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Seasonal Variation In The Biomass, Tuber Density, And Photosynthetic Metabolism Of Hydrilla In Three Florida Lakes[1]

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ABSTRACT

Biomass, tuber densities and various water parameters were measured throughout 1977 in mats of hydrilla (*Hydrilla verticillata* Royle) in three Florida lakes: Jackson, Orange, and Trafford. In the northern lakes, Jackson and Orange, no mats were present in winter, and a maximum mat biomass of 0.24 Kg dry weight/m^2 was attained in the late fall. In the southern Lake Trafford, mats were present year round, and the maximum biomass of 0.89 Kg/m^2 occurred in the summer. In the hydrosoil of lakes Jackson and Orange, tuber densities reached a peak in the late fall, whereas in Lake Trafford they remained high throughout the year. The differences in mat biomass and tuber densities from north to south indicate that control techniques and costs may differ drastically, both seasonally and regionally. In all three lakes the presence of hydrilla mats substantially altered the local aquatic environment. During the day, stratification occurred in the mat but not in open water. High levels of O_2, pH, and temperature in the mat surface water, and low light penetration, produced unfavorable conditions for plant growth. Hydrilla plants from all three lakes altered their photosynthetic metabolism from winter to spring, as demonstrated by a shift in the CO_2 compensation points from high to low values. In the spring, a reduction in potential photorespiratory and respiratory activity, and a concomitant increase in net photosynthesis, increased the potential productivity and growth of the plants. It is suggested that submersed aquatic macrophytes belong to a new photosynthetic category.

INTRODUCTION

Since its introduction into Florida, hydrilla has become a major aquatic weed problem in freshwater (2, 8, 10). Various methods may be used for the control of submersed aquatic plants, such as hydrilla. These include mechanical harvesting techniques (13), the application of herbicides (5, 6, 9), water drawdowns (6), and also biological control (1, 6, 9, 14). Often, harvesting techniques and herbicides must be applied several times a year in order to keep the water clear of hydrilla; making these forms of control expensive. Furthermore, due to the cost factor, control in a heavily infested body of water usually can only be achieved over limited areas. A knowledge of the seasonal growth patterns and biomass changes of hydrilla in different regions of Florida could be advantageous in the local planning for timing, intensity of application, and relative cost effectiveness of different control measures.

In the summer, hydrilla can form dense areas of vegetation (mats) where most of the biomass is concentrated near the surface (8). For northern Florida lakes this condition usually does not persist throughout the year (1). Rather, a marked decline occurs in the late fall; the mat breaks up by winter and sinks to the bottom, presumably releasing nutrients to add to the eutrophic state of the lake. Though presently the cause or causes of the decline are uncertain, they may include infectious organisms, physiological changes in the plants, or environmental influences. In this study, photosynthetic, photorespiratory, and dark respiratory characteristics have been investigated on a seasonal basis for hydrilla from a northern and a southern Florida lake to ascertain whether any physiological changes in the plants are involved in the decline. An estimate of the relative photosynthetic efficiency of a plant (in terms of photosynthesis versus photorespiration) can be obtained by determining the CO_2 compensation point (3); that is the concentration of CO_2 at which photosynthetic CO_2 uptake is equivalent to photorespiratory CO_2 loss. High CO_2 compensation points (above about 40-50 μl CO_2/l) indicate substntial photorespiratory CO_2 loss, and possibly a less "efficient" plant. Seasonally measured CO_2 compensation points can thus be used as an

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indicator of the photosynthetic state of the plant. In addition, seasonal variation in several water quality parameters have been monitored to determine possible environmental influences on the decline.

In the spring, regrowth of hydrilla from winter plants and vegetative propagules is usually rapid. A major source for new growth is the tuber, germinating in the hydrosoil (6). An estimated 3 x 10^6 tubers/ha has been reported to occur in ponds well stocked with hydrilla (8), indicating that there is a high potential for future infestation. Tuber production in experimental ponds in northern Florida occurs principally in the fall and winter (7, 16). However, no seasonal study on tuber densities in the hydrosoil of lakes has been reported thus far.

This paper describes seasonal changes that occur in hydrilla physiology, biomass, and tuber densities for three Florida lakes, and an examination of some of the effects that a dense hydrilla mat has on the local aquatic environment. In order to obtain some indication of climatic effects on hydrilla growth, the three Florida lakes chosen for this study were Lake Jackson in the north, Orange Lake which is closer to central Florida, and Lake Trafford in the south.

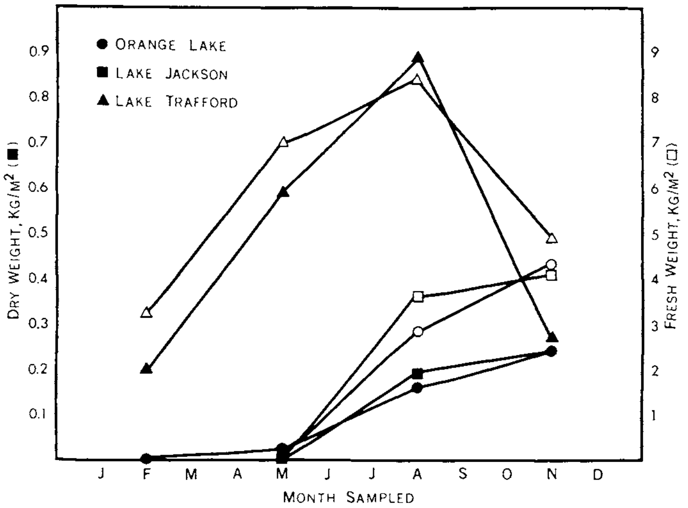

Figure 1. Biomass values, on a dry and fresh weight basis, measured in hydrilla mats of three Florida lakes at various times during 1977. The standard deviations for the dry weight measurements were: Lake Jackson in Aug ±0.05, Nov ±0.8; Orange Lake in May ±0.01, Aug ±0.02, Nov ±0.02; Lake Trafford in Feb ±0.06, May ±0.17, Aug ±0.58, Nov ±0.11.

METHODS AND MATERIALS

Seasonal measurements of biomass for hydrilla were carried out in 1977 on three Florida lakes: Lake Jackson (Leon County), Orange Lake (Alachua County), and Lake Trafford (Collier County). In each case, 3 to 5 replicate samples were taken from 0.5 m^2 quadrats in water 1 m deep by removing all hydrilla material above the hydrosoil. Samples were cleaned and weighed, then oven dried for dry weight determinations. Different, but representative, locations were sampled each measurement period.

Seasonal measurements of tuber density in the hydrosoil were performed in the same lake areas where biomass measurements were made. The samples were obtained as described by Haller and Sutton (8). Each measurement was based on 10 to 12 replicate samplings.

Diurnal measurements of O_2, temperature, pH, and quantum flux density were taken each season in all three lakes, both within hydrilla mats and in open water. Lake water O_2 concentration and temperature were measured with a Yellow Springs O_2/temperature meter, model 54, equipped with a submersible probe. The pH of water samples pumped from various depths was determined with a Brinkmann portable pH meter. Quantum flux density measurements were performed with a Lambda quantum meter, model LI-185, equipped with a submersible quantum probe.

Seasonal measurements of photosynthesis, photorespiration, CO_2 compensation points, and dark respiration were carried out in the laboratory using the techniques and infrared gas analysis system previously described (4, 15). All measurements were made at 25 C. The plants were freshly collected from the same areas used for biomass sampling.

RESULTS AND DISCUSSION

Seasonal changes in hydrilla biomass (fresh and dry weight), for a given area of mat, were evident in all three lakes (Figure 1). In lakes Jackson and Orange, the biomass was negligible in winter but increased during the growing season with the highest measured values being found in the fall (November). There were individual plants present in Lake Jackson in the spring, but no true mat of vegetation, whereas hydrilla mats already existed in Orange Lake by this time. For Lake Trafford, substantial biomass existed even in winter, and the greatest levels were found in August. This peak value was the highest found for the three lakes, being three-fold higher than the maximum in the other two lakes. In all cases the mat areas sampled were virtually monocultures of hydrilla, only occasionally were other plants, such as *Ceratophyllum demersum,* found. The maximum biomass values attained by hydrilla were similar to the value reported for *Ceratophyllum demersum* in a eutrophic lake (17), but two to five-fold greater than those reported for hydrilla in experimental ponds in central Florida (8). Plant density has a considerable effect on the rate of harvesting, and therefore on the cost of this control method (13). Since the biomass of a mat changed during the growing season at different rates for the three lakes examined, the energy and cost required to control hydrilla by harvesting may not only vary seasonally, but also regionally. Similar considerations would also apply to biological control methods.

As with other submersed freshwater angiosperms, the hydrilla biomass values were considerably lower than those normally occurring in terrestrial systems (17), especially on a dry weight basis. Despite this relatively low productivity, the plant is capable of rapidly covering large areas of water (8, 10, 12). This ability is due to several factors: a) a low dry to fresh weight ratio, the dry weight was approximately 6% of fresh weight as reported previously (15); b) a concentration of the biomass at the water surface; and c) germination from large numbers of tubers formed the previous year.

Seasonal differences also occurred in the tuber density of the lake hydrosoil (Table 1). No tubers were found in Lake Jackson until fall. In Orange Lake, tuber density increased during the growing season with the greatest density being

Table 1. Hydrilla tuber density determined seasonally in the hydrosoil of three Florida Lakes. Each value was determined from the mean of 10 to 12 samplings.

Month Sampled	Tuber Density (No./m²) Lake Jackson	Orange Lake	Lake Trafford
Feb	—	—	330
May	0	58	128
Aug	0	245	362
Nov	20	510	120

measured in late fall. In Lake Trafford substantial numbers were found over the entire year with the highest density in the summer. In all three lakes, the period of highest tuber density coincided with the period of greatest biomass. The data for lakes Jackson and Orange are similar to those obtained for hydrilla planted in experimental ponds (7), but the findings for Lake Trafford differ somewhat, as the tuber density there was high throughout the year.

Short days stimulate tuber formation (16), while tuber germination requires an exposure to light and low CO_2 levels (7). Thus in lakes Jackson and Orange, the tuber density would be high in the fall due to tuber formation, whereas the tuber density in the spring would be reduced by germination. However in Lake Trafford, the continual existence of a mat probably limits tuber germination by restricting light penetration and by producing a high CO_2 level in the hydrosoil; thereby maintaining a substantial reserve of tubers throughout the year in the hydrosoil.

The large biomass and high tuber density at all times of the year in Lake Trafford implies that control of hydrilla in southern Florida will be more expensive than in northern Florida, and may require more frequent treatments. The data for lakes Jackson and Orange support the suggestion that destruction of the plants in late summer could reduce tuber formation and the potential for reinfestation the following year (8).

In spring through late fall, the dense structure of hydrilla mats had a noticeable effect on light penetration. In a mat, plant material below 0.3 m received light levels below the photosynthetic light compensation point of hydrilla (4), both in full sun and under an overcast sky (Table 2); whereas in open water, light levels were above the compensation point to a depth of at least 1.3 m. In fact in open areas, saturating light levels for the photosynthesis of a number of submersed aquatic angiosperms (15) were found to a depth of 1.3 m in full sunlight. In the mat, these light saturating conditions were only found at the surface. The data shown (Table 2) is for Lake Trafford, as a representative lake. Very similar results were found for the other two lakes when hydrilla mats were present. The low penetration of light is because the upper 0.5 m of a mat contains over one-half of the hydrilla biomass (8). Consequently, most photosynthesis must occur in the upper portion, and at depths below 0.3 m in a mat there can be no net CO_2 fixation.

Seasonal variation in water temperature was less for Lake Trafford than for lakes Jackson and Orange (Table 3). Lake Jackson, being the farthest north, had the lowest average winter temperature and exhibited the greatest annual temperature fluctuation.

Table 2. Light penetration (μEinstein/m²·sec) in a hydrilla mat as compared to open water. The data are from Lake Trafford in August; they are representative of similar trends in the three lakes studied.

Probe Depth	Full Noon Sun Mat	Full Noon Sun Open	Overcast Sky Mat	Overcast Sky Open
m				
Air	2400	2270	1500	1590
Water Surface	1625	1550	950	975
0.3	25	1100	2	625
0.6	1	900	0	350
1.0	0	675	0	175
1.3	0	450	0	18

Table 3. Seasonally measured daytime temperatures in the surface water of three Florida Lakes.

Month Measured	Daytime Surface Water Temperature (C) Lake Jackson	Orange Lake	Lake Trafford
Feb	14	16	21
May	30	26	29
Aug	31	30	21
Nov	15	17	30

Quite marked diurnal temperature changes occurred in the surface water of the hydrilla mat and in open water areas of all three lakes. Data for Lake Trafford is presented as an example in Table 4. The water temperature during the afternoon at the mat surface was generally higher than in open areas. Because little diurnal temperature fluctuation occurred at a depth of 1 m, the water of the mat became more stratified in the afternoon than did the open water. Similar temperature stratification was noted throughout the growth season in mats of the other two lakes (data not shown).

Table 4. Diurnal temperatures at the surface and at a depth of 1 m in a hydrilla mat as compared to open water. The data are from Lake Trafford in May; they are representative of similar trends in the three lakes studied.

Time Measured	Temperature (C) Surface Mat	Surface Open	One Meter Mat	One Meter Open
hr				
06:00	25.3	25.9	25.8	25.9
09:00	25.2	26.0	24.9	26.0
15:00	33.2	30.0	25.3	26.8
19:00	30.8	29.5	25.7	27.8
21:00	28.3	28.3	27.5	26.1
01:00	26.9	27.2	25.0	26.0

In the surface water of the mat in Lake Trafford, marked diurnal fluctuations in O_2 concentration were found (Table 5). Similar changes were found for lakes Jackson and Orange (data not shown). With surface O_2 levels increasing threefold from 07:00 hr to 13:00 hr in the mat, and little change occurring at a depth of 1 m, the mat became very stratified with respect to O_2 in the afternoon. Even greater diurnal fluctuations in mat O_2 concentrations were observed in Lake Trafford in the spring, with night-time levels dropping to below 1 mg O_2/l. In open water, only slight diurnal O_2 changes were found at either the surface or at a depth of 1 m (Table 5), indicating a lack of stratification.

Table 5. Diurnal O_2 concentrations at the surface and at a depth of 1 m in a hydrilla mat as compared to open water. The data are from Lake Trafford in August; they are representative of similar trends in the three lakes studied.

Time Measured	Oxygen Concentration (mg O_2/l)			
	Surface		One Meter	
	Mat	Open	Mat	Open
hr				
09:00	6.5	5.5	5.1	4.9
13:00	17.8	7.4	4.8	6.2
17:00	15.6	7.7	6.7	6.7
00:00	7.9	6.2	5.9	6.0
07:00	5.1	5.8	5.1	5.2

The pH of the surface water in a mat increased during the day, reaching the highest value by about 17:00 hr, and then declined through the night (Table 6). In contrast, only slight diurnal changes in pH were found at the surface and at a depth of 1 m in open water, or at 1 m in the mat. The data shown in Table 6 is for Lake Trafford, although all three lakes exhibited very similar trends. Thus, as in the case of temperature and O_2, the mat water became stratified with respect to pH, but little or no stratification was found in open water.

Table 6. Diurnal pH values at the surface and at a depth of 1 m in a hydrilla mat as compared to open water. The data are from Lake Trafford in August; they are representative of similar trends in the three lakes studied.

Time Measured	Surface		One Meter	
	Mat	Open	Mat	Open
hr				
06:00	7.6	7.7	7.8	7.7
09:00	7.6	7.8	7.4	7.4
13:00	9.9	7.8	7.6	7.4
17:00	10.1	7.8	7.7	7.7
00:00	8.7	7.8	7.6	7.7

These data indicate that the presence of the hydrilla mat, as contrasted with open water, substantially changes the aquatic environment. The vegetation reduces mixing by wave action or diffusion, thus allowing the daytime temperatures, O_2 concentration, and pH in the mat surface water to rise to values higher than in open areas. Consequently the water in the mat becomes stratified by the afternoon. During the day, the high levels of O_2, pH, and temperature, together with the low light penetration, produce very unfavorable conditions for the growth of plants, including hydrilla itself. At night, the respiratory activity of hydrilla occasionally reduces the O_2 to levels that could cause a fishkill if open water areas were not present.

As with the biomass data, seasonal differences in the photosynthesis and photorespiration of plants from lakes Orange and Trafford were observed (Table 7). The trends were similar for both lakes. Net photosynthesis was lowest during the winter, but increased from February to May. Photorespiration measured as CO_2 evolution into CO_2-free air in the light, was lower in the summer than in the winter (February). As reported previously (15), dark respiration was high relative to net photosynthesis (Table 7). Winter grown plants had the highest respiration rates (measured at 25 C), but these declined by the spring.

The seasonal change in the photosynthetic metabolism of hydrilla cannot explain the existence of a large winter biomass in Lake Trafford, as plants from all three lakes exhibited a similar metabolic shift; yet only Lake Trafford contained mats of vegetation year round. Daytime water temperatures in Lake Trafford in February averaged 5-7 C higher than in the other two lakes. The decline and sinking of a mat may therefore be influenced more by temperature than by direct physiological changes. One possible hypothesis is that low water temperatures reduce photosynthesis and respiration, and thereby reduce the gas content of lacunae, resulting in a loss of buoyancy. Furthermore, optimum growth temperatures are reached earlier in Lake Trafford than in northern Florida lakes, so that rapid regrowth should begin sooner, resulting in the maximum biomass being attained earlier in the year.

For plants from all three lakes, a marked seasonal variation in the CO_2 compensation point was noted. The values were highest in the winter months and lowest in the spring (Table 8). Consistently throughout the year, plants from Lake Jackson had lower CO_2 compensation points than those from lakes Orange or Trafford; the cause of this is unknown. The switch, from high CO_2 compensation points in the winter to much lower values in the spring through the fall months, is further evidence that the photosynthetic carbon metabolism of the plants from all three lakes changed from winter to spring. In the winter, the low net rates of photosynthetic carbon fixation were due, at least in

Table 7. Seasonal values of net photosynthesis, photorespiration, and dark respiration for hydrilla plants freshly collected from Orange Lake and Lake Trafford (μmol CO_2/mg Chl·hr)

Month Measured	Net Photosynthesis		Photorespiratory CO_2 Evolution in the Light		Respiratory CO_2 Evolution in the Dark	
	Orange Lake	Lake Trafford	Orange Lake	Lake Trafford	Orange Lake	Lake Trafford
Feb	2.2 ± 0.3†	1.6 ± 0.2	1.7 ± 0.1	2.8 ± 0.3	3.4 ± 1.0	2.3 ± 0.1
May	3.2 ± 0.1	3.4 ± 0.3	1.6 ± 0.1	0.5 ± 0.1	2.0 ± 0.1	2.0 ± 0.2
Aug	2.4 ± 0.1	2.7 ± 0.1	1.0 ± 0.2	0.9 ± 0.1	1.7 ± 0.3	1.3 ± 0.1
Nov	3.8 ± 0.6	2.2 ± 0.9	1.3 ± 0.2	1.4 ± 0.3	2.2 ± 0.5	1.7 ± 0.3

† Mean of two replicates ± standard deviation.

part, to potentially high photorespiratory, and possibly "dark" respiratory, activity in the light (3, 15). Similarly high photorespiratory rates have been reported for *Najas flexilis* and *Scirpus subtermenalis* based on *in situ* lake measurements (11). The low net photosynthetic rates of winter-grown hydrilla indicate a lower potential for net primary productivity, and thus growth, during winter months or in cooler climates. However in spring, the shift in photosynthetic metabolism apparently increases the efficiency of net carbon fixation and thereby raises the potential for more rapid growth. Such a dramatic seasonal shift in photosynthetic/photorespiratory metabolism has not been reported, to date, with any terrestrial plants. It suggests that submersed aquatic macrophytes (SAM species) are a unique photosynthetic group (3).

TABLE 8. CO$_2$ COMPENSATION POINT VALUES AT 25 C DETERMINED SEASONALLY FOR HYDRILLA PLANTS FRESHLY COLLECTED FROM THREE FLORIDA LAKES. EACH VALUE IS THE MEAN OF THREE REPLICATES.

Month Measured	CO$_2$ Compensation Point (μl CO$_2$/l)		
	Lake Jackson	Orange Lake	Lake Trafford
Feb	31	75	85
May	17	37	27
Aug	38	39	45
Nov	27	26	49
Mar	—	90	66

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