Adaptation To Low Light Levels By Hydrilla[1]

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ABSTRACT

Mature, apical stem sections of hydrilla (*Hydrilla verticillata* (L.F.) Royle) were collected at Orange Lake, Florida to determine their adaptability to low light levels. These plants were grown in controlled environment chambers at quantum flux densities varying from below the photosynthetic light compensation point to near light saturation. Growth rates, expressed as fresh weight, dry weight and stem length, were measured over a 5-week period. Concomitantly, chlorophyll content, photosynthetic, photorespiratory, and respiratory characteristics were determined. The plants adapted their photosynthetic and respiratory characteristics to make more effective use of the lower light levels. Young shoots, developing from tubers, exhibited similar adaptations to low light. Tuber size influenced both shoot survival and shoot length when they were germinated and held in complete darkness. The largest tubers produced shoots that survived longer and had longer stems. The lowest light level to which hydrilla plants could adapt was 10 to 12 μeinstein/m$^2 \cdot$sec. Below this quantum flux density the plants were incapable of increasing in dry weight.

INTRODUCTION

Within the 15 years since its introduction into the State, hydrilla has become the most serious aquatic weed problem in Florida. The rapid spread of this plant within a body of water and its dominance over native aquatic vegetation are probably related to its low light requirement for photosynthesis. Van et al. (9) compared the photosynthetic responses of four submersed aquatic plants to increasing irradiance. Hydrilla required the least light to achieve the light compensation point, where the amount of CO_2 produced by respiratory processes is equivalent to the amount taken up in photosynthesis. Similarly, hydrilla required significantly less light than the other species to drive photosynthesis at half-maximum rate. These features would enable hydrilla to outcompete other species in conditions of low irradiance, such as during regrowth from the hydrosoil at the bottom of a lake. They would also be advantageous in dense vegetation, since in a hydrilla mat most of the photosynthetic activity occurs early in the morning when light is limiting (9). Brown et al. (5) have

also reported a correlation between the photosynthetic responses to light by a number of exotic submersed macrophytes and their ability to displace native vegetation in New Zealand lakes.

Light is also an important factor controlling the zonation of submersed aquatic macrophytes (7). Species with greater shade tolerance are usually able to colonize deeper waters. Thus it might be possible to estimate the depth range for infestation by a rooted, submersed aquatic plant, such as hydrilla, if the light compensation point of the plant and the light penetration into the water were known. This information potentially could be used as a tool to predict, at an early stage of infestation, how much of a lake, left untreated, might be covered by the weed.

However, the light compensation point of terrestrial species is known to vary, within limits, with the environmental conditions for growth. Björkman et al. (3) have shown that within a single genotype the rates of several of the component processes in photosynthesis can be modified by growing the plants under different light levels. Bowes et al. (4) suggested that adaptation to the light intensity received during growth may explain the large differences in maximum photosynthetic rate and light saturation intensity that have been observed with soybean. Two species of the aquatic plant *Potamogeton*, *P. polygonifolius* and *P. obtusifolius* which are shallow- and deep-water species respectively, also reportedly adapt to the prevailing light conditions during growth (8). The potential range of individual adaptation differs considerably between the shallow-water and the deep-water species, which suggests that limits to the adaptations caused by light are genetically determined.

The following study, with apical stem sections from mature hydrilla plants and shoots germinated from hydrilla tubers, was undertaken to determine the limits of adaptation to light in an attempt to predict the lowest light level at which hydrilla might be expected to survive and grow.

METHODS AND MATERIALS

Hydrilla plants were collected from surface waters of Orange Lake, Florida. Hydrilla tubers were collected in the Kenwood area of Rodman Reservoir from the hydrosoil under a water depth of approximately 1 m. Mature, 10-cm long apical stem sections were planted 25 to an aquarium in a layer of washed sand 3 cm in depth. Two 20-liter aquaria were used for each light treatment. The aquaria were filled with water from Orange Lake and placed in growth chambers at 25 C with a 16-hr day. The lake water was replaced every 2 weeks. The quantum flux density pro-

vided by a combination of fluorescent and incandescent lamps, was varied with neutral density filters to obtain four different quantum flux density levels (400-700 nm) incident on the plants. These levels, measured in μeinstein/m²•sec with a Model LI 185 Lambda Quantum Meter were: 6 (low light), 30 and 120 (intermediate light), and 300 (high light). Previous work (9) indicated that the low light was below the light compensation point of the plants, while the high light was close to saturation for photosynthesis. Over a 5-week period, six plants were measured each week at each light level to determine changes in stem length, fresh weight, and dry weight. Photosynthetic and respiratory characteristics were measured on six of the plants after a 3-week period.

Photosynthetic and respiratory rates were measured at air-levels of CO_2 and pH 5.5 with a Beckman 215A infrared gas analyzer as described previously (9). Photorespiration was determined as the rate of CO_2 released by the plants under saturating light at a CO_2 level of 5 μl CO_2/liter in the circulating gas mixture. The chlorophyll content was determined by the method of Arnon (1).

Tubers were treated in a similar manner to the apical stem sections, except they were germinated in the dark before being placed in the aquaria under the different quantum flux densities. Fresh and dry weights of a sample were measured to determine the initial tuber weight. In the experiment to determine survival and the maximum shoot length that a tuber could support, the ungerminated tubers were divided into four weight classes. Twenty to thirty tubers from each weight class were planted to a depth of 1 cm in sand contained in glass columns 200 cm in length filled with lake water and maintained in complete darkness. The water was aerated with an air pump. Shoot lengths and survival were determined periodically under a green safelight.

RESULTS AND DISCUSSION

Apical Stem Sections. Plotted in Figure 1 are the photosynthetic rates, as a function of light, of the apical stem sections of hydrilla grown under four different quantum flux densities. The data indicate an adaptation of photosynthesis to the quantum flux density received during growth, so that the plants were able to make more effective use of the light level under which they were grown. The quantum flux density required to saturate photosynthesis (i.e. the light saturation point) was increased four-fold by growing the plants at the high light as opposed to the low light (Figure 1). Plants grown under the low light required

the least light to achieve the light compensation point and the half-maximal photosynthetic rate. Thus, at very limiting light intensities, plants grown under low and intermediate light exhibited the higher photosynthetic rates (Figure 1).
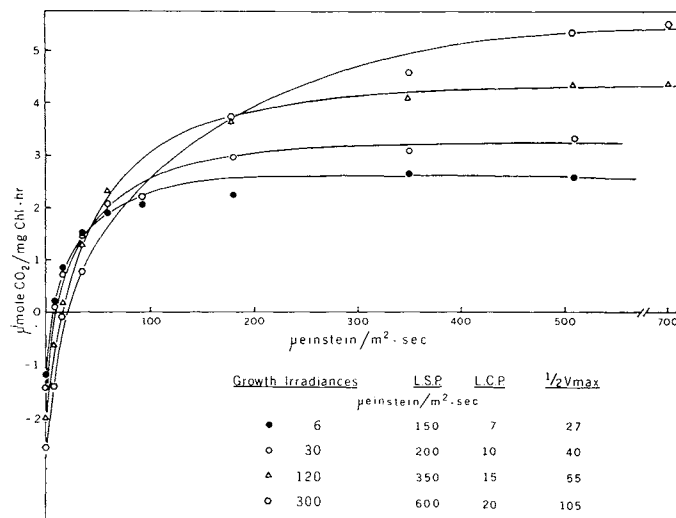

Figure 1. Effect of light on the photosynthetic CO_2 fixation rates of apical stem sections from hydrilla grown for 3 weeks under various quantum flux densities. L.S.P.: quantum flux density at the light saturation point; L.C.P.: quantum flux density at the light compensation point; $\frac{1}{2}$Vmax: quantum flux density required for half-maximal photosynthetic rate.

The plants grown under high light had a light saturated photosynthetic rate of 5.4 μmole CO_2/mg Chl• hr (Table 1). Similar values have been reported for hydrilla freshly collected from surface waters of lakes exposed to full sun (9). The rate exhibited by plants grown under low light was less than half of this value (Table 1). A similar adaptive reduction has been reported for the light saturated photosynthetic rate of terrestrial plants grown at low light intensities (3), and in certain instances the reduced rate appears to correlate with reduced activity of the primary carboxylation enzyme (4). The dark respiration rates were reduced in a manner similar to the photosynthetic rates in plants grown at the lower light levels (Table 1), and thus for all treatments the dark respiration rate was approximately 45% of the photosynthetic rate. Photorespiration rates appeared to be unaffected by the quantum flux density during growth (Table 1). Table 1 also shows that the chlorophyll concentration in the plants increased as the quantum flux density during growth decreased, except for

TABLE 1. THE EFFECT OF VARIOUS QUANTUM FLUX DENSITIES DURING A 3-WEEK GROWTH PERIOD ON THE CHLOROPHYLL CONTENT, PHOTOSYNTHETIC, RESPIRATORY, AND PHOTORESPIRATORY RATES OF APICAL STEM SECTIONS OF HYDRILLA.

Quantum Flux Density During Growth (μeinstein/m²•sec)	Chlorophyll Content (mg/ g fr wt)	Light-saturated Photosynthetic Rate (μmole CO_2/mg Chl• hr)	Rate of Dark Respiration (μmole CO_2/mg Chl• hr)	Rate of Photorespiration (μmole CO_2/mg Chl• hr.)
6	0.976 ± 0.107†	2.6 ± 0.3	1.2 ± 0.9	1.1 ± 0.4
30	1.330 ± 0.222	3.3 ± 0.4	1.4 ± 0.2	1.6 ± 0.3
120	1.290 ± 0.124	4.3 ± 0.2	2.0 ± 0.3	1.2 ± 0.4
300	1.131 ± 0.106	5.4 ± 0.6	2.5 ± 0.2	1.0 ± 0.2

† Mean of six measurements ± standard deviation.

33

the plants grown at low light, where the incoming radiant energy was probably too low to support many synthetic reactions.

It has been suggested (3) that photosynthetic and respiratory adaptations to low light are primarily related to energy conservation, involving an increase in the capacity of the light harvesting system and a concomitant decrease in the capacity of the CO_2 fixation reactions. High levels of the carboxylation enzyme, for example, would be of little use under limiting light conditions and the synthesis and maintenance of such levels would require substantial expenditures of energy via respiration. The data for hydrilla supports this hypothesis.

All plants, including those under the lowest light level exhibited an increase in length and fresh weight over the experimental period (data not shown). Despite this increase in length, the plants grown under low light exhibited a decrease in dry weight (Figure 2), indicating that the quantum flux density of 6 μeinstein/m²•sec was below the light compensation point of the plants. The report (2) that certain aquatic plants can "grow" at light levels as low as 10 ft-c (approximately equal to 2 μeinstein/m²•sec) may be misleading in that this conclusion was based on measurements of length (i.e. etiolation) and not increases in mass (i.e. dry weight).
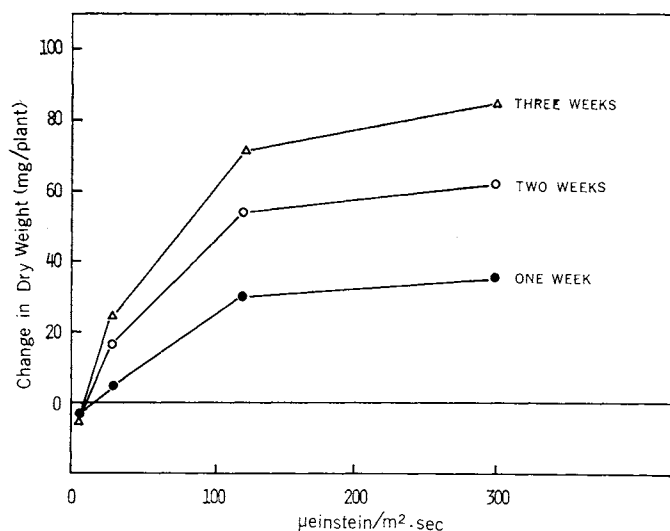

Figure 2. Effect of light during a 3-week growth period on the change in dry weight of apical stem sections from hydrilla. Each point is the mean of six replications.

From the changes in dry weight of the plants grown under different quantum flux densities (Figure 2), long term light compensation points could be estimated. The light compensation point values progressively decreased over the experimental growth period, reaching a final value of 12 μeinstein/m²•sec. This value is slightly higher than that derived from the photosynthetic measurements in Figure 1, probably because it incorporates all parts of the plant including the non-photosynthetic root tissue, and an 8-hr period of dark respiration each day.

Tubers. It has been estimated that a 1-ha area of hydrilla may produce several million underground vegetative propagules or tubers (6). Rapid regrowth from tubers in the

hydrosoil constitutes one of the major problems encountered in controlling hydrilla. Reserves in the tuber may support growth of the germinating shoot for an extended period of time in the complete absence of light. However, the young shoots must eventually reach a light level higher than their light compensation point in order for them to survive and increase their dry weight. Table 2 shows the maximum shoot length that could be supported solely by tuber food reserves. Because of natural variations in size, the tubers were divided into four weight classes which were then germinated and the shoots allowed to etiolate in complete darkness. A correlation was obtained between tuber weight and the maximum shoot length that could be supported. The largest tubers produced an average shoot length of approximately 73 cm (Table 2). They also exhibited the greatest capacity for survival after germination. This may be expected on the basis of the quantities of reserves available to the shoot.

TABLE 2. SURVIVAL RATES AND MAXIMUM SHOOT LENGTHS PRODUCED BY HYDRILLA TUBERS OF DIFFERENT SIZES WHEN INCUBATED IN DARKNESS OVER A 4-MONTH PERIOD.[a]

Tuber Classes (mg fr wt)	2 Months		4 Months	
	Survival (%)	Shoot Length (mm)	Survival (%)	Shoot Length (mm)
80 - 125	20	257 c	0	—
150 - 200	25	262 c	0	—
200 - 280	49	346 b	0	—
300 - 400	82	425 a	11	725

[a] Values followed by the same letter are not significantly different at the 5% level as determined by the Duncan's Multiple Range Test.

Figure 3 shows the photosynthetic responses to light of shoots germinated from tubers that were exposed to the four quantum flux densities for 3 weeks. Shoots grown at the low and intermediate light required less light to achieve the light compensation point and the half-maximal photosynthetic rate. These results indicate that young shoots produced by germinating tubers have about the same capacity for adaptation to a low light environment as the mature plant (Figure 1).

In Figure 4 is plotted the change in dry weight of the young shoots developing from tubers over a 5-week period versus the quantum flux density to which they were exposed. Samples were taken weekly to determine the change in dry weight of the tuber and shoot. During the 1st week after germination, the germinating tubers in all the different light regimes exhibited a decrease in dry weight, suggesting that any photosynthetic activity of the developing shoot was insufficient to overcome respiratory CO_2 loss. By the 2nd week, the tubers with developing shoots in the intermediate and high light regimes had begun to gain dry weight (Figure 4). By 3 weeks, a light compensation point of approximately 50 μeinstein/m²•sec was apparent. With the development of further photosynthetic tissue this value dropped to 20 μeinstein/m²•sec by the 5th week. It is likely that further development of the shoots would have resulted in a light compensation point value similar to that observed with mature plants. Tubers kept in darkness or at the low light
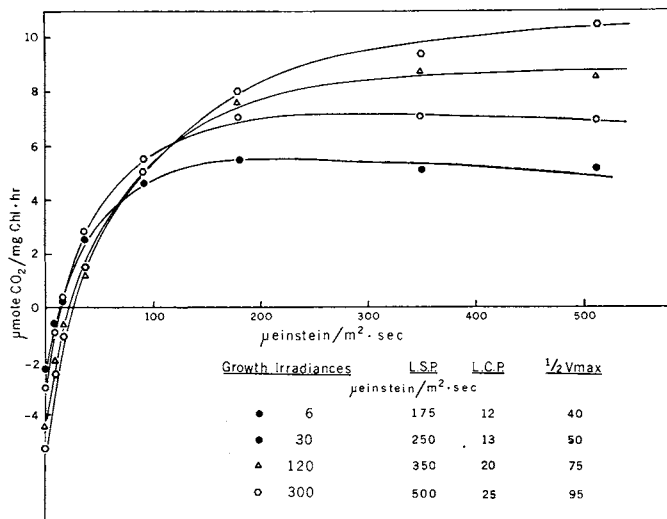
34

Figure 3. Effect of light on the photosynthetic CO_2 fixation rates of shoots germinated from hydrilla tubers and exposed to various quantum flux densities for 3 weeks. L.S.P.: quantum flux density at the light saturation point; L.C.P.: quantum flux density at the light compensation point; ½Vmax: quantum flux density required for half-maximal photosynthetic rate.

level of 6 μeinstein/m²•sec showed a progressive decrease in dry weight over the entire experimental period, despite large increases in shoot length. This is to be expected as they were existing at light levels well below the compensation point of the developing shoot.

These results indicate that a shoot developing from a tuber must reach a quantum flux density of at least 12-20 μeinstein/m²•sec within 0.5 to 0.75 m above the hydrosoil, or it cannot survive. In lake areas where light penetration is less than this, regrowth of hydrilla from tubers is unlikely to be a major problem.

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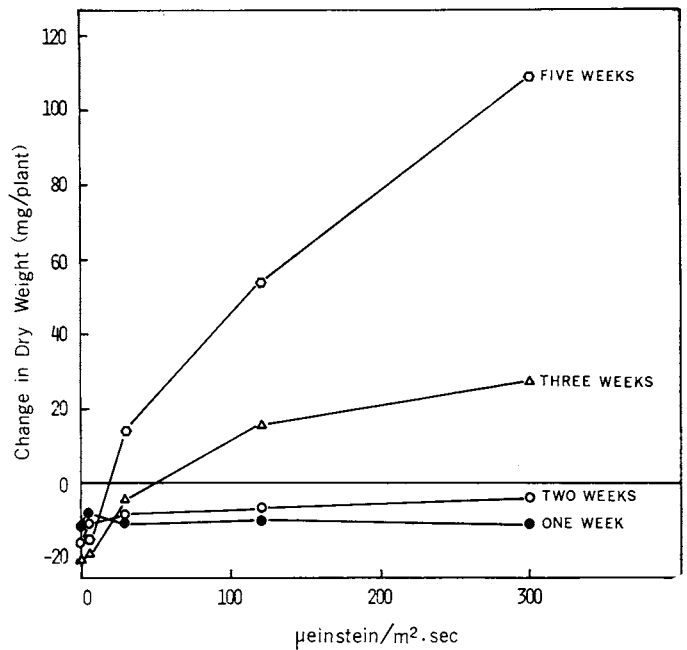
Figure 4. Effect of light during a 5-week growth period on the change in dry weight of shoots germinated from hydrilla tubers. Each point is the mean of six replications.

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