CONFERENCE ON SOLAR ENERGY: THE SCIENTIFIC BASIS.

AT THE

UNIVERSITY OF ARIZONA, TUCSON,

1955 OCTOBER 31 AND NOVEMBER 1,

MONDAY AND TUESDAY.

THE YIELD OF SUNLIGHT CONVERSION BY CHLORELLA.*

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SECTION B Business Administration Building, ROOM 111

DAY Monday HOUR 4:00 p.m.

One often finds photosynthesis simply formulated as:

$$\text{light} + CO_2 + H_2O \longrightarrow (C\ H_2O) + O_2$$

But, in fact does the diversity of the anabolic processes driven by the light prohibit any distinct definition. The ultimate products of photosynthesis are oxygen and new plant cells.

For the present discussion this difficulty is immaterial, since our interest concentrates upon sizable amounts of calories, food or protein, we can hope to harvest from a given amount of sunlight.

Fig. 1 shows the results of experiments, in which algae were grown under exactly known conditions of illumination. The final harvest was chemically analyzed or combusted in a calorimeter. Under optimal conditions more than 20 percent of the absorbed radiation energy (590 m u) was converted into organic material. The pigments of green cells only absorb light of wave-lengths shorter than 700 m u and therefore only about half of the total solar radiation. The sodium light used for the expts. of fig. 1 represents about the mean of the visible solar spectrum and thus we drew the conclusion that the best possible yield of sunlight conversion by green cells is around 20% of absorbably radiation i.e. in the order of 10% of total solar radiation. This value is not typical for green algae: it could be shown, though in less exacting experiments, that under optimal conditions higher plants are also capable of light conversion with an about equal yield.

In temperate and tropical regions the total amount of solar radiation ranges from 70-170 kcal per cm^2 per annum. If we, under natural conditions, could realize growth efficiencies close to the maximum of 10%, our domesticated plants would yield harvests of 50-100 tons of dry weight per acre (30-80 gr/m^2 day).

* 137th Communication of this laboratory; 47th Communication on Photosynthesis.

It is well known that the actual farmland and forestry crops are a full order of magnitude lower. The caloric value of the total yields of dry weight (including roots and stalks) does not exceed 0.5 - 1% of the incident solar energy. In itself it would be a program of major importance to quantitatively analyze the various factors responsible for this 10 to 20 fold discrepancy. A number of requirements have to be fulfilled to ensure optimal growth-rates of plants, few of these we may expect to be met under natural conditions.

We hardly need to again sum up the many advantages which algal mass cultures a priori offer in this respect: water supply is automatically taken care of and the concentrations of nutrients and carbondioxide are easily controllable. Light losses, due to incomplete absorption or to incomplete coverage for the exposed area either in time or space, can be avoided. There are, however, two factors left which largely escape control in mass cultures under natural conditions: Light intensity and temperature. It is therefore that we presently want to discuss a few aspects of these factors.

If measured in a thin suspension of algae, the curve describing the relation between photosynthetic rate and intensity, has an hyperbolic shape, but can for most practical purposes adequately be described as an exponential function:

$$R = R_m(1-e^{I/I_s}). \qquad (1)$$

The meaning of the symbols is shown in fig. 2, curve a. This formulation has the advantage that for a complete characterisation only two rate measurements suffice: one in weak light (yielding $\phi = R_m/I_s$) and one in strong light (yielding R_m). As long as sufficiently thin suspensions are used for this measurement, the computed value of I_s is independent of the concentration of the algae and therefore can be used to characterize the particular batch studied at the prevailing temperature.

On the basis of (1) we can theoretically predict the response of the studied algae if they were illuminated at the same temperature in a thick totally absorbing layer. As is shown in fig. 3, also in a thick suspension the yield of conversion drops heavily below the value ϕ (accepted 20%), if the incident intensity I_o surpasses factorfold the saturation intensity I_s.

No strain of algae has been found yet which is capable of utilizing bright sunlight with full efficiency. The I_s values observed in experiments as described above even at elevated temperatures range several fold lower than full sunlight intensity. This would imply outdoor growth efficiencies far below the maximum value discussed above.

The limited photosynthetic capacity of algae thus appears to severely restrict the possible yields of outdoor growth. Still another factor enters the picture: bright light in addition exerts inhibitory effects upon photosynthesis. This is illustrated in fig. 2b, which shows that exposure to excessive light may decrease both the quantum yield and the saturation rate.

Our recent work therefore was mainly directed towards a better understanding of the rate limiting steps in photosynthesis and an analysis of photoinhibition.

The so far obtained results are summarized in fig. 4, in which the kinetics of the two photochemical processes and the rate determining dark-steps are described:

The light absorbing pigments are grouped together in functional units, each comprising 200-400 molecules (indicated as dots). Each group has a final energy acceptor (U), to which a light quantum absorbed by one of the pigment molecules is

passed on. The final excitation of U leads to a stable product (U*) and further absorption acts within the unit are fruitless unless U* is restored to U. This occurs in a dark-reaction, in which the excitation energy is taken over by an intermediate (indicated by E $\longrightarrow$ E*). The excitation energy of E* is further used in a reaction, which ultimately yields oxygen and reduced components. This mechanism is illustrated in the right hand part of fig. 4 (bold arrows).

The more the intensity is increased, the more frequent do successive absorption acts occur within each pigment molecule and within each unit. It now could be shown, that if two excitations occur within a given brief time interval, the unit may "explode". This "double hit" process underlies the above mentioned process of photoinhibition.

It looks as if in most cases an effective coincidence inactivates a complete unit but that it is also possible that only part of the pigment chain is knocked off. This sequence of events is visualized in the left hand part of fig. 4, which also indicates that relatively slow, temperature-dependent dark-reactions may restore the inactivated pigment complexes (cf. also fig. 2 curves c and d).

The consequences of this photoinhibition are obvious: inactivation of pigment molecules or complexes leads to ineffective light absorption and thus decreases the yield in weak light. No obvious changes in absorption spectrum occur. But, since the units themselves are involved in a photosynthetic dark-reaction, also the saturation rate decreases and this the sooner the greater the relative role the first dark-reaction plays in co-determining this rate.

The reaction sequence shown in fig. 4 in many cases suffices for a complete kinetic description of the rate limiting photosynthetic reactions. In weak light the collection of lightquanta is rate determining - it will be more effective, the more pigment molecules are arranged within each unit and the more units are present per molecule of enzyme E. (Indeed cells grown in weak light are usually characterized by high chlorophyll content per cell, as well as per unit).

In strong light the two dark-reaction steps, characterized by velocity constants K_2U_0 and k_3, respectively, cannot keep pace with the formation of U*, and the rate of photosynthesis becomes independent of intensity but dependent upon temperature.

The photosynthetic saturation rate is equal to:

$$R_m = \frac{k_3 E_0}{1 + \alpha} \qquad (2)$$

in which $E_0 = E + E^*$, $U_0 = U + U^*$. The value of $\alpha = k_3/k_2U_0$ ranges from 0.25 - 1.0 dependent upon the type of algae and their pre-treatment. At a given temperature (k_3), R_m thus is primarily determined by the amount of enzyme E present per given amount of light absorbing pigment or pigment complexes. Evidently opposing demands are put upon the photosynthetic machinery (the ratio pigment/E_0) for either optimal use of weak light or of strong light. The high pigment content of "shadow cells" (and their units) is of no use in strong light and does moreover strongly increase their susceptibility to photoinhibition.

It thereforeis not amazing that large quantitative variations were found to exist among different algae.

In addition algae appeared to respond to a change in light intensity with a rearrangement of their photosynthetic apparatus. Such "light adaptations" are quite pronounced in thin suspensions; they may at least partly be regulated by the photoinhibition reactions described above. Cells, pre-exposed to strong light show a poor quantum yield, low chlorophyll content and a high saturation rate if calculated per unit chlorophyll.

It is noteworthy, that the saturation rate is found to be decreased, if calculated per unit dry weight. By an analogous reasoning we might deduce that in strong light the total photosynthetic outfit of the cell is larger than required for supplying its maximal needs for complete growth. The maximal growth-rate of algae thus is probably limited by other systems than their photosynthetic apparatus.

The above adaptations affects are also observed in dense cultures, such as used for outdoor growth more than twofold variations of the various magnitudes may occur.

Similar adaptation phenomena are found in connection with the temperature response of algae: Fig. 3 shows that in sufficiently bright light (I_s/I_o small) the expected yield increases nearly proportionally with the value of I_s. Since one would a priori expect the limiting dark-reactions to at least double their rate for each temperature increment of 10°C, use of high temperatures seems to be indicated.

Fig. 5 shows six intensity-assimilation curves as measured with "high temperature" algae in short-term experiments at three temperatures. Two samples of originally identical algae were used -- one was precultivated during a few days at 23°C, the other at 42°C. The influence of temperature upon the maximum rate is quite different in the two cases. Noteworthy is the small difference between the two curves for which the temperatures of measurement were close to the temperatures of pretreatment. Obviously the high saturation rate observed after the 23°C sample was exposed at 45°C is only a temporary phenomenon. Conversely we may expect the low rate observed at 25°C with the sample pretreated at 42°C to increase if the cells are exposed for a longer time to the low temperature. Below 25°C temperature has a more marked and lasting influence and low temperatures therefore should be avoided during exposure of cultures to bright sunlight, especially since photoinhibition plays a greater role under such conditions. The time responses of light and temperature adaptations are presently subject to study and probably range in the order of hours.

It is evident that a growing culture cannot be treated as a static system, the less so under the natural conditions characterized by diurnal and seasonal variations. Characterization of algae and expectations for their outdoor growth on the basis of simple laboratory experiments and calculations as given in eq. (1) and figs. 2 and 3 are bound to be over simplified. Some of the phenomena touched above will be described elsewhere in greater detail. The off-hand conclusion is that a trial and error approach towards increased yields of algal cultures might quicker yield results than the quantitative exploration of all factors involved (tempting as the latter approach may be for the physiologist).

So far, under "static" conditions in the laboratory, the best yields we observed in intensities close to that of full sunlight amounted to the conversion of 6% of absorbed energy. If we account for the diurnal variations of the sunlight, we may expect much higher values under outside conditions.

Fig. 6 shows the results of an outdoor growth experiment, the daily yield is plotted vs. the daily quantity of total light received by the suspension. The drawn slope represents an efficiency of conversion of 4% of total incident radiation,

which on the average would correspond to about 10% conversion of the photosynthisable radiation. This efficiency comes close to half the maximum value and was approached even on very bright days, during which harvests over 30 gr/m^2 day were observed. These high yields were obtained (in Holland) in flat, closed culture devices containing rather thin layers of algae.

Radiation, completely absorbed by water and algae, heated the culture with a short time response, often well beyond the temperature of the surrounding air, and therefore light and temperature showed a close parallelism. In extreme cases the diurnal temperature variations exceeded 30°C.

We expect that realisation of such yields may be quite generally possible, be it that local climatic conditions may require different designs of the culture system. Economic aspects, however, are likely to play a decisive role in the design of large scale massculture outfits and may necessitate a compromise between capital investment and optimal yield.

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Fig. 1 Yield of light conversion in suspensions of green algae under various conditions.

Fig. 2 Relation between light intensity (I) and photosynthetic rate (R) as measured on one sample of algae in four experiments each lasting about 30 minutes.
Curve a was measured first, with a sample of algae grown in relatively weak light. The two asymptotes of the light-curve are $\emptyset$: the maximum efficiency (in weak light) and R_m: the maximum rate (in strong light). I_s is defined the saturation intensity.
Curve b was measured after the cells had been briefly exposed to very bright light, the rates both in weak and in strong light appear to be decreased.
Curve c and d successively measured after b and show a recovery of the rates in darkness and weak light.

Fig. 3 Yield of light conversion as a function of the ratio I_s/I_o. Calculated for a thick suspension on the basis of equation (1).

Fig. 4 Illustration of the photochemical and dark reaction steps, which kinetically describe the processes of photosynthesis (bold arrows) and photoinhibition (thin arrows).

Fig. 5 Intensity rate curves measured in short lasting experiments at different temperatures with differently pretreated algae.

Fig. 6 Daily yields of dry weight as observed in an outdoor culture of Scenedesmus spec. Data collected during six weeks are plotted versus the total amount of incident solar radiation.

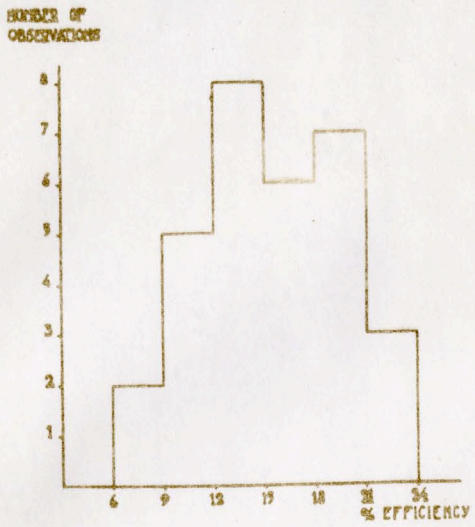

FIG. 1

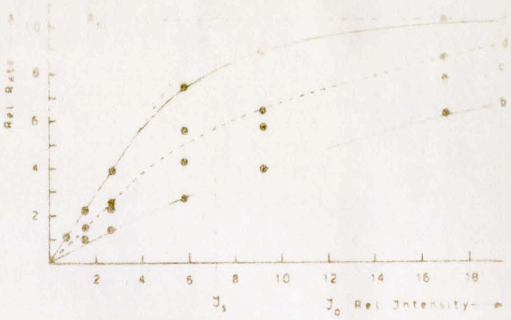

FIG. 2

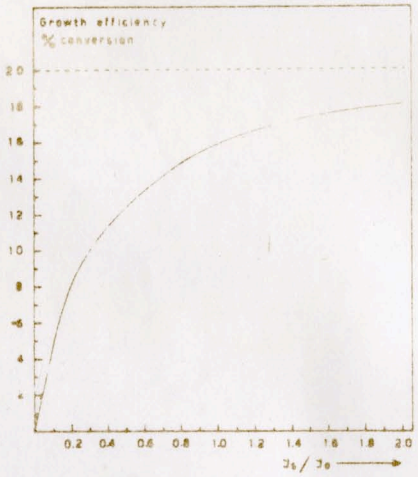

FIG. 3

FIG. 4

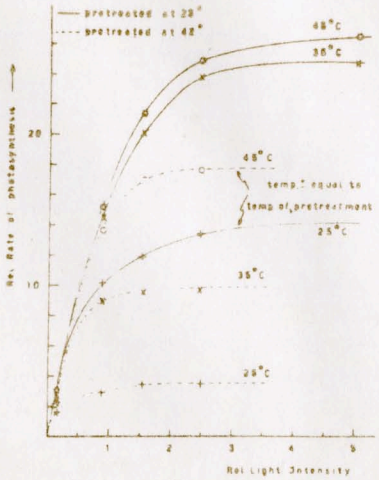

FIG. 5

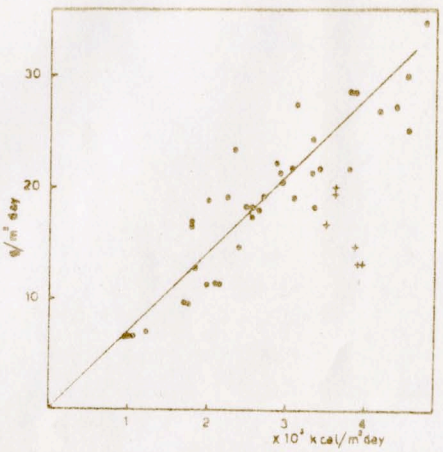

FIG. 6