

Temperature and Daylength Effects on Growth and Tuber Formation in Hydrilla

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ABSTRACT

Under controlled environmental conditions, growth and tuber formation in hydrilla [*Hydrilla verticillata* (L. f.) Royle] were examined over a range of temperatures (20 - 30 C), during 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 builders' 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 daylength interacted significantly in affecting tuber production.

Key words: photoperiod, sediment, interaction, biomass, tuber production.

INTRODUCTION

Hydrilla [*Hydrilla verticillata* (L. f.) Royle] is a highly prolific, rooted, submersed macrophyte (Haller 1976, Van

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et al. 1978a, Cook and Luond 1982, Yeo et al. 1984). For three decades since its introduction to Florida (Blackburn et al. 1969), hydrilla has extended its invasion of freshwater systems mainly throughout southern regions of the country (Steward et al. 1984, Spencer and Anderson 1986). The ability of hydrilla to displace favorable native submersed aquatic vegetation is attributed to several photosynthetic and reproductive characteristics (Haller 1976, Van et al. 1978a). These include a 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 (Steward and Van 1985, Salisbury and Ross 1985).

Ecological studies of growth and tuber formation in hydrilla have focused primarily on response to specific environmental variables. Major consideration has been given to effects of daylength, temperature, and sediment fertil-

ity. Research to date indicates that short photoperiod induces tuber formation in hydrilla (Haller 1976, Haller et al. 1976, Van et al. 1978a and b, Bowes et al. 1979), and that under these conditions, tuber formation increases with increased biomass and water temperatures up to about 33 C (Van et al. 1978b). Reductions in both growth and tuberization due to inadequate sediment fertility have been demonstrated in studies of Van and Haller (1979), Bruner and Batterson (1984), Barko and Smart (1986), and McFarland and Barko (1987). Whereas daylength, 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.

In this article, we examine the effects of temperature, daylength, and their interaction on growth and tuber formation in dioecious hydrilla under controlled environmental conditions. Responses are contrasted across two sediments differing in texture and nutrient availability. Assessments here are intended to further the knowledge of processes regulating growth and perennation of hydrilla in different habitats, and, ultimately, to contribute to the advancement of practices in aquatic plant management.

METHODS AND MATERIALS

The research was conducted in two 10-wk phases in a greenhouse facility of the Waterways Experiment Station (WES), Vicksburg, MS (Barko and Smart 1981). 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 hrs (List 1951).

In both phases, three 1200-L white fiberglass tanks were used to provide separate 5-degree increments in experimental temperatures from 20 to 30 C. The tanks were filled 83 cm deep with the culture solution described in Smart and Barko (1985). The solution was continuously circulated and thermally controlled (± 1 C) by liquid circulators connected independently to each tank.

The sediment used in this study was collected from Brown's Lake at WES; it was a fine-textured, inorganic substrate (characterized in Barko and Smart 1986) with particle size fractions of 5% coarse ($>50\mu$ dia) and 95% fine ($<5\mu$ dia) by dry mass. At the beginning of each phase, the sediment was mixed thoroughly (while wet) and divided into two portions. One of these was amended with washed builders' sand, an infertile addition that resulted in a 22% coarse, 78% fine particle size distribution; and the other with NH_4Cl (30.8 mg N L^{-1} of sediment) to ensure sufficient nitrogen availability (Barko unpublished data) over the 10-wk 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 1700 ml.

Dioecious hydrilla was obtained from our greenhouse stock established from an earlier collection made in Lake Seminole, FL. This stock was subcultured over 6-wk periods, on fresh (unamended) Brown's Lake sediment. Subcultures were grown at 25 C, under naturally-occur-

ring photoperiods, i.e. either 11-12 hrs daylight immediately prior to the short-day phase, or 13-14 hrs daylight immediately prior to the long-day phase. Four 12-cm long apical cuttings (approximately 0.08 g dry mass) were planted to a depth of 5 cm per container. A thin layer of clean sand was placed on the sediment surface to minimize particle disturbance and nutrient diffusion into the water column (Smart and Barko 1985). Consistent with pretreatment culture procedures, neutral-density shade fabric was positioned over the tanks reducing ambient irradiance levels by 33%. Midday photosynthetically active radiation inside the tanks was about 1000 and 600 $\mu\text{E m}^{-2} \text{s}^{-1}$ during long and short days, respectively.

Each study phase was terminated at 10 weeks to avoid the onset of senescence (Barko and Smart 1981, Smart and Barko 1985). 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 treatments on tuber number were evaluated by direct counting. All data 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% or less.

RESULTS

Total biomass in hydrilla was greater under long-day than short-day conditions, and was generally stimulated on the fertile (N-amended) sediment (Figure 1). 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 daylengths, 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.

Temperature and daylength interacted significantly in affecting tuber formation (Figure 2). Under short days, tuber formation was inhibited at 20 C, while under long days tuber number was greatest at this temperature. Under long days, no tubers were formed at 30 C; however, at this temperature tuber number was greatest under short-day conditions. Over all temperature and sediment conditions, short-day tuber number was about 4 times greater than long-day tuber number.

Although daylength effected only minor differences in tuber mass (i.e. total tuber mass per container, Figure 2), individual tuber mass was substantially reduced under short days. Based on data pooled for tuber-producing replicates, the mean mass (\pm std. err.) per tuber formed during long days was 147.9 (\pm 42.0) mg, while the short-day mean was 24.9 (\pm 0.3) mg per propagule, reflecting a six-fold difference in individual tuber mass between daylengths.

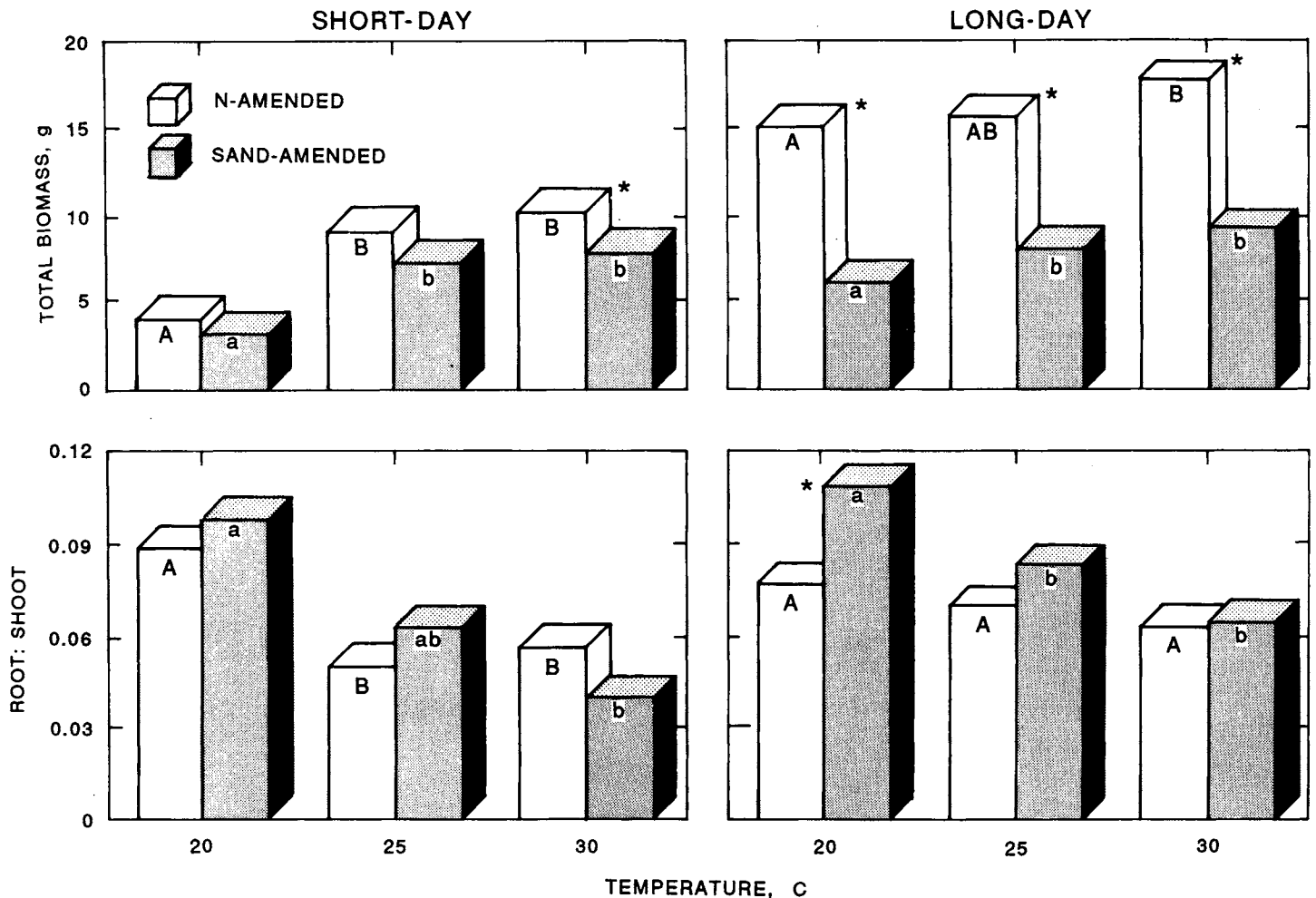


Figure 1. Effects of temperature and sediment type on growth of hydrilla under long-day and short-day conditions. Within each subfigure, biomass values or root-to-shoot ratios sharing the same letter (upper case for N-amended sediment and lower case for sand-amended sediment) do not differ significantly from each other. Asterisks denote significant effects of sediment type on growth. Duncan's Multiple Range Test was used to determine statistical significance at $P < 0.05$.

DISCUSSION

Results of this investigation are in general agreement with those of others demonstrating that temperature and daylength strongly influence growth and tuber production in hydrilla (e.g. Van et al. 1978b, Barko and Smart 1981, Spencer and Anderson 1986, McFarland and Barko 1987, Steward and Van 1987). However, unique to the present study is the demonstrated interaction of these variables affecting tuber formation. As in the present investigation, a positive effect of increasing temperature on tuber formation in dioecious hydrilla was reported under short-day conditions (Van et al. 1978b). However, under long-day conditions, increasing temperature appears to have a negative effect on tuber formation in both dioecious (this study) and monoecious (McFarland and Barko 1987) hydrilla. In monoecious hydrilla, the response was magnified substantially (compared to results of the present investigation) due to the tendency of this biotype to produce greater numbers of tubers than the dioecious biotype (Steward and Van 1987). Interactions between temperature and daylength appear to be important in the turion production of other

aquatic species as well, e.g. curlyleaf pondweed, *Potamogeton crispus* L. (Sastroutomo 1980), and European frogbit, *Hydrocharis morsus-ranae* L. (Glück 1906 as cited in Sastroutomo 1980, Vegis 1955).

As predicted by our findings and those 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 in Lake Trafford, Florida, Bowes et al. (1979) reported high tuber densities throughout 1977, with peak densities occurring in February, and notably in August. Our data suggest that moderate water temperature (about 21 C, from Bowes et al. 1979) coupled with long daylengths of summer may have extended the period of tuber production in Lake Trafford. Further, we speculate 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.

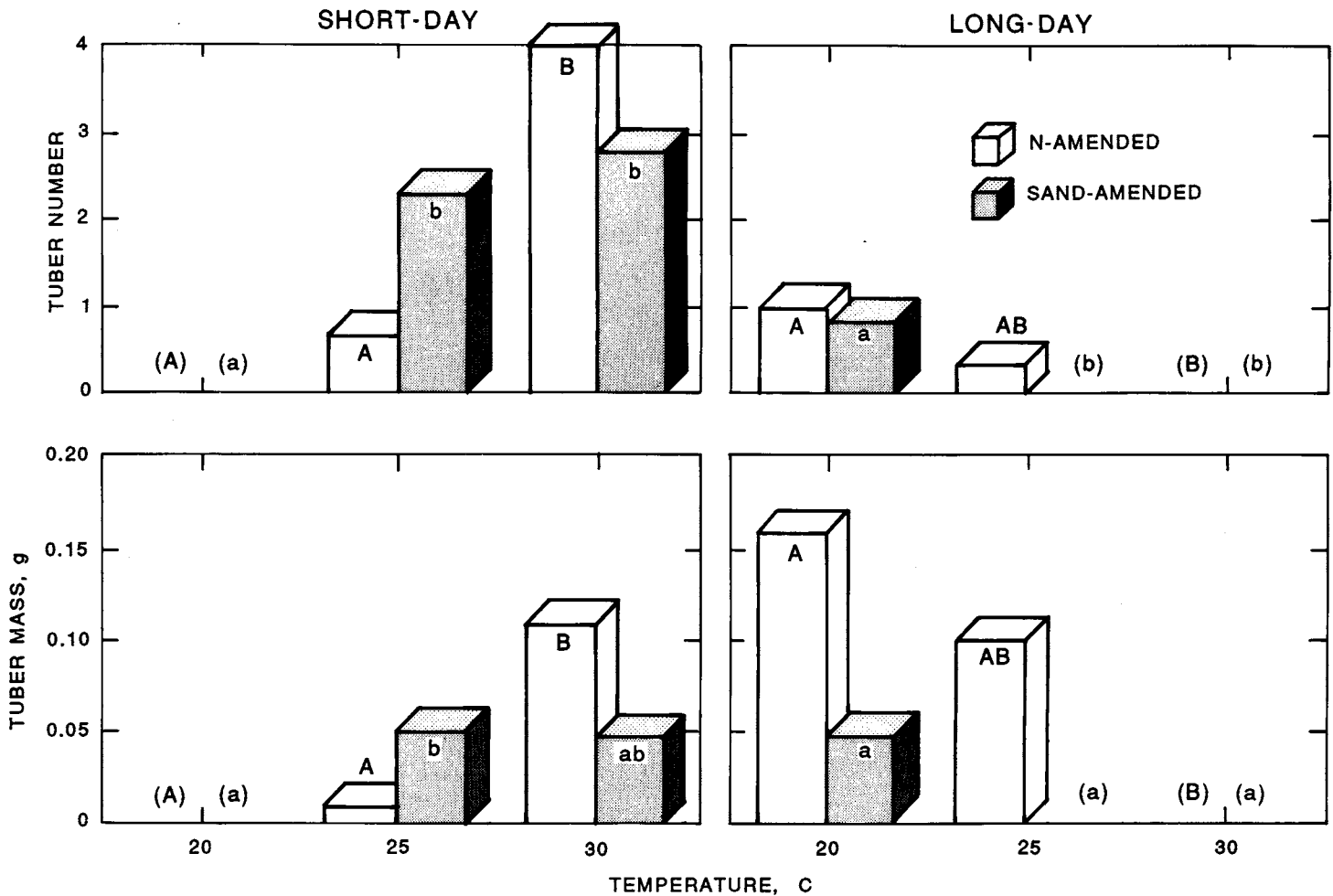


Figure 2. Effects of temperature and sediment type on tuber formation in hydrilla. Within each subfigure, tuber number or tuber mass sharing the same letter (upper case for N-amended sediment and lower case for sand-amended sediment) do not differ significantly from each other. Units for tuber number represent number per container. Asterisks denote significant effects of sediment type on tuber formation. Duncan's Multiple Range Test was used to determine statistical significance at $P < 0.05$.

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), our 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. Further investigation of the occurrence and mass-related vigor of long-day propagules would be useful in assessing potential recruitment and competitive success of hydrilla under different conditions.

Growth of hydrilla in this 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 Patterson 1984, Steward 1984, Sutton 1985, Barko and Smart 1986). Yet, despite sediment conditions causing significant reductions in biomass, tuber for-

mation was not significantly affected. Bruner and Battersson (1984) have hypothesized that the number of tubers produced and sustained by hydrilla is a function of sediment fertility. However, our results indicate that tuber production may be more dependent upon other environmental cues (e.g. temperature and daylength) 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 and ours suggest that sediment composition may be a better indicator of hydrilla growth potential than an indicator of tuber density in nature. Considering the great 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.

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