

High-Temperature Effects on Growth and Propagule Formation in Hydrilla Biotypes

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ABSTRACT

In consecutive greenhouse studies, growth and propagule formation were examined first in monoecious hydrilla [*Hydrilla verticillata* (L.f.) Royle], then in dioecious hydrilla, at three temperature levels (25, 30, and 35 C) and contrasted over three periods of growth (8, 12 and 16 wks). Each biotype was grown under natural photoperiods, decreasing from 14 hrs (in Aug) over 8, 12, and 16 wks respectively to 12, 11, and 10 hrs (in Oct, Nov, and Dec). For both biotypes, total biomass and root-to-shoot ratios were significantly reduced at 35 C; greater biomass was produced both at 25 and 30 C. Increases in growth period generally enhanced total biomass and shoot production; however, shoot length was unresponsive to growth periods beyond 8 wks. The 35 C treatment strongly impeded tuber formation and eliminated the production of axillary turions; the number and biomass of these propagules peaked at lower temperatures under short photoperiods after 12 to 16 wks. Shoot elongation was stimulated with increases in temperature and was especially pronounced in the dioecious biotype. Notably, in the monoecious biotype, the number of shoots as a potential source of fragments, and tuber production (although reduced) occurred at relatively high levels under unfavorably high-temperature (35 C) conditions. These results suggest that monoecious hydrilla may be better adapted to high temperatures than previously shown, and that the distribution of both biotypes in the U.S. could overlap further in southern states.

Key words: *Hydrilla verticillata*, biomass, morphology, tubers, turions, reproduction, thermal conditions, photoperiod.

INTRODUCTION

Investigations in aquatic ecology have long shown temperature to be a major factor influencing the growth of submersed aquatic macrophytes. Thus far, numerous studies have documented marked effects of temperature on biomass production and morphological development (Barko et al. 1982, McFarland and Barko 1987, McFarland and Barko 1990), photosynthetic rates (Titus and Adams 1979, Barko and Smart 1981), oxygen consumption (Anderson 1969), and growth cycle duration (Anderson 1969, Grace and Tilly 1976, Barko and Smart 1981). For many submersed macrophyte species, high temperatures within the range of 28 to 32 C promote biomass production with accompanying increases

in shoot number and length (Barko and Smart 1981, Barko et al. 1982). Changes in the composition of submersed macrophyte communities due to alterations in thermal regimes have also been reported (Anderson 1969, Allen and Gorham 1973), suggesting temperature to be important in affecting interactions among coexisting species (Barko et al. 1986).

The role of temperature in regulating the production of submersed macrophyte propagules has received less investigative attention. Due to the apparent infrequency of sexual reproduction in submersed macrophytes (Sculthorpe 1967), studies of population dispersal and perennation have focused mainly on vegetative propagules, e.g., regenerative fragments, tubers, turions, rhizomes, stolons, and root crowns. Among these propagules, tubers and turions are important in facilitating regrowth following winter and other adverse conditions (Weber 1973, Basiouny et al. 1978, Sasstroutomo 1982). In temperate species, the production of tubers and turions typically begins under short photoperiods in autumn (Spencer and Anderson 1987). Van et al. (1978) found that under a short (10-hr) photoperiod, the number of tubers in dioecious hydrilla [*Hydrilla verticillata* (L.f.) Royle] increases as temperature increases to 33 C. Also, Weber and Nooden (1976) found that under short-day conditions, turions of water milfoil (*Myriophyllum verticillatum* L.) can be induced at 15 C and lower, but not at 20 C. Further understanding of the effects of temperature on propagule formation would be useful to predict the survival of submersed macrophytes from one growing season to the next. Additionally, knowledge of how propagule production is affected by temperature and other conditions may be valuable in allowing timely application of control methods, and could suggest more effective means of regulating the number of propagules produced.

Currently, two biotypes of hydrilla represent a persistent menace to aquatic resources in North America. The dioecious biotype (pistillate only) was introduced into Florida, probably from India, in the mid-1950s (Blackburn et al. 1969). Since that time, it has spread simultaneously across the sunbelt states to California (Spencer and Anderson 1986, Dechoretz 1989, Schmitz et al. 1991) and up the east coast to North Carolina (Haller 1976, Schmitz et al. 1991). Most recently, dioecious hydrilla was reported in Connecticut, thus marking its northernmost extension on this continent to date (Les et al. 1997). In the early 1980s, a monoecious biotype was discovered in the Potomac River near Washington, DC (Steward et al. 1984). Its appearance was presumably the result of a separate introduction, although the foreign source has not been determined (Steward et al. 1984). Presently, monoecious hydrilla is found in at least five northeastern states, including North and South Carolina, Virginia,

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Maryland, and Delaware (Langeland and Smith 1984, Verkleij and Pieterse 1986). Sightings of the monoecious biotype have also been reported on the west coast for several lakes in Washington². Investigations of both biotypes show that efficient propagule production and germination at low to moderate temperatures better suit monoecious hydrilla than dioecious hydrilla to northerly environments (Anderson 1985, Spencer et al. 1987, Steward and Van 1987, Spencer and Ksander 1991).

The research presented here revisits two earlier studies (McFarland and Barko 1987 and 1990) wherein growth of monoecious and dioecious hydrilla was examined over a range of temperatures from 16 to 32 C. In this article, we provide further information on the growth of these biotypes but with greater emphasis on tuber and turion production. This research was specifically designed to determine how warm water temperatures extending into autumn may affect the growth of hydrilla biotypes and their perennating structures. Data were collected over three periods of growth (up to 16 wks) to ensure adequate time for propagule development under short photoperiods (≤ 12 hrs) and to allow assessments of response over an extended period of time.

MATERIALS AND METHODS

Plant Preparation and Growth Conditions. The research consisted of two 16-wk (Aug to Dec) studies performed in a greenhouse facility, at the U.S. Army Engineer Waterways Experiment Station (WES), Vicksburg, MS. The first study was conducted with monoecious hydrilla in 1993, and the second with dioecious hydrilla in 1994. Apical stems of each biotype were clipped 15 cm in length from 4-wk-old plants in the WES greenhouse stocks: the monoecious stock was established from a population in the Potomac River, Virginia; the dioecious stock was cultured from collections in Lake Seminole, Florida.

The studies were conducted in white fiberglass tanks, 150 cm long, by 90 cm wide, by 90 cm deep. Each tank was filled to a depth of 83 cm with the low-alkalinity culture solution described in Smart and Barko (1985). The solution, prepared with reagent-grade salts and deionized-distilled water, provided major cations ($\text{Na}^+ = 16.0$, $\text{K}^+ = 6.0$, $\text{Ca}^{+2} = 25.0$, and $\text{Mg}^{+2} = 6.8$ mg L⁻¹) and anions ($\text{Cl}^- = 44.2$, $\text{HCO}_3^- = 51.8$, and $\text{SO}_4^{-2} = 26.9$ mg L⁻¹) but lacked N and P, specifically omitted to minimize algal growth in the tanks. Upon preparation (at 25 C), the solution had a pH of 7.9 and an electrical conductivity of 278 $\mu\text{S cm}^{-1}$. Two air lifts per tank provided filtered humidified air to enhance air/water CO₂ exchange. The solution was continuously circulated and thermally controlled (± 1 C) using Remcor circulators with both heating and cooling capacities.

Surficial sediment dredged from Brown's Lake, WES provided the rooting medium in these studies. This sediment is a fine-textured, inorganic medium with particle size fractions of 10 percent coarse ($> 50 \mu$ dia) and 90 percent fine ($< 50 \mu$

dia) by dry weight (McFarland and Barko 1987). The sediment was amended with ammonium chloride (0.6 g L⁻¹ wet sediment) to ensure sufficient N to support 16 wks of growth. The amended sediment was poured 8 cm deep in polyethylene containers (24.3 cm long, by 24.3 cm wide, by 10.0 cm deep) and was allowed to settle for several days just prior to planting. Table 1 summarizes physical and chemical characteristics of the sediment (after fertilization) as determined by analytical procedures described by Barko et al. (1988).

All plants were grown under natural photoperiod beneath a neutral-density (75 percent) shade fabric positioned over the greenhouse roof. At this location (i.e., in Vicksburg, MS; 32°23'N, 90°52'W), the duration of daylight declined by about 1 hr mo⁻¹, from a maximum of 14 hrs at the beginning of both studies (in Aug) to 12, 11, and 10 hrs respectively at 8, 12, and 16-wk harvests³. Maximum midday photosynthetically active radiation (PAR) levels inside the tanks decreased from approximately 400-325 $\mu\text{E m}^{-2}\text{sec}^{-1}$ during long days (> 12 hrs daylight) and 300-225 $\mu\text{E m}^{-2}\text{sec}^{-1}$ during short days (< 12 hrs daylight).

Study Design and Execution. Each study employed a 3 × 3 factorial design in which responses of hydrilla were examined at 25, 30 and 35 C over growth periods of 8, 12, and 16 wks. Six replicate containers were planted for each of the resulting nine treatment combinations and were placed in prepared tanks. Four apical cuttings of hydrilla (i.e., monoecious in the first study; dioecious in the second study) were spaced evenly in each container, with basal ends buried 3 cm in the sediment. After planting, a thin layer of washed silica sand was placed over the sediment surface to prevent physical mixing with the culture solution.

At the end of each growth period, aboveground plant material was clipped at the sediment surface, and shoot number and length were recorded. Belowground plant material was washed free of sediment by rinsing over a fine (1-mm) mesh sieve. All plant materials were oven-dried to constant weight at 80 C. Dry weights obtained for shoot (aboveground) and root (belowground) biomass were used to calculate total biomass and root-to-shoot ratio. Tubers and turions were counted directly and weighed after oven-drying for separate determinations of tuber and turion biomass. Individual propagule (i.e., tuber or turion) biomass was calculated for

TABLE 1. SEDIMENT CHARACTERISTICS.*

Parameter	Study 1: Monoecious	Study 2: Dioecious
Moisture, %	42.12 ± 0.16	43.57 ± 0.02
Organic Matter, %	5.63 ± 0.12	6.19 ± 0.03
Dry Weight Density, g/ml	0.87 ± 0.01	0.88 ± 0.00
Extractable Nutrients, mg/g		
Nitrogen	0.16 ± 0.01	0.17 ± 0.00
Phosphorus	0.14 ± 0.01	0.15 ± 0.01

*Values are means and standard errors based on three (in Study 1) or four (in Study 2) replicate sediment samples.

²Hamel, K. 1995 (pers. comm.). Department of Ecology, Washington State University. Sighting Report Form submitted to the Nonindigenous Aquatic Plant Species Program, U.S. Geological Survey, Florida Caribbean Science Center, Gainesville, FL 32653 (<http://nas.er.usgs.gov/monocots>).

³List, R. J. 1951. Smithsonian Meteorological Tables, 6th ed. Smithsonian Institution, Washington, DC.

each replicate by dividing total propagule biomass by total propagule number; these calculated values were then used to obtain a mean biomass per propagule per treatment.

Data Analysis. All data were analyzed using analysis of variance (ANOVA) and post-ANOVA capabilities of the Statistical Analysis System (SAS Institute, Inc. 1991). Response variables presented in Figures 1 to 4 are given as means ($n = 6$) with associated standard error bars. Separation of means across temperature and growth period was accomplished using Duncan's Multiple Range Test. Hereafter, statements of statistical significance without specific indication of probability level refer to $P < 0.05$.

RESULTS

Results of two-way ANOVAs (Table 2) indicate the relative significance of independent and interactive effects of temperature and growth period on responses of monoecious and dioecious hydrilla. In nearly all cases, independent effects of temperature and growth period were highly significant and explained greater treatment-related variance than did the interaction terms. However, interactions between these variables did occur and affected the magnitude of most measured responses [e.g., effects of temperature increased over prolonged growth periods (12 to 16 wks), and effects of growth period were greatest at favorable temperatures (25 to 30 C); see below].

Study 1: Responses of Monoecious Hydrilla. Total biomass in monoecious hydrilla responded to both temperature and growth period but showed no significant interactive effects (Figure 1). At 8 wks, total biomass did not differ among temperature treatments. Peak biomass levels were achieved by 12 wks at 25 and 30 C, and were greater than at 35 C. Beyond 12 wks, temperature effects grew less pronounced owing to slight increases in biomass at 30 and 35 C.

Ratios of root-to-shoot biomass were greatest at 25 C and generally declined with increases in temperature to 35 C (Figure 1). In 25 and 30 C treatments, these ratios increased significantly with increases in growth period up to 16 wks; peak ratios in the 35 C treatment were reached by the harvest at 12 wks. Reductions in root-to-shoot ratio in response to high temperature treatment were magnified over time; i.e., ratios obtained at 16 wks differed twice as much between 25 and 35 C as did those obtained at 8 wks in corresponding temperature treatments.

Growth periods beyond 8 wks had little effect on shoot length, but had a positive effect on the number of shoots produced (Figure 1). Maximum shoot production occurred in plants grown for 12 to 16 wks, with about 20 percent more shoots than those grown for 8 wks. There was no distinct pattern in shoot number relative to temperature treatments in this study, although shoot length increased by 18 to as much as 27 percent between 25 and 35 C.

Tuber production (i.e., tuber number and tuber biomass) increased over time but was clearly inhibited at 35 C (Figure 2). At 8 wks, the number of tubers at 30 C was significantly lower than at 25 C, but this initial lag in the 30 C treatment was overcome by the harvest at 12 wks. Differences in tuber production were most apparent by 16 wks when nearly 3 times as many tubers (161.0 ± 5.6 vs 58 ± 6.3 tubers) and 6.5

times as much tuber biomass (12.9 ± 0.5 vs 2.0 ± 0.2 g) occurred at 25 as at 35 C. Tuber biomass was related closely and significantly to tuber number ($r = 0.94$, $P < 0.001$) and to belowground biomass ($r = 0.96$, $P < 0.001$). Overall, the contribution of tubers to belowground biomass ranged from 66 to 91 percent from 8 to 16 wks.

Likewise, turion production (i.e., turion number and turion biomass) reflected strong effects of temperature, growth period and the interaction between these variables. No turions were produced at 35 C, and the number and biomass of those obtained at 30 C were markedly low (Figure 2). Most turions were produced at 25 C, with maximum production occurring between 12 to 16 wks.

Changes in mean biomass per propagule (i.e., tuber or turion) showed that prolonged growth periods allowed greater propagule development and magnified differences in response to temperature treatments. For example, mean biomass (\pm std. err.) per tuber at 8 wks varied by 21 percent, from 0.047 ± 0.003 g at 25 C down to 0.037 ± 0.003 g at 35 C ($F = 3.93$, $P = 0.0443$). By 16 wks the respective difference was 61 percent ($F = 72.09$, $P = 0.0001$), with a maximum of 0.080 ± 0.002 g per tuber occurring at 25 C. The mean biomass per turion at 25 C increased from 0.011 ± 0.003 g at 8 wks to 0.044 ± 0.001 g at 16 wks ($F = 172.01$, $P = 0.0001$), and by that time, had 34 percent more biomass than those in the 30 C treatment ($F = 9.92$, $P = 0.0198$). Under optimal conditions for the production of both propagule types, the mean biomass per tuber (0.080 ± 0.002 g) was nearly twice that per turion (0.044 ± 0.001 g).

Study 2: Responses of Dioecious Hydrilla. Total biomass in dioecious hydrilla was high in all temperature treatments, although at 35 C the response was slightly reduced (Figure 3). Levels of biomass production were similarly high at 25 and 30 C and peaked in all temperature treatments between 12 and 16 wks.

On the whole, ratios of root-to-shoot biomass were affected by treatment to a greater extent than was total biomass production (Figure 3). Unlike total biomass, root-to-shoot ratios were reduced sharply at 35 C and remained consistently low in that treatment over all growth periods. In 25 and 30 C treatments, ratios obtained at 12 to 16 wks were approximately 2 to 4 times greater than those obtained at 8 wks. Differences due to temperature increased through time and by 16 wks, ratios at 25 and 30 C exceeded those at 35 C by nearly eightfold.

Shoot length in the dioecious biotype primarily reflected influences of temperature, with plants at 30 and 35 C achieving the greatest stem lengths (Figure 3). There were no significant differences in stem length due to growth period or to the interaction of growth period and temperature.

Greater numbers of shoots were produced at 30 C than at either of the other two temperatures (Figure 3). The number of shoots produced at 25 and 35 C remained relatively stable between harvests, but at 30 C, shoots nearly doubled in number between 8 and 12 wks. At maximum production levels in the 30 C treatment, shoot numbers were approximately 40 and 60 percent greater than in the 25 and 35 C treatments, respectively.

Essentially no tubers were produced at 35 C (Figure 4). Tuber production occurred predominately at 25 and 30 C

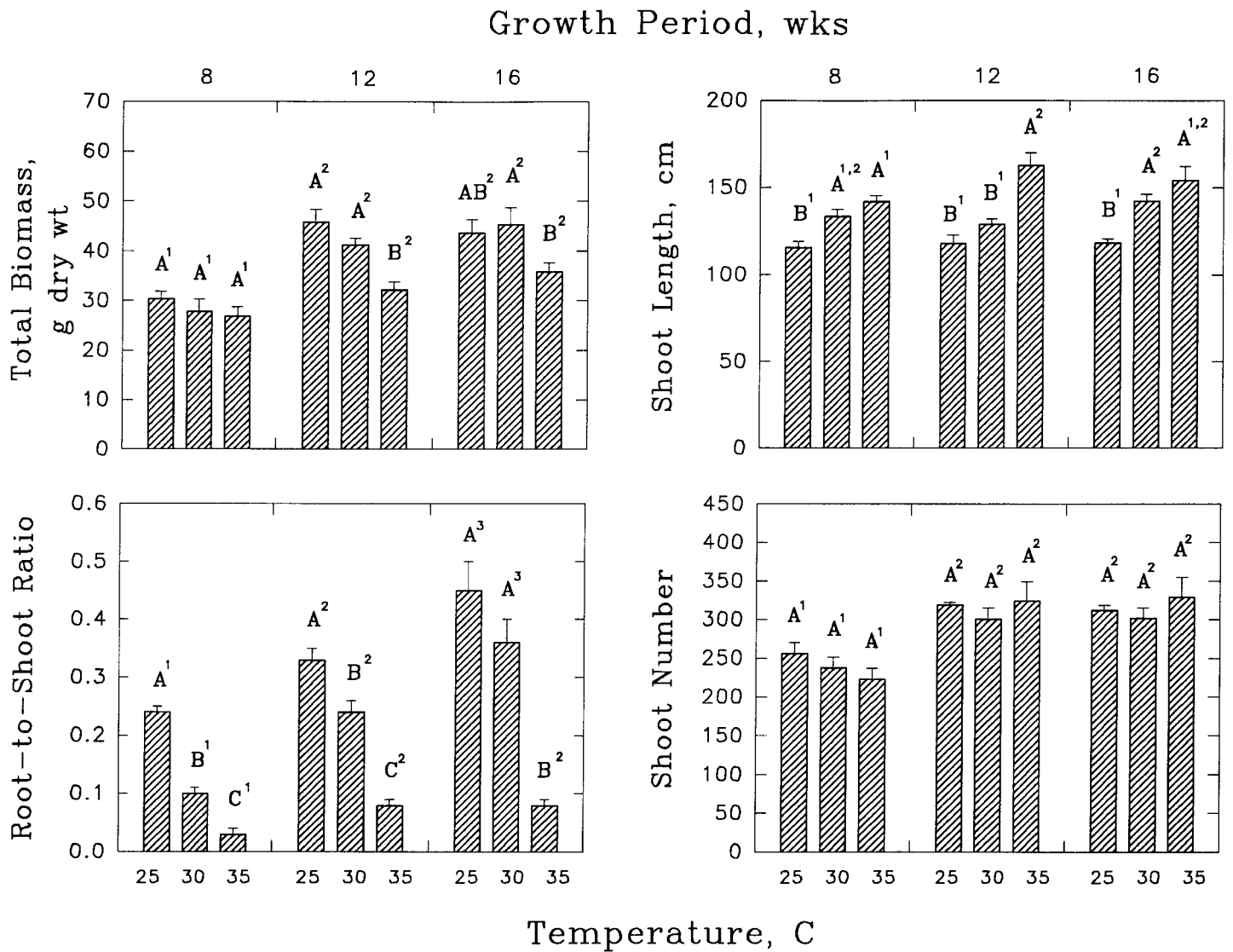


Figure 1. Effects of temperature and growth period on total biomass (top left), root-to-shoot ratio (bottom left), shoot length (top right) and shoot number (bottom right) in monoecious hydrilla. Each bar represents the mean \pm 1 standard error based on six replicate containers per treatment. Within each growth period, uppercase letters denote results of comparisons made across temperature. For each temperature, superscripts denote results of comparisons made across growth period. Bars sharing the same letter or superscript do not differ significantly from each other. Duncan's Multiple Range Test was used to determine statistical significance at $P < 0.05$.

and showed marked increases with growth periods up to 16 wks. In the 12 and 16-wk harvests, tuber biomass did not differ between 25 and 30 C treatments, despite elevated tuber numbers at 30 C. The opposite response was observed in the harvest at 8 wks when tuber number and biomass were greater at 25 C due to significant interactive effects. Correlation analysis showed strong positive relationships between tuber biomass and tuber number ($r = 0.89$, $P < 0.001$) and between tuber biomass and belowground biomass ($r = 0.92$; $P < 0.001$). From 8 to 16 wks, contributions of tubers to belowground biomass ranged from 17 to 52 percent.

The interaction of temperature and growth period exerted the greatest overall effect on turion production (i.e., turion number and biomass). At 30 and 35 C, production of

these propagules was inhibited completely (Figure 4). Turions developed only in the 25 C treatment where they were found in very low numbers at the end of 16 wks.

Increases in temperature severely limited biomass accrual in individual propagules. In the 25 C treatment, the mean biomass (\pm std. err.) per tuber ranged from 0.090 (\pm 0.012) to 0.167 (\pm 0.009) g between 8 and 16 wks, respectively. In the 30 C treatment, the corresponding range was 0.015 (\pm 0.12) to 0.087 (\pm 0.008) g. Increases in growth period allowed further tuber development as was indicated by the aforementioned findings. In treatments where both tubers and turions were formed, i.e., at 25 C by 16 wks, individual tubers outweighed individual turions by a factor of 4.

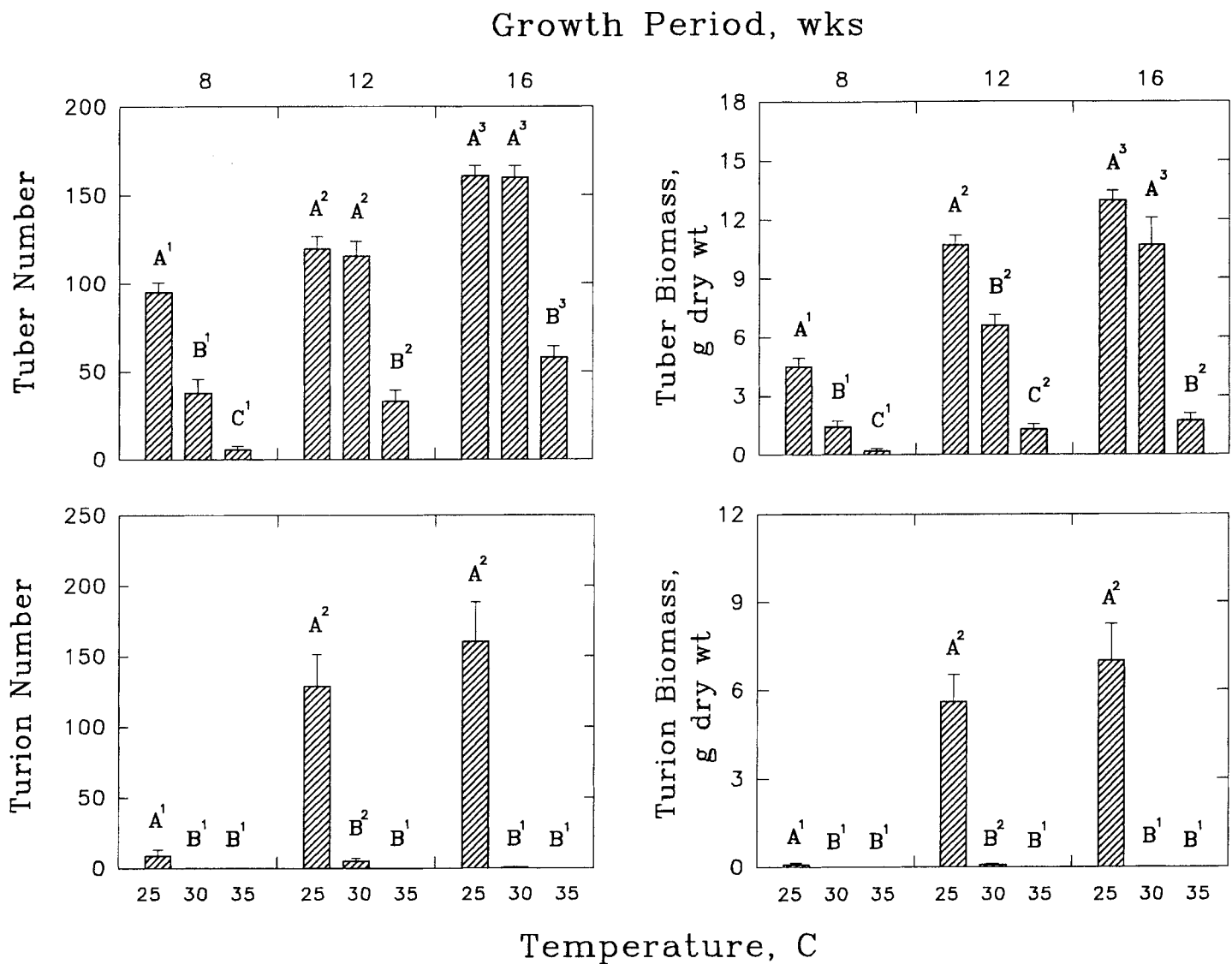


Figure 2. Effects of temperature and growth period on tuber number (top left), tuber biomass (top right), turion number (bottom left) and turion biomass (bottom right) in monoecious hydrilla. Each bar represents the mean \pm 1 standard error based on six replicate containers per treatment. Within each growth period, uppercase letters denote results of comparisons made across temperature. For each temperature, superscripts denote results of comparisons made across growth period. Bars sharing the same letter or superscript do not differ significantly from each other. Duncan's Multiple Range Test was used to determine statistical significance at $P < 0.05$.

DISCUSSION

The results presented here are evidence that extended growth periods can allow continued tuber and turion production in monoecious and dioecious hydrilla. These positive responses to growth period are thought to have resulted from exposure to shorter and shorter photoperiods. Increases in tuber production under short-day conditions have been widely documented for both hydrilla biotypes (Haller et al. 1976, Van et al. 1978, Spencer and Anderson 1986, Steward and Van 1987, McFarland and Barko 1990, Spencer et al. 1994). Information on daylength effects on turion production is less available; however, our data support findings of Miller et al. (1993) and Spencer et al. (1994) showing greater numbers of turions in hydrilla under short day lengths.

Total biomass, and tuber and turion production were reduced in both biotypes at 35 C, presumably due to metabolic losses associated with increased respiration rates (cf. Barko and Smart 1981). Yet, compared to the dramatic decline in propagules in that treatment, total biomass showed a relatively small decline. From a management standpoint, these results may be useful in identifying cases (e.g., shallow systems) where due to high temperature exposure, plants accrue substantial amounts of biomass at the expense of tuber and turion formation, resulting in low population densities at the beginning of the next growing season. Patterns of propagule production in hydrilla biotypes in these studies indicate a high temperature threshold, between 30 and 35 C for tubers and between 25 and 30 C for turions, which severely inhibits formation of these propagules.

Growth Period, wks

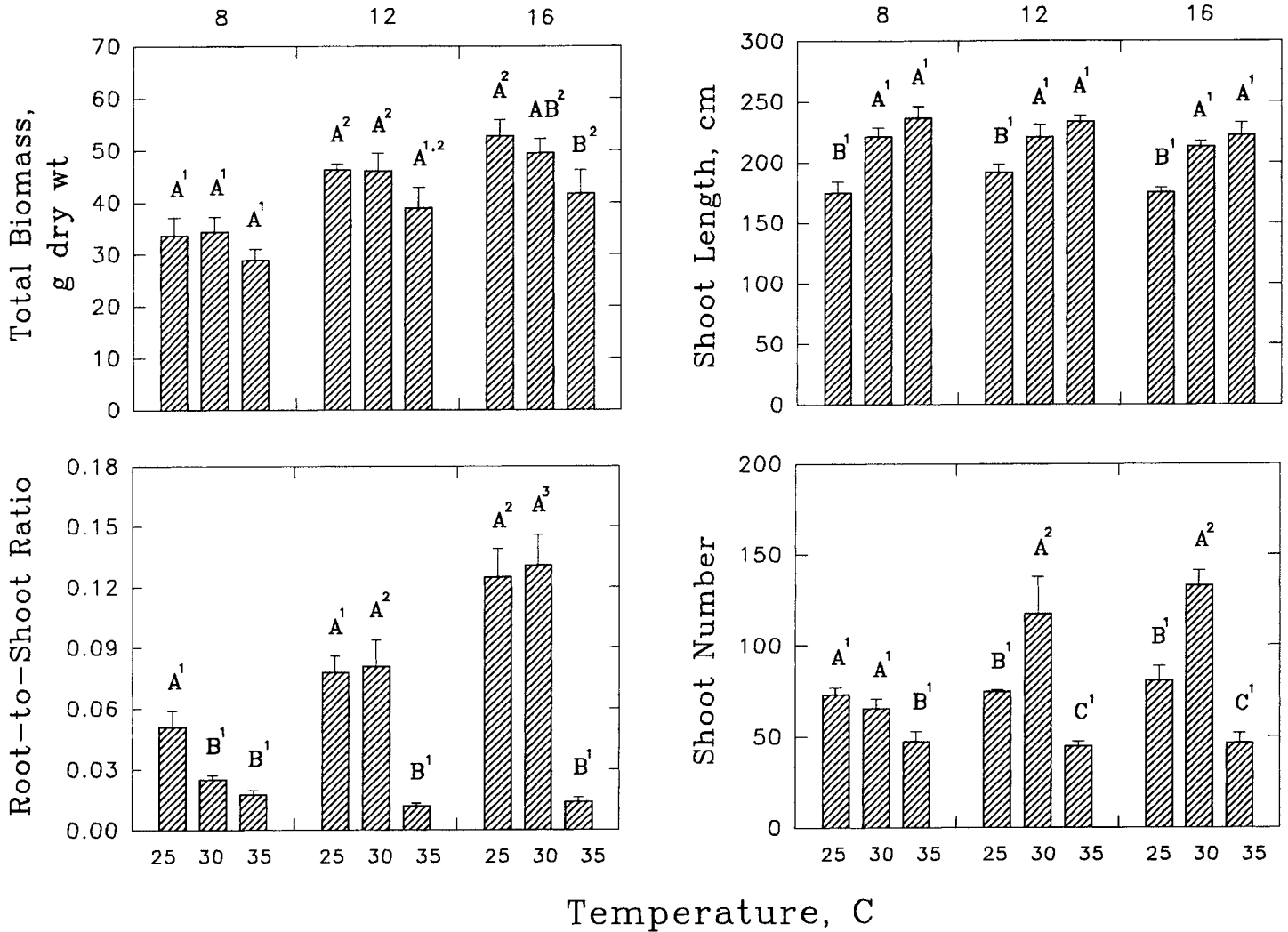


Figure 3. Effects of temperature and growth period on total biomass (top left), root-to-shoot ratio (bottom left), shoot length (top right) and shoot number (bottom right) in dioecious hydrilla. Each bar represents the mean \pm 1 standard error based on six replicate containers per treatment. Within each growth period, uppercase letters denote results of comparisons made across temperature. For each temperature, superscripts denote results of comparisons made across growth period. Bars sharing the same letter or superscript do not differ significantly from each other. Duncan's Multiple Range Test was used to determine statistical significance at $P < 0.05$.

Our calculations of mean biomass per propagule revealed that increases in temperature, from 25 to 35 C for tubers and to 30 C for turions, can significantly reduce individual propagule biomass. Although these results were determined indirectly, they provide a preliminary indication that exposure to high temperature can affect propagule size. At present, influences of tuber and turion biomass on the success of hydrilla are not completely known. However, in recent studies of monoecious hydrilla in our laboratory, emergence from different burial depths and from different sediment types was influenced directly by tuber biomass (unpubl. data). Furthermore, for *Potamogeton pectinatus* L., germination and initial growth rate have been shown to be positively related to tuber fresh weight (Spencer 1986). Differences in individual propagule biomass effected by temper-

ature may also influence other processes in hydrilla (e.g., competitive interactions, propagule longevity, and resistance to disease). Further research of the biomass-related vigor of tubers and turions would be useful in predicting their recruitment and post-germination capabilities in the field.

From results of our studies, tuber production appears to precede the production of axillary turions in both hydrilla biotypes. Spencer et al. (1994) also noted a similar sequence in propagule formation, and suggested that the timing difference could explain the greater abundance of tubers than turions in dioecious populations in the field (Mitra 1955, Haller and Sutton 1975, Sutton and Portier 1985, Harlan et al. 1985). Our data further showed monoecious hydrilla to be better able than dioecious hydrilla to overcome the initial lag in turion formation, and quickly achieve similarly large num-

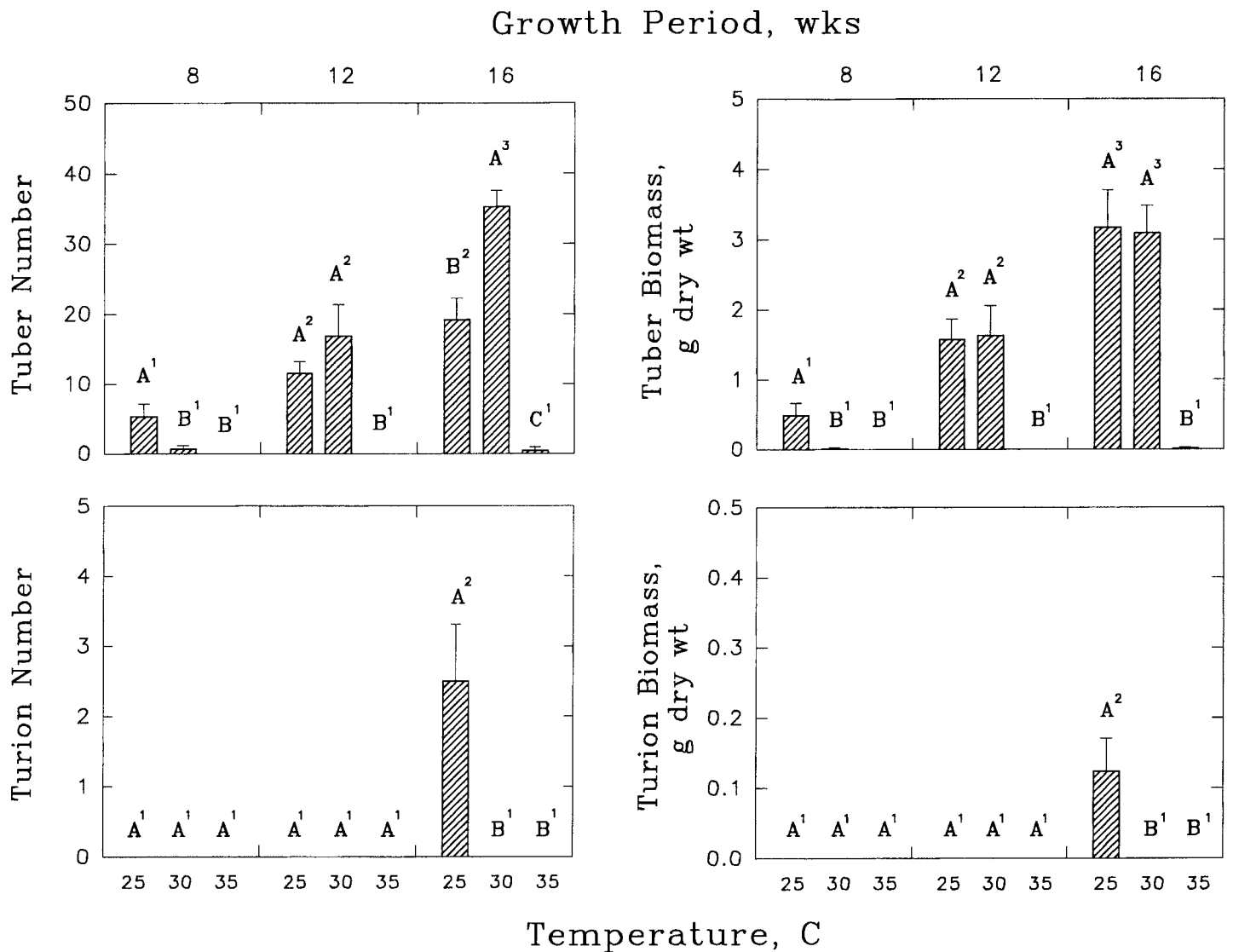


Figure 4. Effects of temperature and growth period on tuber number (top left), tuber biomass (top right), turion number (bottom left) and turion biomass (bottom right) in dioecious hydrilla. Each bar represents the mean \pm 1 standard error based on six replicate containers per treatment. Within each growth period, uppercase letters denote results of comparisons made across temperature. For each temperature, superscripts denote results of comparisons made across growth period. Bars sharing the same letter or superscript do not differ significantly from each other. Duncan's Multiple Range Test was used to determine statistical significance at $P < 0.05$.

bers of tubers and turions under favorable conditions (cf. Figures 2 and 4). Due to the later production of turions, adverse environmental conditions (e.g., sudden chilling) that might occur later in the season could potentially impede or prevent the development of these propagules. Such events could preclude turion transport via water movements to other colonizable sites. We further propose that since turion formation occurs more swiftly in the monoecious biotype, periods during which its turion formation could be terminated or interrupted may be shorter than for the dioecious biotype.

Although the northerly distribution of monoecious hydrilla in the U.S. is probably linked to human introduction, it also has been attributed to the rapid production of shoots (as a source of fragments) and tubers of this biotype at mod-

erately low temperatures (Spencer and Anderson 1986, McFarland and Barko 1987, Steward and Van 1987). These capabilities in monoecious hydrilla are advantageous in northern environments where growing seasons are typically short (Spencer and Anderson 1986). Conversely, the ability of the monoecious biotype to produce relatively high densities of shoots and tubers at high temperatures (30 to 35 C) increases its potential for survival in many southern localities, and under high temperature conditions that may occur during drought. Interestingly, Cook and Luond (1982) have reported that on a worldwide scale, monoecious hydrilla is more prevalent than dioecious hydrilla in tropical areas. Results obtained in the present studies generally support their observations.

TABLE 2. SYNOPTIC TWO-WAY ANOVAS FOR RESPONSES OF MONOECIOUS AND DIOECIOUS HYDRILLA (IN STUDIES 1 AND 2, RESPECTIVELY) RELATIVE TO TEMPERATURE AND GROWTH PERIOD.

Response	Source ¹	Monoecious		Dioecious	
		F value	P	F value	P
Total Biomass	pd	35.03	0.0001	20.41	0.0001
	temp	11.50	0.0001	5.48	0.0074
	pd * temp	2.27	0.0804	0.27	0.8937
Root: Shoot Ratio	pd	56.03	0.0001	31.42	0.0001
	temp	150.46	0.0001	56.10	0.0001
	pd * temp	7.11	0.0003	9.94	0.0001
Shoot Length	pd	2.52	0.0918	3.75	0.0610
	temp	45.83	0.0001	23.02	0.0001
	pd * temp	2.52	0.0544	2.53	0.0537
Shoot Number	pd	17.46	0.0001	6.67	0.0029
	temp	1.14	0.3284	36.42	0.0001
	pd * temp	4.13	0.0062	5.47	0.0011
Tuber Number	pd	99.74	0.0001	43.66	0.0001
	temp	143.09	0.0001	51.78	0.0001
	pd * temp	8.91	0.0001	16.15	0.0001
Tuber Biomass	pd	130.68	0.0001	34.36	0.0001
	temp	213.98	0.0001	34.04	0.0001
	pd * temp	19.57	0.0001	8.69	0.0001
Turion Number	pd	15.07	0.0001	9.62	0.0003
	temp	66.40	0.0001	9.62	0.0003
	pd * temp	14.37	0.0001	9.62	0.0001
Turion Biomass	pd	16.70	0.0001	7.01	0.0022
	temp	65.81	0.0001	7.01	0.0022
	pd * temp	16.38	0.0001	7.01	0.0002

¹Abbreviations: pd = growth period; temp = temperature; pd * temp = interaction between growth period and temperature.

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LITERATURE CITED

- Allen, E. D., and P. R. Gorham. 1973. Changes in the submerged macrophyte communities of Lake Wabamun as a result of thermal discharge. In: Proceedings of the Symposium on the Lakes of Western Canada. University of Alberta, Edmonton, pp. 313-324.
- Anderson, L. W. J. 1985. Preliminary research on monoecious hydrilla. Misc. Paper A-85-4, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS, pp. 185-189.
- Anderson, R. R. 1969. Temperature and rooted aquatic plants. Chesapeake Sci. 10: 157-164.
- Barko, J. W., M. S. Adams, and N. L. Cleseri. 1986. Environmental factors and their consideration in the management of submersed aquatic vegetation: a review. J. Aquat. Plant Manage. 24: 1-10.
- Barko, J. W., D. G. Hardin, and M. S. Matthews. 1982. Growth and morphology of submersed macrophytes in relation to light and temperature. Can. J. Bot. 60: 877-887.
- Barko, J. W., and R. M. Smart. 1981. Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. Ecol. Monogr. 51: 219-235.
- Barko, J. W., R. M. Smart, D. G. McFarland, and R. L. Chen. 1988. Interrelationships between the growth of *Hydrilla verticillata* (L.f.) Royle and sediment nutrient availability. Aquat. Bot. 32: 205-216.
- Basiouny, F. M., W. T. Haller, and L. A. Garrard. 1978. The influence of growth regulators on sprouting of *Hydrilla* tubers and turions. J. Exp. Bot. 29: 663-669.
- Blackburn, R. D., L. W. Weldon, R. R. Yeo, and T. M. Taylor. 1969. Identification and distribution of similar appearing aquatic weeds in Florida. Hyacinth Contr. J. 8: 11-21.
- Cook, C. D. K., and R. Luond. 1982. A revision of the genus *Hydrilla* (Hydrocharitaceae). Aquat. Bot. 13: 485-504.
- Dechoretz, N. 1989. Hydrilla program in California: current status. Misc. Paper A-89-1, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS, pp. 6-10.
- Grace, J. B., and L. J. Tilly. 1976. Distribution and abundance of submerged macrophytes including *Myriophyllum spicatum* L. (Angiospermae) in a reactor cooling reservoir. Arch. Hydrobiol. 77: 475-487.
- Haller, W. T. 1976. *Hydrilla*: a new and rapidly spreading aquatic weed problem. Circular S-245, Agricultural Experiment Station, IFAS, University of Florida, Gainesville, FL, 13 pp.
- Haller, W. T., J. L. Miller, and L. A. Garrard. 1976. Seasonal production and germination in hydrilla vegetative propagules. J. Aquat. Plant Manage. 14: 26-28.
- Haller, W. T., and D. L. Sutton. 1975. Community structure and competition between *Hydrilla* and *Vallisneria*. Hyacinth Control J. 13: 48-50.
- Harlan, S. M., G. Davis, and G. J. Pesacreta. 1985. *Hydrilla* in three North Carolina lakes. J. Aquat. Plant Manage. 23: 68-71.
- Langeland, K. A., and C. B. Smith. 1984. Hydrilla produces viable seed in North Carolina lakes—a mechanism for long distance dispersal. Aquatics 6: 20-21.
- Les, D. H., L. J. Mehrhoff, M. A. Cleland, and J. D. Gabel. 1997. *Hydrilla verticillata* (Hydrocharitaceae) in Connecticut. J. Aquat. Plant Manage. 35: 10-14.
- McFarland, D. G., and J. W. Barko. 1987. Effects of temperature and sediment type on growth and morphology of monoecious and dioecious *Hydrilla*. J. Freshwat. Ecol. 4: 245-252.
- McFarland, D. G., and J. W. Barko. 1990. Temperature and daylength effects on growth and tuber formation in Hydrilla. J. Aquat. Plant Manage. 28: 15-19.

- Miller, J. D., W. T. Haller, and M. S. Glenn. 1993. Turion production by dioecious hydrilla in north Florida. *J. Aquat. Plant Manage.* 31: 101-105.
- Mitra, E. 1955. Contributions to our knowledge of Indian freshwater plants. 1. On some aspects of the structure and life history of *Hydrilla verticillata* Presl. with notes on its autoecology. *J. Asiatic Soc.* 2: 1-16.
- SAS Institute, Inc. 1991. SAS Version 6.03. SAS Institute, Cary, NC, 1028 pp.
- Sastroutomo, S. S. 1982. The role of turions in the re-establishment process of population in submerged species. *Ecol. Rev.* 20: 1-13.
- Schmitz, D. C., B. V. Nelson, L. E. Hall, and J. D. Schardt. 1991. Exotic aquatic plants in Florida: a historical perspective and review of the present aquatic plant regulation program. *Proc. Symp. on Exotic Pest Plants.* Univ. Miami, Nov. 2-3, 1988, Miami, FL.
- Sculthorpe, C. D. 1967. *The Biology Aquatic Vascular Plants.* Edward Arnold (Publ.) Ltd., London, 610 pp.
- Smart, R. M., and J. W. Barko. 1985. Laboratory culture of submersed freshwater macrophytes on natural sediments. *Aquat. Bot.* 21: 251-263.
- Spencer, D. F. 1986. Tuber demography and its consequences for *Potamogeton pectinatus* L. *Proceedings, Europ. Weed Res. Soc., Assoc. Appl. Biol., 7th Symp. on Aquatic Weeds, Loughborough*, pp. 321-325.
- Spencer, D. F., and L. W. J. Anderson. 1986. Photoperiod responses in monoecious and dioecious *Hydrilla verticillata*. *Weed Sci.* 34: 551-557.
- Spencer, D. F., and L. W. J. Anderson. 1987. Influence of photoperiod on growth, pigment composition and vegetative propagule formation for *Potamogeton nodosus* Poir. and *Potamogeton pectinatus* L. *Aquat. Bot.* 28: 103-112.
- Spencer, D. F., L. W. J. Anderson, M. D. Ames, and F. J. Ryan. 1987. Variation in *Hydrilla verticillata* (L.f.) Royle propagule weight. *J. Aquat. Plant Manage.* 25: 11-14.
- Spencer, D., L. Anderson, G. Ksander, and S. Klaine. 1994. Vegetative propagule production and allocation of carbon and nitrogen by monoecious *Hydrilla verticillata* (L.f.) Royle grown at two photoperiods. *Aquat. Bot.* 48: 121-132.
- Spencer, D. F., and G. G. Ksander. 1991. Comparative growth and propagule production by *Hydrilla verticillata* grown from axillary turions or subterranean turions. *Hydrobiologia* 222: 153-158.
- Steward, K. K., and T. K. Van. 1987. Comparative studies of monoecious and dioecious hydrilla (*Hydrilla verticillata*) biotypes. *Weed Sci.* 35: 204-210.
- Steward, K. K., T. K. Van, V. Carter, and A. H. Pieterse. 1984. Hydrilla invades Washington, DC and the Potomac. *Am. J. Bot.* 71: 162-163.
- Sutton, D. L., and K. M. Portier. 1985. Density of tubers and turions of hydrilla in south Florida. *J. Aquat. Plant Manage.* 23: 64-67.
- Titus, J. E., and M. S. Adams. 1979. Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Valisneria americana* Michx. *Oecologia* 40: 273-286.
- Van, T. K., W. T. Haller, and L. A. Garrard. 1978. The effect of daylength and temperature on hydrilla growth and tuber production. *J. Aquat. Plant Manage.* 16: 57-59.
- Verkleij, J. A. C., and A. H. Pieterse. 1986. Identification of *Hydrilla verticillata* (L.f.) Royle strains by means of isoenzyme patterns. *Europ. Weed Res. Soc., Assoc. Appl. Biol., 7th Symp. on Aquatic Weeds, Loughborough*, pp. 381-388.
- Weber, J. A. 1973. Induction, dormancy and germination of the turions of *Myriophyllum verticillatum*. Ph.D. Dissertation, University of Michigan, Ann Arbor, MI. 219 pp.
- Weber, J. A., and L. D. Nooden. 1976. Environmental and hormonal control of turion formation in *Myriophyllum verticillatum*. *Plant Cell Physiol.* 17: 721-731.