at lower temperatures during the long photoperiod, and at higher temperatures during the short photoperiod. Thus, temperature and day length interacted significantly in affecting tuber formation in dioecious *Hydrilla*.

Accession For	
GRA&I	☒
TAB	☐
Unannounced	☐
Classification	
Distribution/	
Availability Codes	
Avail and/or	
Special	
A-1	



PREFACE

The research reported herein was conducted and documented as part of the Aquatic Plant Control Research Program (APCRP), US Army Engineer Waterways Experiment Station (WES). The APCRP is sponsored by the Headquarters, US Army Corps of Engineers (HQUSACE), Directorate of Civil Works (DAEN-CW). Funds were provided by DAEN-CW under Department of the Army Appropriation No. 96X3122, Construction General. Technical Monitor for HQUSACE was Mr. E. Carl Brown.

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

Principal investigator was Dr. John W. Barko (APEG), who coauthored this report with Mrs. Dwilette G. McFarland (APEG). Studies were designed by Drs. Barko and R. Michael Smart (APEG), with contributions from Drs. Marc C. Bruner, US Department of Agriculture, and T. R. Batterson, University of Florida. Data analysis and interpretation were performed by the authors. Technical assistance from the APEG was provided by Mmes. Avis Helmuth, M. Susan Hennington, and Ramona Warren, and Messrs. J. Conley and D. Schwartz. Sediment from Buckhorn Lake, Ontario, was collected by Dr. S. Painter, Ministry of Environment, Ontario, Canada.

This report is based on articles accepted for publication in the Journal of Aquatic Plant Management and the Journal of Freshwater Ecology. Technical reviews within EL were provided by Drs. Thomas L. Hart, Nancy J. McCreary, and William D. Taylor. Mrs. Janean C. Shirley of the Information Technology Laboratory, WES, was the editor.

COLS Dwayne G. Lee and Larry B. Fulton each served as Commander and Director of WES during the course of these studies and preparation of this manuscript. Dr. Robert W. Whalin was Technical Director.

This report should be cited as follows:

McFarland, D. G., and Barko, J. W. 1990. "Interactive Influences of Selected Environmental Variables on Growth and Tuber Formation in *Hydrilla*," Technical Report A-90-6, US Army Engineer Waterways Experiment Station, Vicksburg, MS.

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INTERACTIVE INFLUENCES OF SELECTED ENVIRONMENTAL VARIABLES
ON GROWTH AND TUBER FORMATION IN HYDRILLA

PART I: INTRODUCTION

Background

1. The establishment of *Hydrilla verticillata* (L. f.) Royle in the United States apparently resulted from at least two separate introductions. The female dioecious biotype, initially introduced in Florida around 1960 (Blackburn et al. 1969), has become one of the most prolific submersed aquatic plants in southern regions of the country (Haller 1976). Dioecious *Hydrilla* occurs throughout the Southeast, most abundantly in Florida; it extends northward up the east coast to South Carolina, and across the South as far west as California. A more recently discovered monoecious biotype of *Hydrilla* was identified in 1982 in the Potomac River near Washington, DC (Steward et al. 1984). Since then, monoecious *Hydrilla* has been reported in North Carolina (Langland and Smith 1984) and elsewhere in the Northeast. Based on isoenzyme banding pattern and chromosome number, Verkleij et al. (1983) confirmed that the two biotypes of *Hydrilla* in this country are genetically distinct. These genetic distinctions suggest possible differences in response to environmental gradients.

2. Competitive success and associated high rate of spread in *Hydrilla* have been attributed, among other factors, to its minimal light requirement for photosynthesis (Van et al. 1976, Bowes et al. 1977), a high rate of dry matter production (Singh and Sahai 1977), and both diverse and effective means of asexual reproduction (Haller and Sutton 1975, Pieterse 1981). Dispersal and perennation of *Hydrilla* are facilitated by a variety of vegetative propagules, i.e., regenerative fragments, rhizomes, stolons, tubers, and turions (Pieterse 1981). Among these propagules, tubers (or subterranean turions) appear to be most important in reestablishing *Hydrilla* populations following adverse climatic conditions or application of control operations (Weber 1973, Basiouny et al. 1978). Tubers form on stolon apices embedded in the sediment, and thus are protected from most chemical treatments of aboveground plant mass (Steward 1969, Basiouny et al. 1978). Tubers are also structurally sound, affording greater resistance to mechanical disturbance, heat loss, and

desiccation of stolon meristematic tissues (Salisbury and Ross 1985, Steward and Van 1985).

3. Ecological studies of growth and tuber formation in *Hydrilla* have focused on response to a wide variety of environmental factors. Major consideration has been given to the effects of day length, temperature, and sediment fertility. Research to date indicates that short photoperiods induce tuber formation in *Hydrilla* (Haller 1976, Haller et al. 1976, Van et al. 1978a and b, Bowes et al. 1979), and that under short-day conditions, tuber formation increases with increased biomass and water temperatures up to about 33° C (Van et al. 1978b). Reductions in both growth and tuber formation due to inadequate sediment fertility have been demonstrated in studies of Van and Haller (1979), Bruner and Batterson (1984), and Barko and Smart (1986). Whereas day length, temperature, and sediment fertility have all been shown to have strong independent effects on growth and tuber formation in *Hydrilla*, it is possible that in nature interactions among these variables may significantly modify plant response.

Objectives and Scope

4. Considering the potential for adaptive differences between monoecious and dioecious *Hydrilla*, determinations of growth trends peculiar to each biotype (in response to specific environmental conditions) are of interest. This report presents results of an investigation designed to contrast the growth of these *Hydrilla* biotypes over a range of temperatures (12° to 32° C) on two sediments differing intrinsically in fertility, one an organic sediment with low nutrient availability and the other an inorganic sediment with high nutrient availability (cf. Barko and Smart 1986). Additional information is provided for dioecious *Hydrilla*, based on a separate investigation of growth and tuber formation in relation to temperature, sediment fertility, and photoperiod. An underlying objective of the studies reported here is the identification of interactions among major environmental factors affecting growth and perennation of *Hydrilla* in different locations. Results of these investigations are intended to contribute to the advancement of aquatic plant management practices.

PART II: MATERIALS AND METHODS

Primary Investigation

5. The investigation was conducted during August and September in the Environmental Laboratory greenhouse facility, located in Vicksburg, MS (described in Barko and Smart 1981a). Twelve 1,200-ℓ white fiberglass tanks were filled with a culture solution (Smart and Barko 1985) to a depth of 83 cm. The solution was a moderately alkaline medium with a pH upon preparation of 8.3. Nitrogen and phosphorus were omitted from the solution to minimize algal growth inside the tanks (cf. Smart and Barko 1985). Continuous circulation of the solution and temperature control were provided by liquid circulators connected independently to each tank. During the study, temperatures were monitored twice daily and minor thermostat adjustments were made as necessary.

6. Monoecious and dioecious *Hydrilla* used in the study were obtained from stocks routinely subcultured in the greenhouse at 6-week intervals. Monoecious *Hydrilla* was established initially from tubers collected from the Potomac River, Virginia. Dioecious *Hydrilla* was established initially from stem apices clipped from plants in Lake Seminole, Florida.

7. Six experimental tanks were allotted per biotype; these were assigned different temperatures in 4-deg increments between 12° and 32° C. Four 2-ℓ replicates of an organic sediment from Buckhorn Lake, Ontario, and four 2-ℓ replicates of an inorganic sediment from Brown's Lake, Mississippi, were assigned to each tank. Table 1 summarizes fundamental sediment characteristics determined by analytical procedures described in Barko and Smart (1986). Sediment containers were planted separately with four 15-cm-long apical clippings of either monoecious or dioecious *Hydrilla*. Immediately after planting, the tanks were covered with a neutrally absorptive shade fabric that reduced natural irradiance by 51 percent.

8. At the end of 5 weeks, plants were harvested, measured, oven-dried at 80° C to constant mass, and weighed as discrete components of above- and belowground biomass. Response variables included total biomass, root-to-shoot biomass ratio, shoot length, shoot number, tuber number, and tuber mass. All tubers (irrespective of size) were included in the tuber count.

Secondary Investigation

9. Owing to a need for more detailed information on tuber formation in relation to factors affecting growth of dioecious *Hydrilla*, a secondary investigation was conducted in two 10-week phases in the greenhouse. At this location, 32°23' N, 90°52' W, the initial short-day phase (Nov-Jan) provided an approximate 10-hr daylight exposure; the subsequent long-day phase (May-Jul) allowed a daylight exposure of about 14 hr (List 1951).

10. In both phases, three 1,200-ℓ white fiberglass tanks were used to provide separate 5-deg increments in experimental temperatures from 20° to 30° C. The tanks were filled 83 cm deep with the culture solution described above; liquid circulators installed singly to each tank provided continuous circulation and thermal control ($\pm 1^\circ$ C) of the solution.

11. The sediment used in the secondary investigation was collected from Brown's Lake, and was quite similar in composition to sediment collected earlier from the same location (Table 1). At the beginning of each phase, the sediment was mixed thoroughly and divided into two portions. One of these was amended with washed builder's sand, an infertile addition that resulted in a 22-percent coarse, 78-percent fine particle size distribution; NH_4Cl was added to the other (30.8 mg N ℓ^{-1} of sediment) to ensure sufficient nitrogen availability (Barko, unpublished data) over the 10-week study period. The two sediment treatments were replicated six times in each of the three tanks. Sediment containers provided a sediment depth of 15 cm, a surface area of 145 cm^2 , and a sediment volume of 1,700 ml.

12. Planting procedures were essentially identical to those described above. When planting was completed, neutral-density shade fabric was positioned over the tanks, reducing ambient irradiance levels by 33 percent. Mid-day photosynthetically active radiation inside the tanks was about 1,000 and 600 $\mu\text{E m}^{-2} \text{ sec}^{-1}$ during long and short days, respectively.

13. After 10 weeks of growth in each study phase, above- and belowground plant structures were harvested, oven-dried (at 80° C), and weighed. Evaluations of *Hydrilla* growth were based on measurements of total biomass (roots and shoots), with differentiation of tuber contributions to root mass. Effects of treatment on tuber number were evaluated by direct counting. Data from both primary and secondary investigations were analyzed statistically using analysis of variance (ANOVA) procedures of the Statistical Analysis System (Raleigh, NC). Hereafter, statements of statistical significance refer to probability levels of 5 percent or less.

PART III: RESULTS

Response of *Hydrilla* Biotypes to Environmental Conditions

14. Results of two-way analyses of variance (Table 2) show the relative significance of independent and interactive effects of temperature and sediment type (i.e., inorganic versus organic) on the growth of monoecious and dioecious *Hydrilla*. In many cases, the main effects of temperature and sediment type were of approximately equal importance, and explained far greater treatment-related variance in plant response than the interaction terms. However, significant interactions between these variables did occur, and these influenced biomass and morphological responses in both biotypes (see below).

15. Biomass production in both monoecious and dioecious *Hydrilla* was severely inhibited at 12° and 16° C (Figure 1). Above 16° C, growth increased approximately linearly with increasing temperature up to 28° C; the thermal optimum for total biomass production in these biotypes occurred between 28° and 32° C. Biomass production on the organic sediment was less than half that on the inorganic sediment over temperatures ranging from 20° to 32° C. Ratios of root-to-shoot biomass in both biotypes declined with increasing temperature up to about 24° C (Figure 1). At 12° and 16° C, these ratios for monoecious *Hydrilla* on the inorganic sediment were about twice as great as ratios for dioecious *Hydrilla*.

16. Although total biomass (Figure 1) and shoot biomass (not presented) were rather similarly affected in both biotypes by temperature and sediment type, the manner in which biomass was allocated to shoots differed distinctly between biotypes (Figure 2). With increasing temperature, dioecious *Hydrilla* elongated more extensively overall than monoecious *Hydrilla*. Based on pooled means, shoots in the dioecious biotype were about 25 percent and 10 percent longer than in the monoecious biotype on inorganic and organic sediments, respectively. In contrast, monoecious *Hydrilla* produced higher shoot densities than dioecious *Hydrilla* on both sediments; based on pooled means, the former produced about 50 percent and 25 percent more shoots than the latter on inorganic and organic sediments, respectively.

17. Only monoecious *Hydrilla* produced a measurable number of tubers, probably because the period of growth (5 weeks) provided in this particular study was too brief for tuber production in the dioecious biotype (cf. Spencer and Anderson 1986). In neither biotype were tubers produced at 12° C, and unlike the response of biomass to temperature (essentially linear), tuber

production was maximal at intermediate temperatures (Figure 3). More tubers and a greater overall tuber mass were produced on the inorganic sediment than on the organic sediment. The effect of sediment type was greatest at 24° C, where tuber number varied over an approximate threefold range between sediments. Total tuber mass was highly and significantly correlated with tuber number ($r = 0.87$ at $P < 0.01$); however, the mass of individual tubers was quite variable (mean and standard deviation = 0.16 ± 0.11 mg dry mass per tuber).

Tuber Formation in Relation to Growth of Dioecious *Hydrilla*

18. Total biomass of *Hydrilla* was greater under long-day than short-day conditions, and was generally stimulated on the fertile (N-amended) sediment (Figure 4). The effect of sediment fertility was most pronounced under long-day conditions, whereas under short days, growth was limited on both sediments by reduced daylight exposure. Patterns of biomass production in relation to temperature were similar under both conditions of photoperiod. Biomass increased with increasing temperature to at least 25° C. Under both day lengths, root-to-shoot ratios declined somewhat with increasing temperature. Although these ratios were generally higher on the sand-amended sediment, a significant difference due to sediment type occurred only under long days at 20° C.

19. Temperature and day length interacted significantly in affecting tuber formation (Figure 5). Under short days, tuber formation was inhibited at 20° C, while under long days, tuber formation was greatest at this temperature. Under long days, no tubers were formed at 30° C. However, at this temperature tuber formation was greatest under short-day conditions.

20. The effect of day length on tuber number was most marked. Overall temperature and sediment conditions, short-day tuber number was about four times greater than long-day tuber number. Although day length caused only minor differences in total tuber mass (i.e., total tuber mass per container, Figure 5), individual tuber mass was substantially reduced under short days. Based on data pooled for tuber-producing replicates, the mean mass ($\pm$ standard error) per tuber formed during long days was 147.9 (± 42.0) mg, while the short-day mean was 24.9 (± 0.3) mg per propagule, reflecting a sixfold difference in individual tuber mass between day lengths.

PART IV: DISCUSSION

Independent and Interactive Effects of Environmental Variables

21. Results of these investigations are in general agreement with those of others demonstrating that temperature, day length, and sediment type can all strongly influence the growth and morphology of *Hydrilla* (Van et al. 1978b; Barko and Smart 1981a and b; 1983, and 1986; Steward and Van 1985, 1986, 1987; Spencer and Anderson 1986). As evidenced here, the interaction between variables significantly affected the magnitude of measured independent responses. In the primary investigation, effects of sediment type on the growth and morphology of both *Hydrilla* biotypes were greatest at higher temperatures, and effects of temperature were greatest on the favorable inorganic sediment. In the secondary investigation, the effect of sediment fertility on growth was much more pronounced under long-day conditions than under short-day conditions.

22. While numerous studies have determined major independent effects of temperature and day length on tuber production in *Hydrilla* (Van et al. 1978b; Steward and Van 1985, 1987; Spencer and Anderson 1986), unique to the present research is the demonstrated interaction between these variables on tuberization in this species. Similar to the current findings, a positive effect of increasing temperature on tuber formation in dioecious *Hydrilla* grown under short-day conditions was reported by Van et al. (1978b). However, under long-day conditions, increasing temperature appears to have a negative effect on tuber formation in both monoecious and dioecious biotypes (these studies). Interaction between temperature and day length appears to be important in the formation of turions in other aquatic macrophytes as well, e.g., curlyleaf pondweed, *Potamogeton crispus* L. (Sastroutomo 1980), and European frogbit, *Hydrocharis morsus-ranae* L. (Vegis 1955).

23. As predicted in this research and in that of others conducted under controlled environmental conditions (Van et al. 1978b, Spencer and Anderson 1986), tuber formation by *Hydrilla* in nature occurs primarily during short days, between autumn and spring (Haller et al. 1976, Bowes et al. 1979). However, seasonal trends in tuber formation are often lacking in systems supporting dense year-round stands of this species (Bowes et al. 1979, Sutton and Portier 1985). In one such study conducted at Lake Trafford, Florida, Bowes et al. (1979) reported high tuber densities throughout 1977, with peak

densities occurring in February, and notably in August. The current data suggest that moderate water temperature (about 21° C, from Bowes et al. 1979) coupled with long-day lengths of summer may have extended the period of tuber production in Lake Trafford. It is further speculated that prolonged cool-water temperatures in other aquatic systems, e.g., Floridian springs, may also support tuber formation in *Hydrilla* beyond seasons of short photoperiod.

24. Whereas short photoperiod clearly contributes to the production of larger numbers of tubers by *Hydrilla* (Van et al. 1978b, Spencer and Anderson 1986, Steward and Van 1987), the current study indicates that long photoperiod can promote greater individual propagule mass. The effects of tuber mass on the success of *Hydrilla* are presently not well known. However, for sago pondweed, *Potamogeton pectinatus* L., germination and initial growth rate have been shown to be positively related to tuber fresh weight (Spencer 1986). Differences in mass between long- and short-day tubers may also influence these processes in *Hydrilla*.

25. Growth of *Hydrilla* in the secondary study was limited on the sand-amended sediment as compared with the fine-textured nutrient-amended sediment, presumably due to high substrate density and associated nutrient deficiencies (cf. Bruner and Batterson 1984, Steward 1984, Sutton 1985, Barko and Smart 1986). Yet, despite sediment conditions causing significant reductions in biomass, tuber formation was not significantly affected. Bruner and Batterson (1984) have hypothesized that the number of tubers produced and sustained by *Hydrilla* is a function of sediment fertility. However, the results of the current study indicate that tuber production may be more dependent upon other environmental cues (e.g., temperature and day length) than upon nutrition. In agreement with results of our study, Steward (1984) and Sutton (1985) found that substrate nutrient levels were more directly related to biomass yield than to tuber production in *Hydrilla*. These results coupled with the results of the current study suggest that sediment composition may be a better indicator of *Hydrilla* growth potential than an indicator of tuber density in nature. Considering the wide variability in correlations between tuber and biomass production (cf. Van and Haller 1979, Steward 1984), the physiology of tuber formation in *Hydrilla*, particularly under conditions of nutrient stress, warrants further investigation.

Monoecious Versus Dioecious *Hydrilla*

26. Monoecious *Hydrilla* appears to possess reproductive capabilities beyond those of the dioecious biotype. The findings of this study and those of Spencer and Anderson (1986) and Steward and Van (1987) indicate that the reproductive potential of monoecious *Hydrilla* is enhanced substantially by its ability to form tubers rapidly. Although tubers of monoecious *Hydrilla* are generally smaller and weigh less than those of the dioecious biotype (Anderson 1985, Spencer et al. 1987), they are produced in greater numbers and are capable of germinating at lower water temperatures (Steward and Van 1987). The production of high densities of shoots that serve as a source of fragments may also increase the reproductive capacity of monoecious *Hydrilla*, especially in flowing water systems. Efficient reproduction at low-to-moderate temperatures may provide an added competitive advantage for this biotype in areas with relatively short growing seasons (Spencer and Anderson 1986, Steward and Van 1987). In part, these responses could explain the effective establishment of monoecious *Hydrilla* in many northern localities, and the Potomac River as well. Tuber production by monoecious *Hydrilla* on organic sediment suggests that the distribution of this biotype may extend to sediments less tolerated by the dioecious biotype.

PART V: CONCLUSIONS AND RECOMMENDATIONS

27. Several key environmental factors and their interactions exert varying degrees of influence on growth and reproductive responses in *Hydrilla*. Temperature, sediment composition, and photoperiod determine the basic trends in the productivity and morphology of this species, while interactions among these variables appear to be of generally secondary importance in mediating levels of plant response. However, based on the secondary investigation reported herein, the interaction between water temperature and day length appears to significantly influence tuber formation in dioecious *Hydrilla*. This interaction may be a primary determinant in the seasonal duration, intensity, and character of tuber development in the dioecious biotype.

28. Understanding the relative influences of environmental variables and their interactions on growth of *Hydrilla* is fundamental to the assessment of its potential proliferation in various aquatic systems. Considering combined influences of temperature and day length, future studies of tuber production in *Hydrilla* should examine the mass, number, and maturity of tubers formed under various thermal regimes, at different times of the year. This information would be valuable in applying appropriate management practices directed toward propagule vulnerability due to age or stage of development. Further research of the mass-related vigor and longevity of long- versus short-day propagules would be useful in predicting recruitment and competitive success of *Hydrilla* under field conditions.

29. It appears that nutrient availability, affected greatly by sediment composition, is of less importance than some other factors (unknown) influencing tuberization in *Hydrilla*. Physiological processes involved in tuber formation of this species need to be better characterized to explain observed response patterns, particularly under conditions of nutrient stress. More importantly from a management perspective, elucidation of these processes is essential if effective means of suppressing tuber formation are to be determined.

30. The above recommendations for future studies should consider differences in tuberization capabilities between monoecious and dioecious *Hydrilla*. Investigations designed to further resolve variations in these capabilities may define improvements needed in the management of both biotypes.

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Table 1
Characterization of Sediments*

<u>Sediment Parameter</u>	<u>Source</u>	
	<u>Brown's Lake, Mississippi</u>	<u>Buckhorn Lake, Ontario</u>
Texture, %		
Fine particles ($\leq 50 \mu\text{m}$ diam)	90.0 $\pm$ 0.0	80.0 $\pm$ 0.0
Coarse particles ($> 50 \mu\text{m}$ diam)	10.0 $\pm$ 0.0	20.0 $\pm$ 0.0
Dry weight density, g ml ⁻¹	0.76 $\pm$ 0.01	0.07 $\pm$ 0.00
Total organic matter, %	5.6 $\pm$ 0.1	50.2 $\pm$ 0.4

* Values are means and standard errors based on duplicate or triplicate determinations.

Table 2
Synoptic Two-Way ANOVA of Growth Difference in Dioecious and Monoecious
Hydrilla Relative to Temperature and Sediment

Response Variable	Environmental Variable*	Dioecious		Monoecious	
		P	F Value	P	F Value
Total biomass	Temp	<0.001	165	<0.001	181
	Sed	<0.001	216	<0.001	348
	Temp x Sed	<0.001	31	<0.001	50
Root:shoot	Temp	<0.001	29	<0.001	22
	Sed	NS	<1	<0.001	13
	Temp x Sed	<0.05	3	<0.001	7
Shoot length	Temp	<0.001	1,606	<0.001	728
	Sed	<0.001	1,299	<0.001	178
	Temp x Sed	<0.001	138	<0.001	16
Shoot number	Temp	<0.001	80	<0.001	71
	Sed	<0.001	15	<0.001	89
	Temp x Sed	<0.01	4	<0.001	11
Tuber number	Temp	<0.05	3	<0.001	12
	Sed	<0.05	6	<0.001	17
	Temp x Sed	NS	2	<0.01	4
Tuber mass	Temp	NS	1	<0.001	7
	Sed	NS	<1	<0.001	29
	Temp x Sed	NS	<1	<0.05	3

* Temp = temperature; Sed = sediment; Temp x Sed = interaction of temperature and sediment.

DIOECIOUS

MONOECIOUS

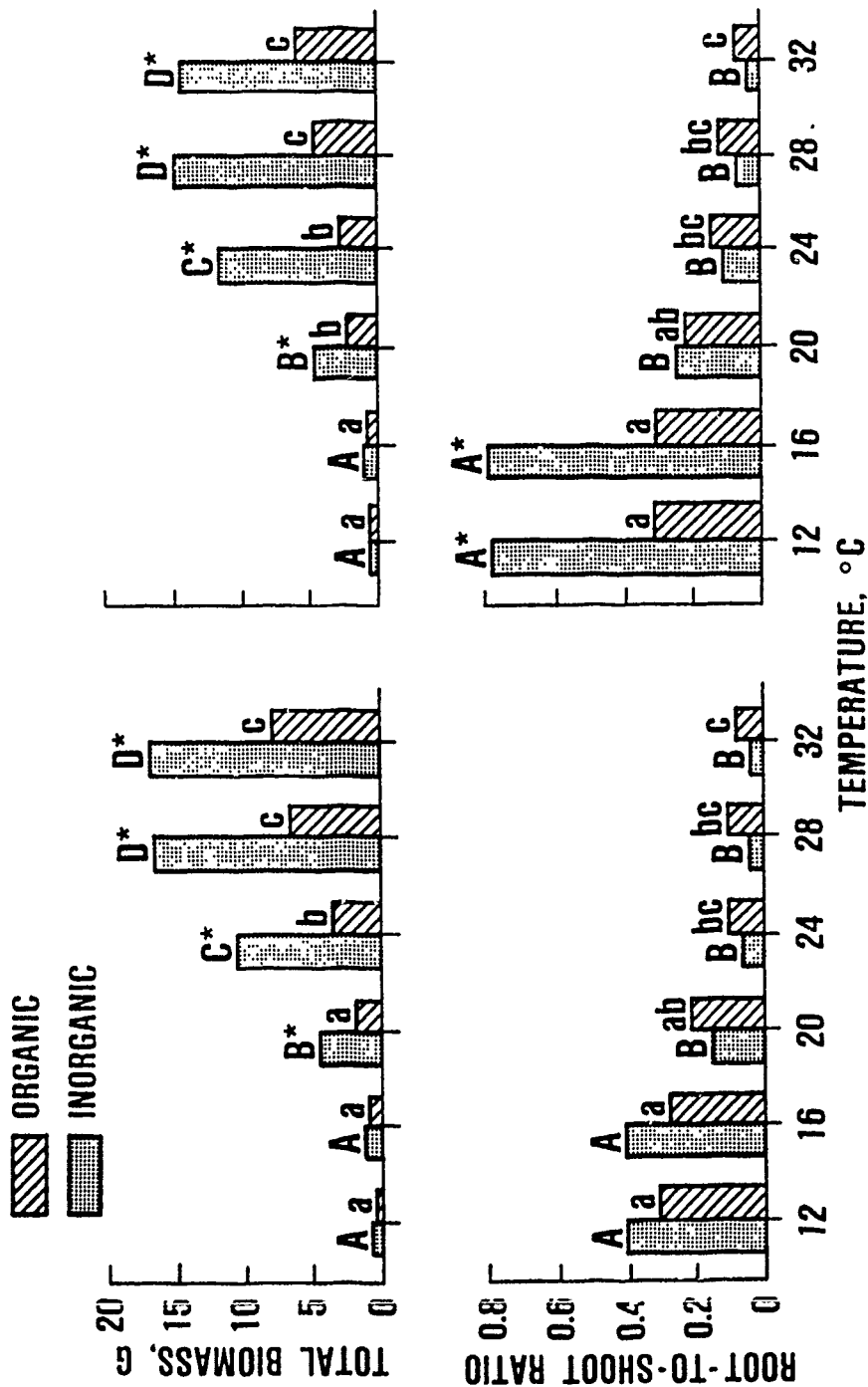


Figure 1. Effects of temperature and sediment type on the growth of dioecious and monoecious *Hydrilla*. [Within each subfigure, biomass values or root-to-shoot ratios sharing the same letter (upper case for inorganic sediment and lower case for organic sediment) do not differ significantly from each other. Asterisks denote significant effects of sediment type on growth. Duncan's Multiple Range Test was used to determine statistical significance at $P < 0.05$.]

DIOECIOUS

MONOECIOUS

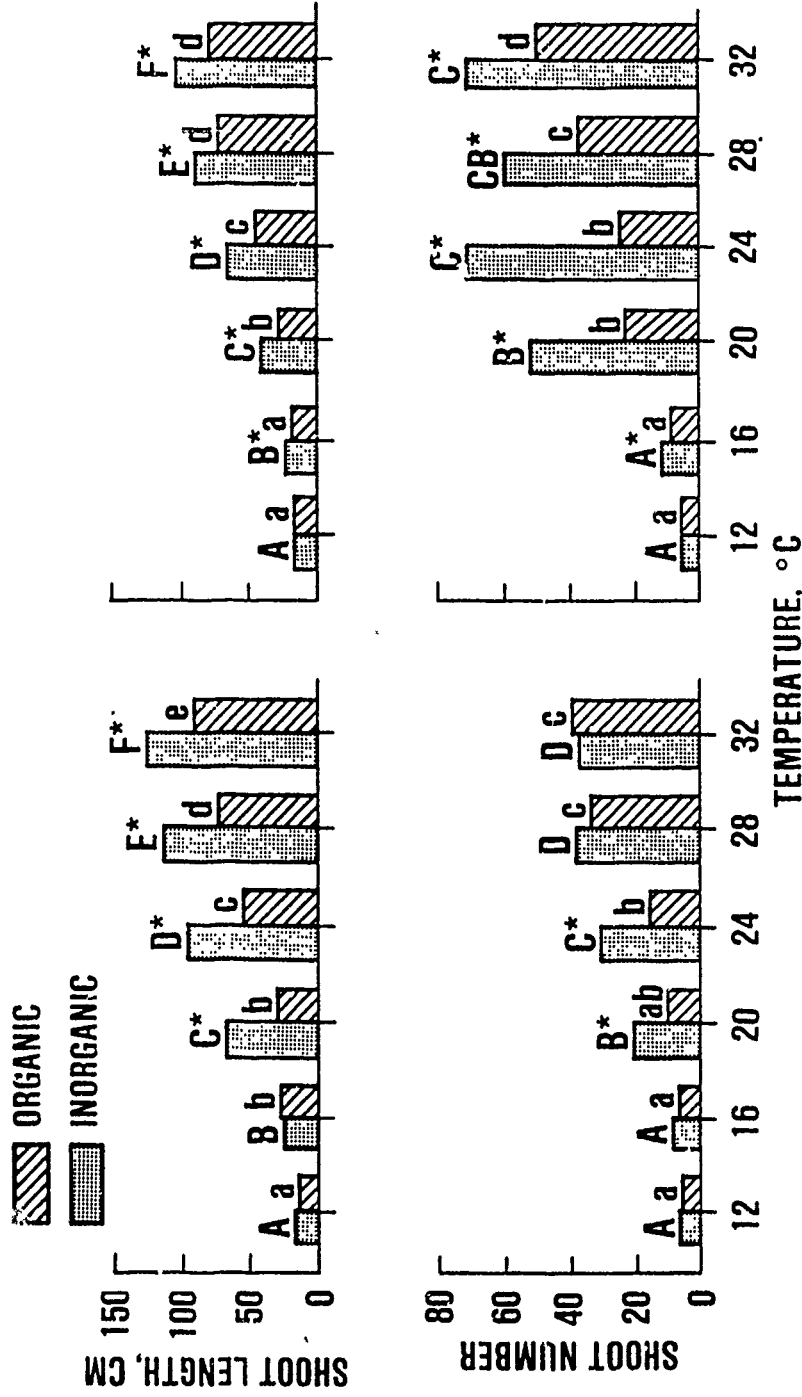


Figure 2. Effects of temperature and sediment type on shoot morphology in dioecious and monoecious *Hydrilla*. [Within each subfigure, shoot lengths or shoot numbers sharing the same letter (upper case for inorganic sediment and lower case for organic sediment) do not differ significantly from each other. Asterisks denote significant effects of sediment type on shoot morphology. Duncan's Multiple Range Test was used to determine statistical significance at $P < 0.05$.]

MONOECIOUS

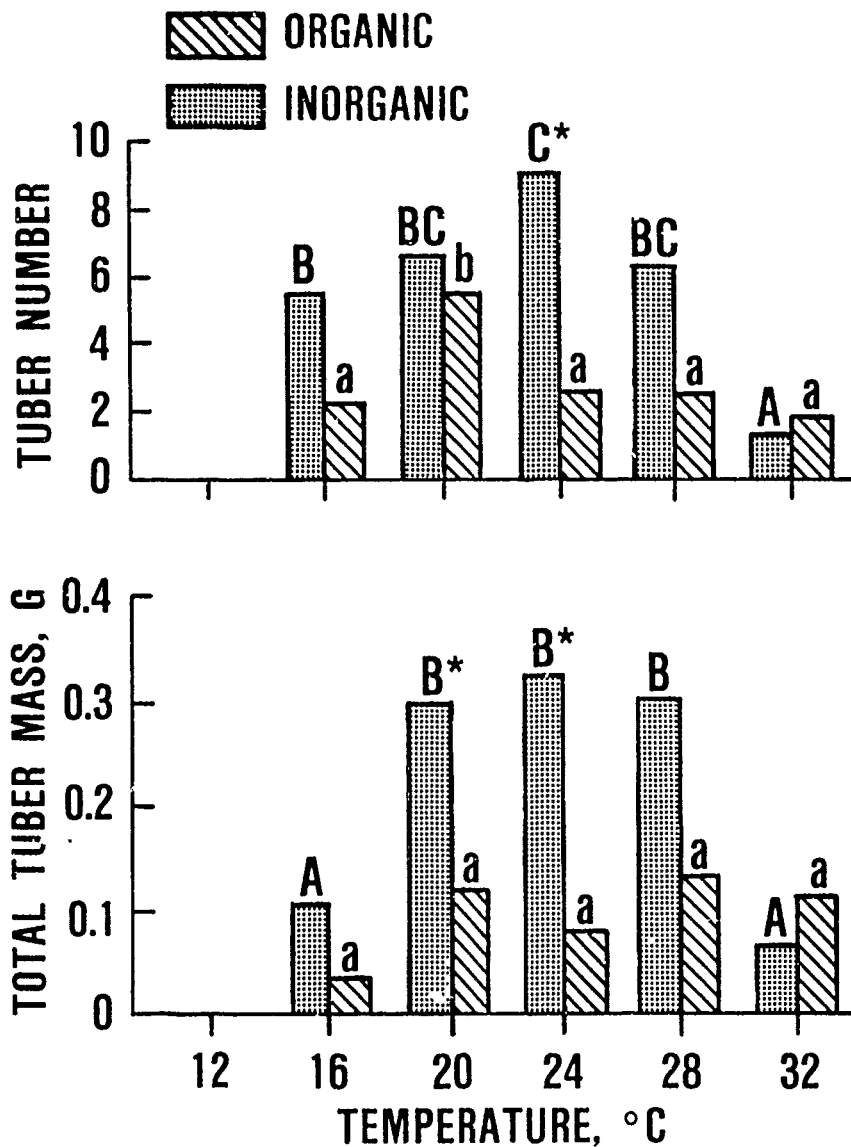


Figure 3. Effects of temperature and sediment type on tuber production in monoecious *Hydrilla*. [Within each subfigure, tuber numbers and tuber mass values sharing the same letter (upper case for inorganic sediment and lower case for organic sediment) do not differ significantly from each other. Asterisks denote significant effects of sediment type on tuber production. Duncan's Multiple Range Test was used to determine statistical significance at $P < 0.05$.]

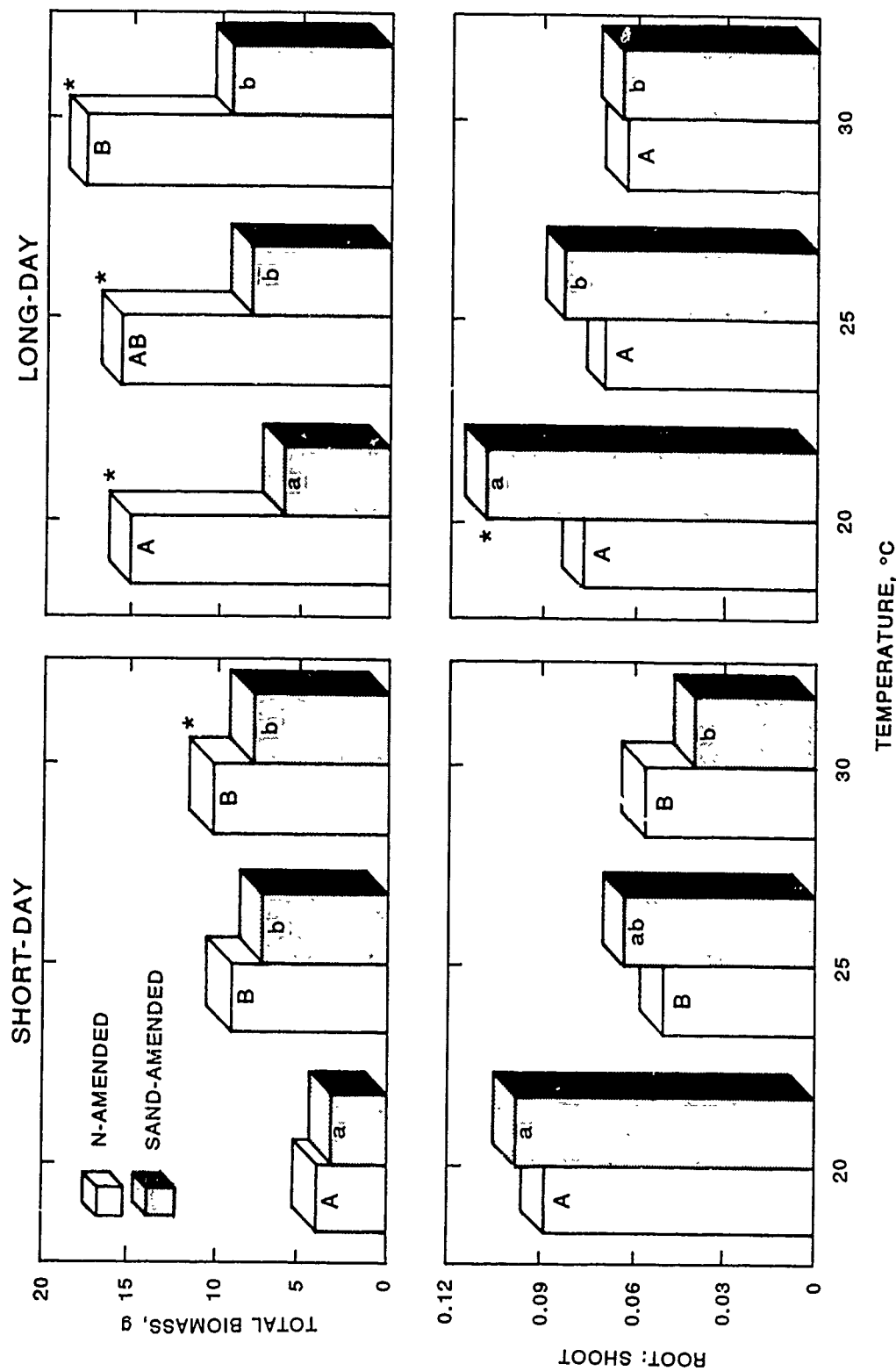


Figure 4. Effects of temperature and sediment type on growth of *Eydrella* under long-day and short-day conditions. [Within each subfigure, biomass values or root-to-shoot ratios sharing the same letter (upper case for N-amended sediment and lower case for sand-amended sediment) do not differ significantly from each other. Asterisks denote significant effects of sediment type on growth. Duncan's Multiple Range Test was used to determine statistical significance at $P < 0.05$.]

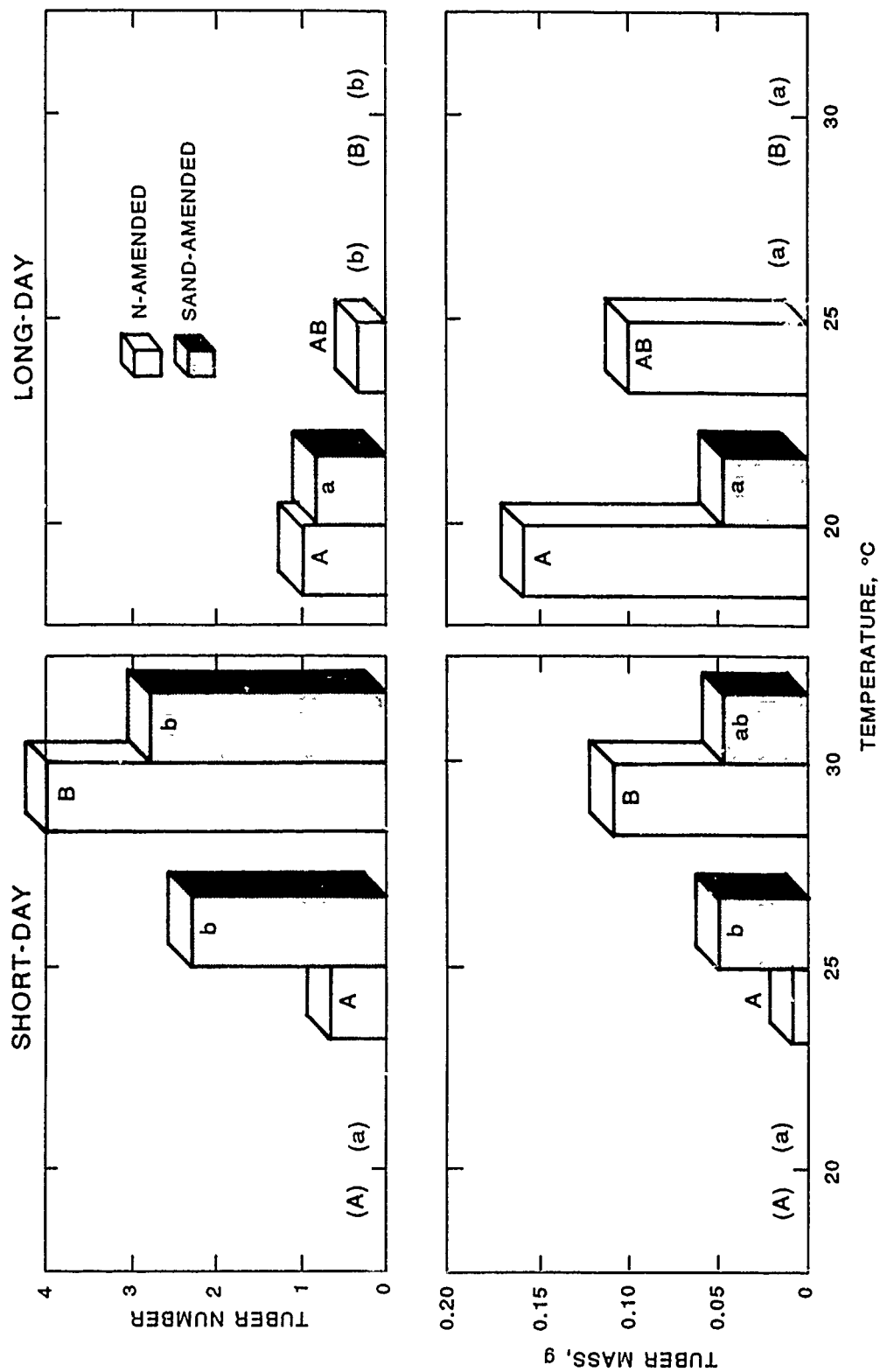


Figure 5. Effects of temperature and sediment type on tuber formation in *Hydrilla*. [Within each subfigure, tuber number or tuber mass sharing the same letter for N-amended sediment and lower case for sand-amended sediment) do not differ significantly from each other. Asterisks denote significant effects of sediment type on tuber formation. Duncan's Multiple Range Test was used to determine statistical significance at $P < 0.05$.]