

PHOTOSYNTHESIS OF NATURAL COMMUNITIES DOMINATED BY *CLADOPHORA GLOMERATA* AND *ULOTHRIX ZONATA*

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The littoral zone in western Lake Erie is populated by attached filamentous algal communities dominated in summer by *Cladophora glomerata* (L.) Kutz., and in winter by *Ulothrix zonata* (Weber & Mohr) Kutz. During 1950-51 these communities were studied to determine their photosynthetic activity under near-natural conditions. Graphs showing the relationship between photosynthesis and light intensity are reproduced and discussed below. These researches were carried out by the senior author at the Stone Institute of Hydrobiology in partial fulfillment of the requirements for the M. S. degree.

METHODS

The method used to measure photosynthesis was similar to that used by Verduin (1951) in studies of phytoplankton photosynthesis. Algae were collected from their natural habitat and studied shortly after collection. Small amounts of algae (1-2 gm) were squeezed manually to remove most of the water, and weighed on a triple-beam balance, having a sensitivity of 0.01 gm. These samples were introduced into glass bottles of 125 ml capacity containing lake water of known pH and total alkalinity (average, 90 ppm, as CaCO₃). Two bottles, blackened to exclude light, were treated similarly to provide an estimate of respiration during the test period (0.5-1.0 hr). The bottles were suspended at one-half meter intervals between 0-3 meters, to subject them to a variety of natural light intensities. Experiments were always performed at about 1:00 P.M. when light was near its maximum intensity for the day. Tests were also made on cloudy days, so surface light intensities varied considerably from one test to another. At the end of the test period the pH of the water in each bottle was determined using a Beckman pH meter. The micromoles of CO₂ absorbed per gm of algae per hr was estimated by reading from a graph relating pH change to CO₂ change (Verduin, 1951, fig. 1.) In the experiments described below final pH values higher than 9.5 were avoided because the lake pH seldom rises above 9.0, so higher experimental values would represent an unnecessary departure from natural conditions.

Light intensities were measured at the depth of each bottle, using a Weston photronic cell enclosed in a water-tight case.

Temperature measurements were made during each experiment using an ordinary mercury thermometer, calibrated in tenths of a degree C.

Estimates of ash-free dry weight of samples were made by drying in an oven, weighing, igniting in a furnace, and reweighing. For these weights a chainomatic balance was used.

RESULTS

A wide range of variability was observed among tests carried out on different days. Figure 1 shows the results of 5 tests made between February 14 and 28, 1951, using samples from the *Ulothrix* community. The photosynthetic rates are graphed against μ amps of current generated by the photronic cell. The rates were calculated using the original pH of the water in the bottles, rather than the

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final pH in the black bottles, as zero point. Thus the points below the zero line represent conditions under which respiration exceeded photosynthesis, and the points on the ordinate represent respiration rates in the black bottles. This figure shows a rather wide scatter of data points, but it is significant that the scatter is not purely random i.e., the points for any single test lie on a fairly smooth curve. The relative position of the curve with respect to the ordinate is the most variable feature, and is primarily caused by variable respiration rates observed from day to day. The causes of the day to day variation have not been studied. Similar variation was observed in *Cladophora* samples; consequently a single test does not represent a very good estimate of the average photosynthetic rate under natural conditions, but the mean of several tests provides a more reliable estimate.

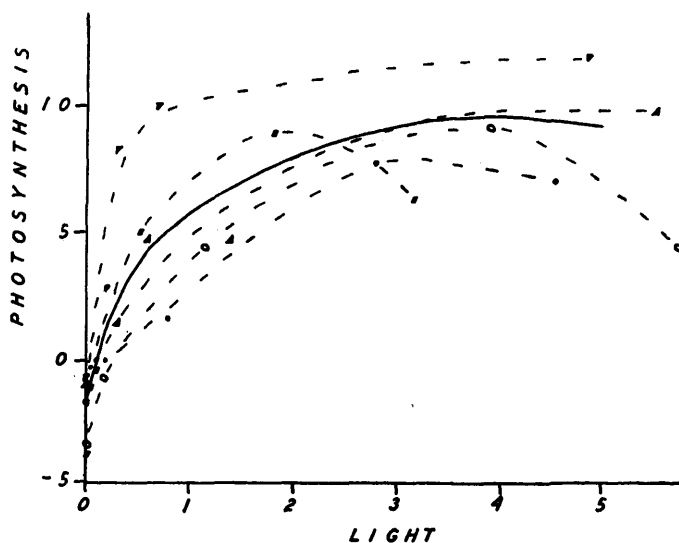


FIGURE 1. Apparent photosynthesis ($\mu\text{moles CO}_2$ absorbed per gm wet wt per hr) of a *Ulothrix* community, graphed against light intensity ($\mu\text{amps Weston photronic cell, } \times 10^{-3}$). The broken lines indicate separate experiments carried out between February 14 and 28, 1951. The solid line represents the average of the five tests shown.

Figure 1 also shows that inhibition of photosynthesis was frequently observed in the surface bottles, but that such inhibition was not associated with a particular intensity of light, but rather with the surface position of the bottle. Thus on February 23 inhibition was observed at a light intensity of only 3200 μamps , although this same, and higher, light intensities, when encountered at a depth of one-half meter on other days, promoted maximal photosynthetic activity. This phenomenon was observed in other tests not shown in figure 1. It suggests that some quality of surface light, rather than its intensity, is responsible for such inhibition. It may be that certain wave-lengths, rapidly absorbed by water layers, are responsible. Tests with *Cladophora* samples never showed reduced rates at the surface.

The solid line in figure 1 represents the mean obtained from the 5 tests shown. The average respiratory rate amounted to about 20% of the total photosynthetic rate at optimal light intensity. The compensation point was reached, on the average, at a light intensity of about 100 μamps . In the data presented below all curves are means of several tests made on different days.

Figure 2 shows four curves: two for *Cladophora*, one obtained during the Autumn of 1950, the other during the Spring of 1951; two for *Ulothrix*, one obtained during February and March, one during April, 1951. The shape of these curves reflects the adaptation of these littoral communities to bright light intensity; they show a relatively low efficiency at dim light intensities. The *Ulothrix* communities, however, showed higher relative efficiency at dim light than did *Cladophora*. For example, in figure 2, *Ulothrix* absorbed one-third as much CO_2 at 500 μamps as at 4000. *Cladophora* used only one-fourth as much CO_2 at 500 μamps as at 4000. This characteristic probably represents an adaptation by *Ulothrix* to the dimmer light of the winter months.

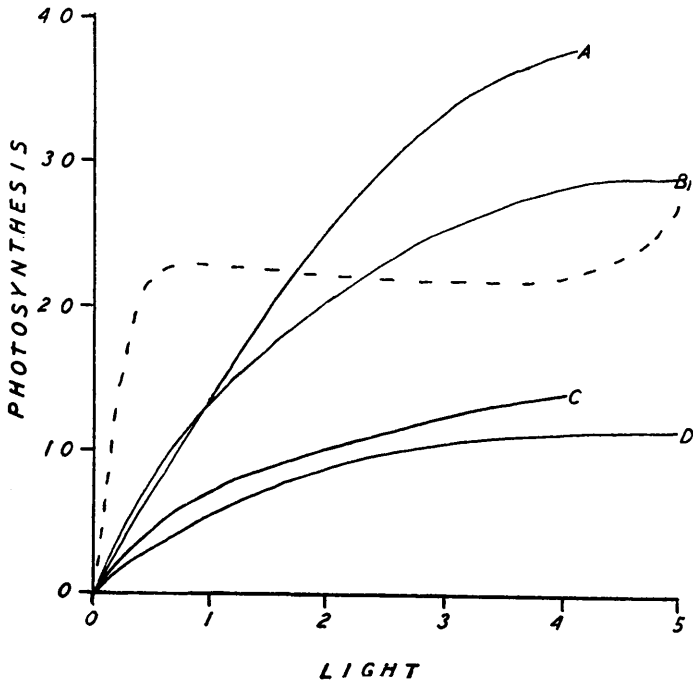


FIGURE 2. Comparison of photosynthesis ($\mu\text{moles CO}_2$ absorbed per gm wet wt per hr) vs. light ($\mu\text{amps Weston} \times 10^{-3}$) curves in *Cladophora* and *Ulothrix* communities. A = *Cladophora*, Autumn, 1950. B = *Cladophora*, Spring, 1951. C = *Ulothrix*, April, 1951. D = *Ulothrix*, January-March, 1951. The broken line represents the curve published by Manning et al. for a species of *Cladophora*.

Manning, Juday and Wolf (1938) have published a graph of photosynthesis *v.* light intensity for an unidentified species of *Cladophora*, showing data from a single experiment. The relative curve shape obtained by them is indicated by the broken line in figure 2. It differs radically from the curves of the present report, although their samples also were collected from an intensely illuminated habitat in shallow water. Plants showing such a curve would thrive at much dimmer light than would the littoral community of Lake Erie. No abrupt increase in photosynthesis in the region of maximal light intensity was ever observed in the Lake Erie material.

Since the photosynthetic rates appearing in figure 2 are based on similar quantities of plant matter, a comparison of the absolute rates exhibited by the different communities may be significant. The most obvious environmental difference

between the communities is that of water temperature. The mean temperature for the autumn tests of *Cladophora* was 18° C. for the spring tests 16°. The mean temperature for the winter tests of *Ulothrix* was 2°, for the April tests 7°. Since photosynthesis under optimal light shows a temperature coefficient of approximately 2 in laboratory experiments (Meyer and Anderson, 1952, p 355) it is interesting to test the hypothesis that the same relationship controls the photosynthetic rates, at optimal light intensity, of two different communities occupying identical space habitats but subjected to different environmental temperatures.

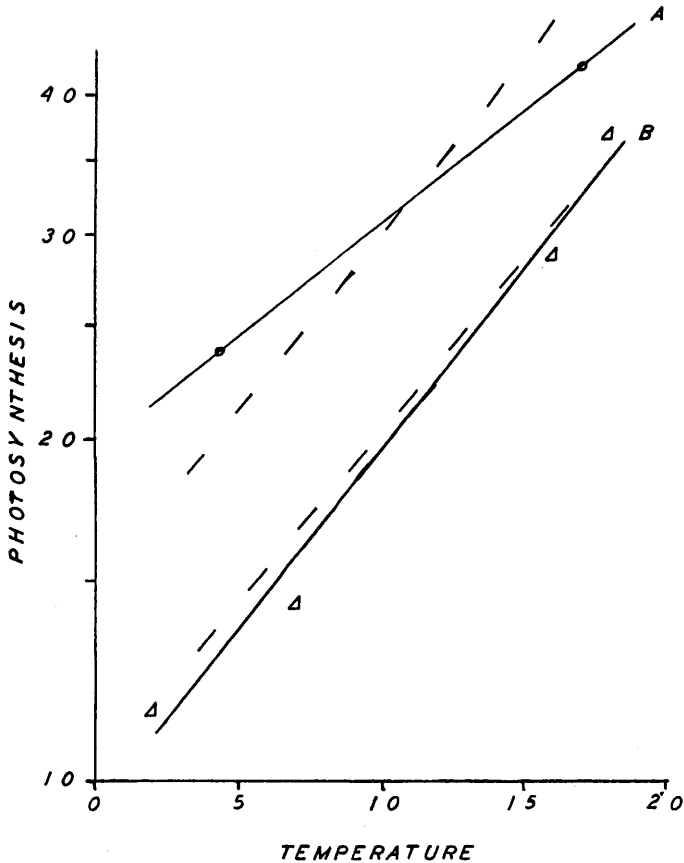


FIGURE 3. The temperature coefficient of photosynthesis at optimal light in natural communities. Temperatures below 10° represent *Ulothrix*, above 15° represent *Cladophora*. The broken lines indicate the slope required for a Q_{10} of 2. A = μ moles CO_2 absorbed per gm ash-free dry wt per hr, $\times 10^{-1}$. Observed Q_{10} about 1.7. B = μ moles CO_2 absorbed per gm wet wt per hr. Observed Q_{10} about 2.1.

The hypothesis is tested in figure 3. Here the photosynthetic rates shown at 4000 μ amps in figure 2 are plotted (logarithmic ordinate) against temperature in degrees C (linear scale). The solid line (B) was drawn, by inspection, through the data points. The broken line represents the slope required for a Q_{10} of 2. It is evident that the points lie reasonably close to a straight line whose slope indicates a temperature coefficient of approximately 2. The data were recalculated as photosynthetic rate per gm ash-free dry wt (line A). On this basis the apparent

Q_{10} is approximately 1.7. Figure 3 shows that the differences observed between the photosynthetic rates of *Cladophora* and *Ulothrix* communities are largely explained by the difference in environmental temperature. It should be pointed out that the temperature coefficient of photosynthesis, as determined in laboratory experiments, refers to photosynthetic rates exhibited by a single species subjected to different temperatures, with all other factors supplied in abundance. It is noteworthy that the relationship seems to be approximately valid for different species studied under near-natural conditions at the temperatures of their natural environment. Moreover, the supplies of CO_2 and other necessary materials, are probably not present in abundance in the natural environment, although they would be approximately the same for both communities in the experiments discussed above. This situation lends support to Baule's (1918) concept of limiting factors, which he has expressed in the form of a general equation (Verduin, 1953). Baule contends that all of the factors influencing a process are operative at all times, the degree of limitation being inversely, and exponentially, proportional to the relative abundance of each factor. Thus, although CO_2 supplies in Lake Erie water are present in less than optimal concentrations, yet a powerful influence of the temperature factor is apparent. Furthermore, the curves in figure 2 remain separate in the region of suboptimal light intensity, suggesting that the temperature factor is still pronounced although both light and CO_2 are supplied at suboptimal intensities.

SUMMARY

Photosynthesis studies of littoral *Cladophora* and *Ulothrix* communities under near-natural conditions showed rates at optimal light of 33 $\mu\text{moles CO}_2$ absorbed per gm (wet) hr for *Cladophora* at temperatures of about 17° C, and 12 $\mu\text{moles CO}_2$ for *Ulothrix* at about 4°. The photosynthesis vs. light curves showed relatively inefficient utilization of low light intensities, differing markedly from a curve for *Cladophora* in the literature. The temperature coefficient estimated from these data was approximately 2. The data seem to support the Baule-Mitscherlich theory of limiting factors.

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