# Potential Productivity of the Sea

## Organic production by marine plankton algae is comparable to agricultural yields on land.

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Under ideal conditions for photosynthesis and growth, what is the maximum potential rate of production of organic matter in the sea? Is this potential ever realized, or even approached? How does the sea compare with the land in this respect? These questions may be approached empirically with some measure of success but, aside from the time and effort required by this method, one can never be certain how close to the optimum a given environment may be and, hence, to what extent the biotic potential is realized.

However, we do know with some degree of certainty the maximum photosynthetic efficiency of plants under carefully controlled laboratory conditions; and there is a considerable literature concerning the effects of various environmental conditions on photosynthesis, respiration, and growth, particularly with respect to the unicellular algae. From such information it should be possible to estimate photosynthetic efficiencies and, for given amounts of solar radiation, organic production under natural conditions. This indirect and theoretical approach cannot be expected to provide exact values, but it does furnish a supplement to the empirically derived data which may help substantiate our concepts both of the environmental physiology of the plankton algae and the level of organic production in the sea.

An attempt has been made to use this joint approach for the marine environment in the following discussion. The only variable considered is light, and the assumption is made that virtually all of the light which enters the water (and remains) is absorbed by plants. Such situations are closely approximated in plankton blooms, dense stands of benthic algae, eelgrass, and other plants. For the rest, it is assumed that temperature, nutrients, and other factors are optimal, or at least as favorable as occur under ideal culture conditions. Given these conditions, I have attempted to calculate the organic yields which might be expected within the range of solar radiation incident to most of the earth. These data are then compared with maximal and mean observed values in the marine environment and elsewhere, and an attempt is made to explain discrepancies.

The calculations which appear below are based, for the most part, upon experimentally derived relationships between unicellular algae and the environment, and are therefore applicable only to this group. This must be kept in mind when, later in the discussion, comparisons are drawn between the theoretical yields and observed values of production by larger aquatic and terrestrial plants.

The values for the efficiency of photosynthesis under natural conditions are based on the utilization of the visible portion of the solar spectrum only (400 to 700 mμ), or roughly half of the total incident radiation. In converting these efficiencies to organic yields, it is assumed that the heat of combustion of the dry plant material is 5.5 kcal per gram, which closely approximates values for unicellular algae reported by Krogh and Berg (*1*), Ketchum and Redfield (*2*), Kok (*3*), Aach (*4*), Wassink *et al.* (*5*), and others.

### Reflection and Backscattering

Of the sunlight which strikes the surface of the ocean, a certain fraction is reflected from its surface and never enters the water. The remainder penetrates to depths which depend upon the concentration of absorbing and scattering particles or dissolved colored substances. While scattering may be as important as absorption in the vertical attenuation of the light, it makes little difference as far as the biological utilization of the radiation is concerned, since the scattered light is eventually absorbed, with the exception of a small fraction which is backscattered up out of the water. The combined reflected and backscattered light is lost to the aquatic system; the rest remains in the water, where, under the ideal conditions postulated, it is absorbed entirely by plants.

The fraction of the incident radiation which is reflected and backscattered has been studied by Powell and Clarke (*6*), Utterback and Jorgenson (*7*), and Hulburt (*8*). The two factors have been treated separately, but they may be considered together here. Their combined effect is rather small, ranging from about 3 to 6 percent, depending somewhat upon who made the measurements and the conditions under which the measurements were made. The highest values were observed when the sky was overcast. Sea states, ranging from flat calm to whitecap conditions, made surprisingly little difference. Reflection and backscattering were also found by Hulburt to be independent of the sun's angle, despite the fact that reflection increases greatly with the angle (from the zenith) of the incident light, particularly at angles above 60°. The explanation for this apparent contradiction lies in the fact that as the sun approaches the horizon, indirect sky light becomes increasingly important, and it eventually exceeds the intensities of the sun itself.

Hulburt's data also indicate that backscattering is not greatly influenced by the amount of particulate matter in the water, since his values in the clear Gulf Stream did not differ appreciably from those made in the turbid waters of Chesapeake Bay.

For the calculations which are made here, it is considered that an average of 5 percent of the incident radiation is lost through the combined effects of reflection and backscattering.

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## Photosynthesis and the Visible Spectrum

We first consider the efficiency of photosynthesis in sunlight at levels below the saturation intensity. Within this range, photosynthesis is directly proportional to the light intensity (or very nearly so), and the efficiency is therefore constant.

Despite the vast numbers of studies of quantum yield (that is, photosynthetic efficiency) in the literature, few data are available for the entire visible spectrum. Figure 1*A* shows two such series of measurements, one with the green alga *Chlorella* (Emerson and Lewis, *9*), the other with the diatom *Navicula minima* (Tanada, *10*). The ordinate is expressed as quantum requirement (the number of quanta required to reduce 1 mole of $CO_2$) rather than a reciprocal, quantum yield (moles of $CO_2$ reduced per quantum) as shown originally by the authors. Although the two organisms have strikingly different pigment complements, the curves are surprisingly similar, with minimal requirements in the red and yellow parts of the spectrum, maximal in the blue-green. *Navicula* appears to be somewhat more efficient than *Chlorella,* but the differences may not be significant.

Figure 1*B* illustrates the fact that the energy per quantum between 400 and 700 mμ decreases from a maximum of 71 kcal per mole quanta of blue light to 41 cal per mole quanta of red light. The heat of combustion of one reduced mole of $CO_2$ (reduced to $CH_2O$) is 112 kcal. A quantum requirement of 10 therefore represents an efficiency of $112/(41 \times 10) = 27.3$ percent in red light and $112/(71 \times 10) = 15.7$ percent in blue light. Figure 1*C* shows the efficiencies of *Chlorella* and *Navicula* throughout the visible solar spectrum.

The spectral distribution of daylight varies with solar altitude and with the water vapor, carbon dioxide, and dust content of the atmosphere. Figure 2 shows the spectral distribution of daylight under average atmospheric conditions and with an air mass of 2 (solar angle = 30° from zenith) as given by Moon (*11*).

If the curves in Fig. 1*C* are averaged and the mean efficiency for the entire visible spectrum is calculated, weighing the mean for the average spectral distribution of sunlight as given in Fig. 2, this value turns out to be 18.4 percent. Taking into consideration a 5-percent reflection and backscattering loss, the efficiency of photosynthetic utilization of visible sunlight *below saturation intensity* incident to the water surface is 17.5 percent.

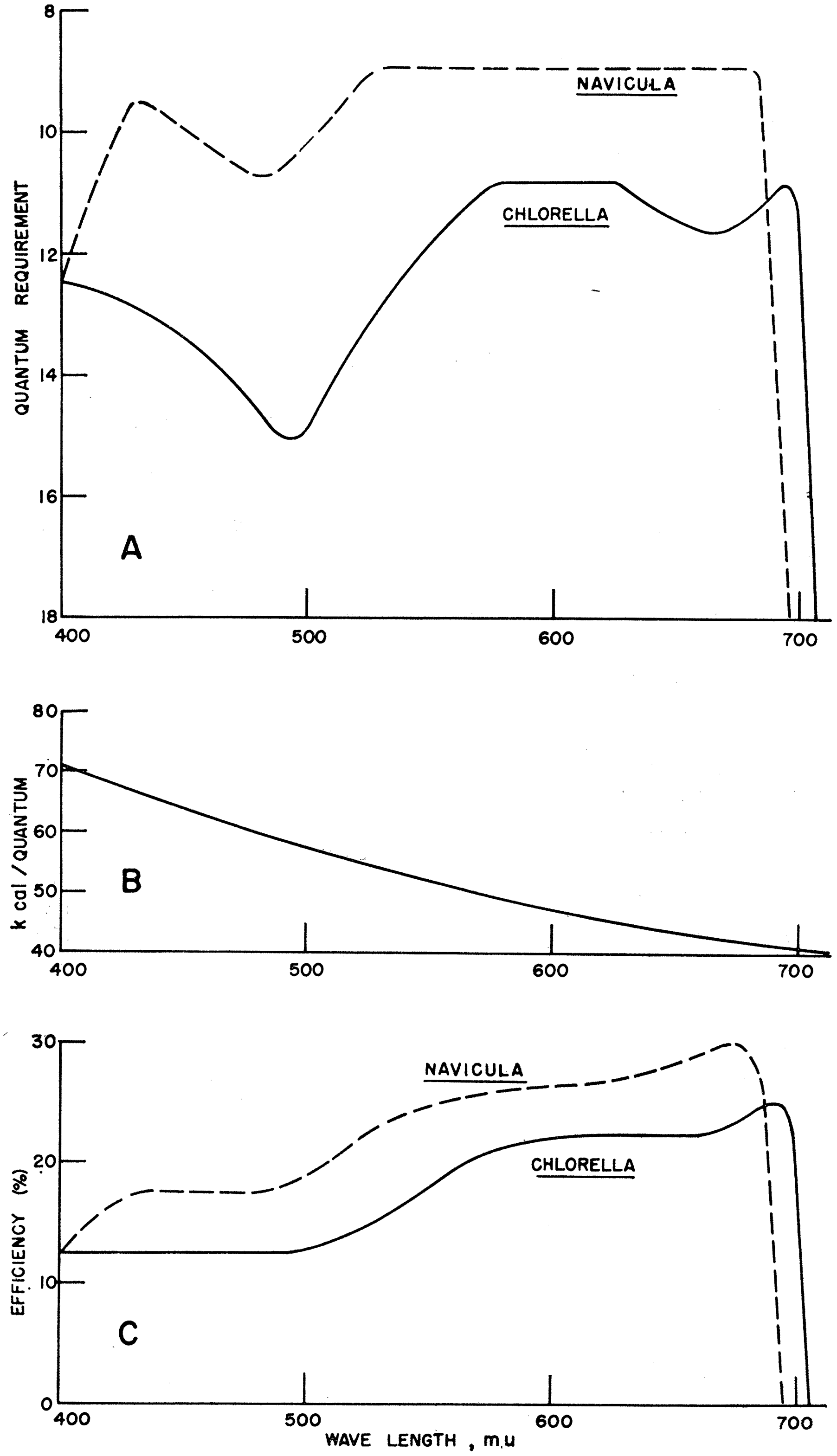

Fig. 1. (*A*) Quantum requirement of photosynthesis as a function of wavelength of light for *Chlorella* [after Emerson and Lewis, *9*] and for *Navicula* [after Tanada, *10*]. (*B*) Energy per mole quantum of light as a function of wavelength. (*C*) Efficiency of photosynthesis as a function of wavelength, calculated from (*A*) and (*B*).

In extremely turbid waters and in those containing organic stains (the "yellow substance" described by Kalle, *12*), blue and green light may be selec-

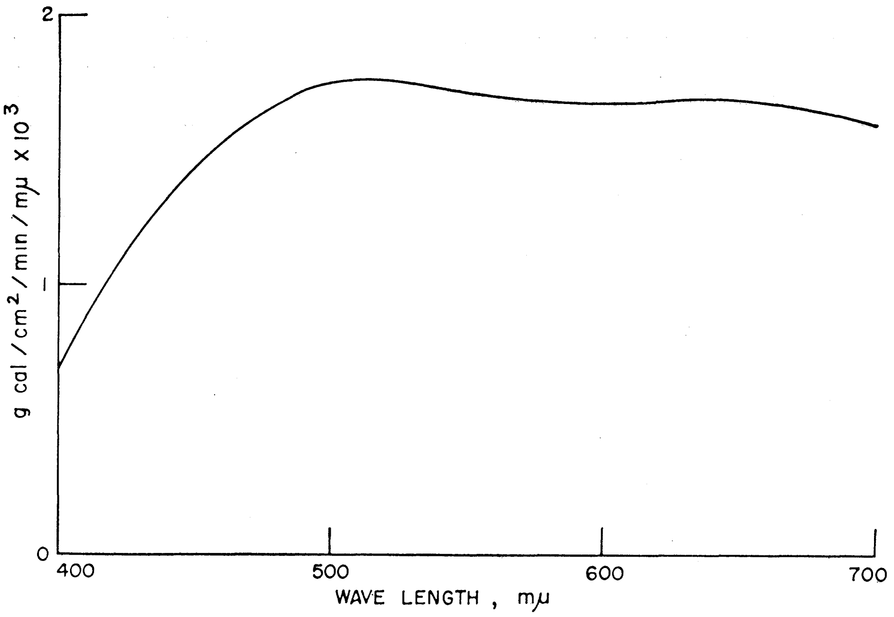

Fig. 2. The spectral distribution of daylight under average atmospheric conditions with air mass equal to 2. [After Moon, *11*]

tively absorbed, resulting in somewhat higher efficiencies in the utilization of the light penetrating to greater depths. On the other hand, in normal, clear oceanic water the red light is selectively absorbed by the water and blue-green light penetrates to the greatest depths, where it is used still less effectively than the average incident daylight considered above. These modifications are not considered in this article, since we are dealing with an idealized situation in which all of the light entering the water is absorbed by plants.

## Intensity Effect

Above the saturation point, photosynthesis does not increase in proportion to light intensity, but remains constant or, at high intensities, is actually depressed, owing to photooxidation or other inhibitory processes.

Figure 3*A* shows a curve of photosynthesis by marine plankton algae as a function of light intensity, from Ryther (*13*). This is a mean curve of experiments with cultures of 14 species of organisms, preconditioned to a variety of different light regimes. Photosynthesis was measured by $C^{14}$ uptake under solar radiation during the 4-hour period (10 A.M. to 2 P.M.) when the intensity is nearly constant and maximum. Graded intensities were obtained with neutral density filters. Almost identical curves were obtained by Steemann Nielsen and Jensen (*14*) for natural plankton populations.

Photosynthetic efficiencies remain constant, or nearly so, up to the saturation point, but then decline sharply at higher intensities. This decrease is illustrated by the difference between the actual photosynthesis curve in Fig. 3*A* and the dotted line, which is an extrapolation of the linear portion of the solid curve and represents photosynthesis if the efficiency remained constant. Figure 3*B* shows relative efficiencies as a function of light intensity, obtained from the ratio between the solid and dotted lines in Fig. 3*A*.

Using the data in Fig. 3*A*, Ryther (*13*) has calculated relative photosynthesis throughout the day and at various depths within the euphotic (illuminated) zone of the ocean for days with different values for total incident radiation. Several curves were thereby produced showing values for total daily photosynthesis at several depths within the euphotic zone relative to the hourly rate of photosynthesis at light saturation.

On extremely dull days, when the intensity never reaches the saturation region, photosynthesis is directly proportional to light intensity at all depths, and the curve of photosynthesis with depth shows an exponential decrease from the surface, as does that of light. On bright, sunny days, intensities at the surface exceed saturation and normally produce inhibition (which occurs at ⅓ or less the intensity of full sunlight). On such days, photosynthesis at the surface is less than that at intermediate depths. In all cases, photosynthesis at depths where the surface light is reduced to 10 percent or less is directly proportional to intensity, and in this region it decreases exponentially, following the light curve.

By extrapolating the lower, exponential portion of the photosynthesis curve to the surface, one may create a hypothetical curve of photosynthesis if the latter maintained the same efficiency at all depths. The ratio of the actual photosynthesis curve to this hypothetical exponential curve will then show the reduction in efficiency caused by light intensities above saturation in the upper waters. This has been done in Fig. 4 for a series of photosynthesis curves on days of varying incident radiation. Since photosynthesis at the various depths is a function of light intensity and not of depth per se, the units on the ordinate of Fig. 4 are natural logarithms of $I_0/I$ and thus represent the depths to which given fractions of the incident radiation penetrate. The curve for the day with lowest radiation (20 gcal/cm² day) is exponential all the way to the surface, indicating that on such a day there is no reduction in photosynthetic efficiency from the effects of light intensity. On days of progressively higher light intensity, the photosynthesis curve departs more and more from the exponential curve illustrating the increasing reduction in efficiency.

If it is assumed that the maximum efficiency (with no intensity effect) is 17.5 percent, as calculated in the previous section, Fig. 5 shows the cumulative intensity effect with efficiencies plotted as a function of total daily incident radiation. The points were obtained from Fig. 4 from the ratio of the actual photosynthesis curves for each value of radiation to the exponential curve of maximum (17.5 percent efficiency. It may be seen that efficiencies decrease from 17.5 percent at low intensities to 6.5 percent on a day when 600 g cal/cm² reaches the earth's surface. It is noteworthy that the efficiency curve does not decrease in a regular way with increasing intensities, but that the rate of decrease becomes less at higher intensities. This is due to the fact that higher values of daily radiation are caused not only by higher intensities of sunlight but to an even greater extent by longer days including more hours of low intensity light.

We are now ready to calculate photosynthesis for different values of incident radiation from the efficiency curve shown in Fig. 5. This is done by multiplying the efficiency by one-half the appropriate values of radiation (that portion of the solar spectrum available for photosynthesis). This gives the amount of energy fixed in photosynthesis. Dividing this by 5.5 (the heat of combustion of a gram of average plant material, as discussed in the first section) we obtain a value which represents grams of organic matter produced per day beneath a square meter of water surface, provided that all the light entering this 1-meter-square column of water is effectively absorbed by plants. These values, shown as the upper broken line in Fig. 5, are equivalent to "real photosynthesis" or "gross production." They are hypothetical in the sense that they cannot be observed as a yield, since the plants must draw upon this organic matter to satisfy their own metabolic requirements. We must therefore subtract an amount of organic matter equivalent to the plants' respiration in order to calculate the amount of material available for harvest, the so-called "net production."

## Respiratory Loss

Under conditions of active growth, photosynthesis at light saturation is some 10 to 20 times as great as dark respiration (see Ryther, *15*). Higher values have been reported, but it seems doubtful that they could represent steady-state conditions in natural populations. If we take a ratio of 15:1 as average for $P:R$ (photosynthesis: respiration) at optimal light, it is obvious that over a 24-hour period, half of which is dark, and within an entire plant community, of which many of the plants are in suboptimal light at all times, respiration must account for a much greater fraction of photosynthesis.

In calculating the ratio $P:R$ in natural communities, the oversimplified assumption will be made that respiration remains constant and independent of light and photosynthesis. While the literature pertaining to this subject is contradictory and in a state of great confusion (see, for example, Rabinowitch, *16*), there is mounting evidence that respiration and photosynthesis are not wholly independent processes. However, since there is no good quantitative formulation of a relationship between them which may be incorporated into our calculations, it must be neglected here.

As mentioned above, the data from Fig. 3*A* together with light intensity values for a group of days with varying total incident radiation have been used to calculate photosynthesis as a function of radiation. (See Ryther, *13*, for a full description of these calculations). The values given by this treatment represent photosynthesis per day beneath a square meter of surface relative to the value for photosynthesis per cubic meter per hour at light saturation. For example, a value of 100 would mean that daily photosynthesis beneath a 1-meter-square water column is 100 times as great as photosynthesis within a 1-cubic-meter aliquot of that water column for 1 hour at optimal light intensity (assuming that the plant population is evenly distributed within this water column).

Since respiration is 1/15 photosynthesis at light saturation and is also stipulated to be constant with respect to light, depth, and time of day, we may calculate total daily respiration in the same relative units as photosynthesis. The curves of photosynthesis and respiration as functions of radiation are shown in Fig. 6. They cross at 100 g cal/cm$^2$ × day, which may be considered the daily compensation level for an entire plant community. The value $(R/P) \times 100$ is the percentage of respiratory loss and is shown as the lower broken line in Fig. 6. It ranges from 100 percent at radiation values of 100 g cal/cm$^2$ day or less to 28 percent on extremely bright, long days.

## Net Production

Returning to Fig. 5, gross production may be reduced by the respiratory loss (Fig. 6), giving the curve of net production, which begins at 100 g cal/cm$^2$ day and reaches a value of 25 g/m$^2$ day under radiation of 600 g cal/m$^2$ day (the lower broken line in Fig. 5).

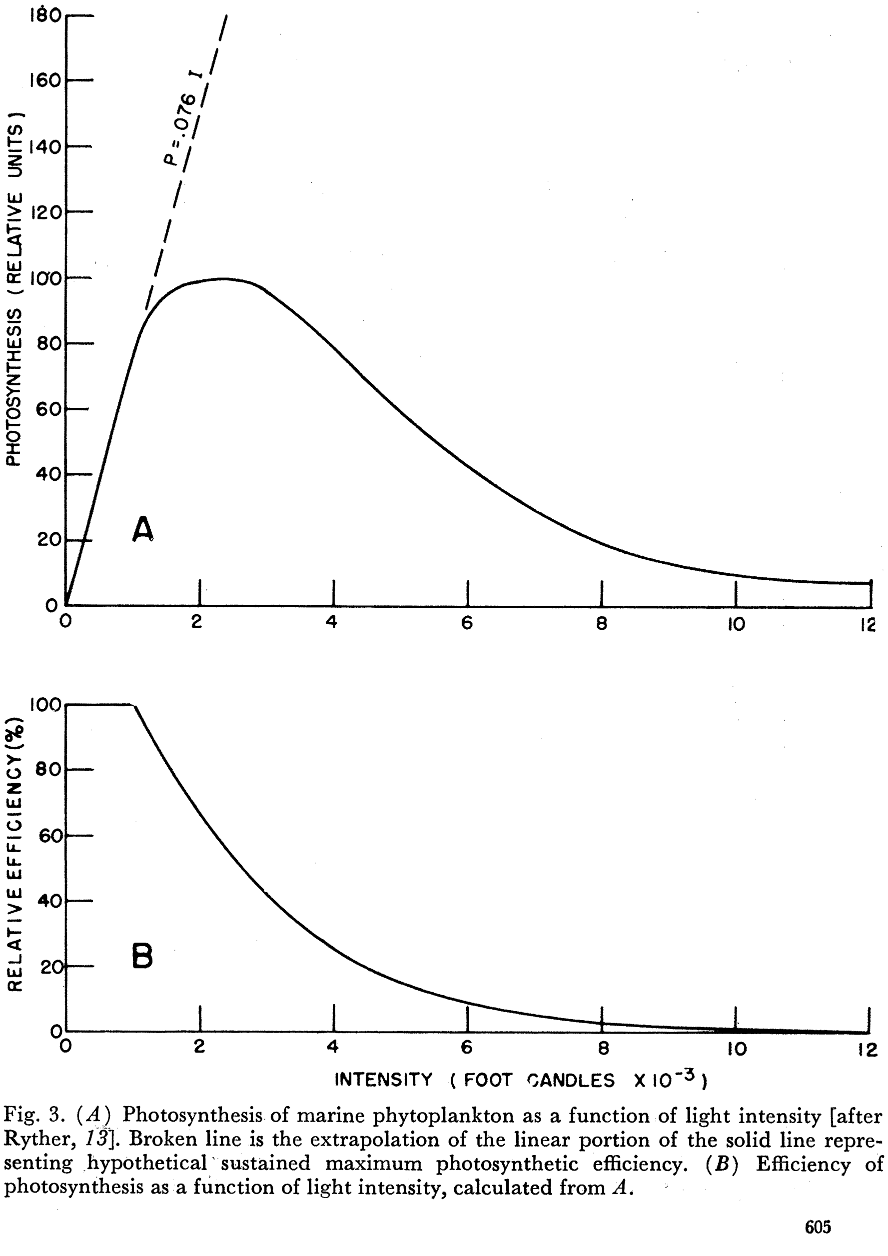

Fig. 3. (*A*) Photosynthesis of marine phytoplankton as a function of light intensity [after Ryther, *13*]. Broken line is the extrapolation of the linear portion of the solid line representing hypothetical sustained maximum photosynthetic efficiency. (*B*) Efficiency of photosynthesis as a function of light intensity, calculated from *A*.

Table 1. Gross and net organic production of various natural and cultivated systems in grams dry weight produced per square meter per day.

| System | Gross | Net |
|---|---|---|
| *A. Theoretical potential* | | |
| Average radiation (200 to 400 g cal/cm$^2$ day) | 23–32 | 8–19 |
| Maximum radiation (750 g cal/cm$^2$ day) | 38 | 27 |
| *B. Mass outdoor* Chlorella *culture* (*26*) | | |
| Mean | | 12.4 |
| Maximum | | 28.0 |
| *C. Land* (*maximum for entire growing seasons*) (*18*) | | |
| Sugar cane | | 18.4 |
| Rice | | 9.1 |
| Wheat | | 4.6 |
| *Spartina* marsh | | 9.0 |
| Pine forest (best growing years) | | 6.0 |
| Tall prairie | | 3.0 |
| Short prairie | | 0.5 |
| Desert | | 0.2 |
| *D. Marine* (*maxima for single days*) | | |
| Coral reef (*27*) | 24 | (9.6) |
| Turtle grass flat (*28*) | 20.5 | (11.3) |
| Polluted estuary (*29*) | 11.0 | (8.0) |
| Grand Banks (Apr.) (*30*) | 10.8 | (6.5) |
| Walvis Bay (*23*) | 7.6 | |
| Continental Shelf (May) (*19*) | 6.1 | (3.7) |
| Sargasso Sea (Apr.) (*31*) | 4.0 | (2.8) |
| *E. Marine* (*annual average*) | | |
| Long Island Sound (*32*) | 2.1 | 0.9 |
| Continental Shelf (*19*) | 0.74 | (0.40) |
| Sargasso Sea (*31*) | 0.88 | 0.40 |

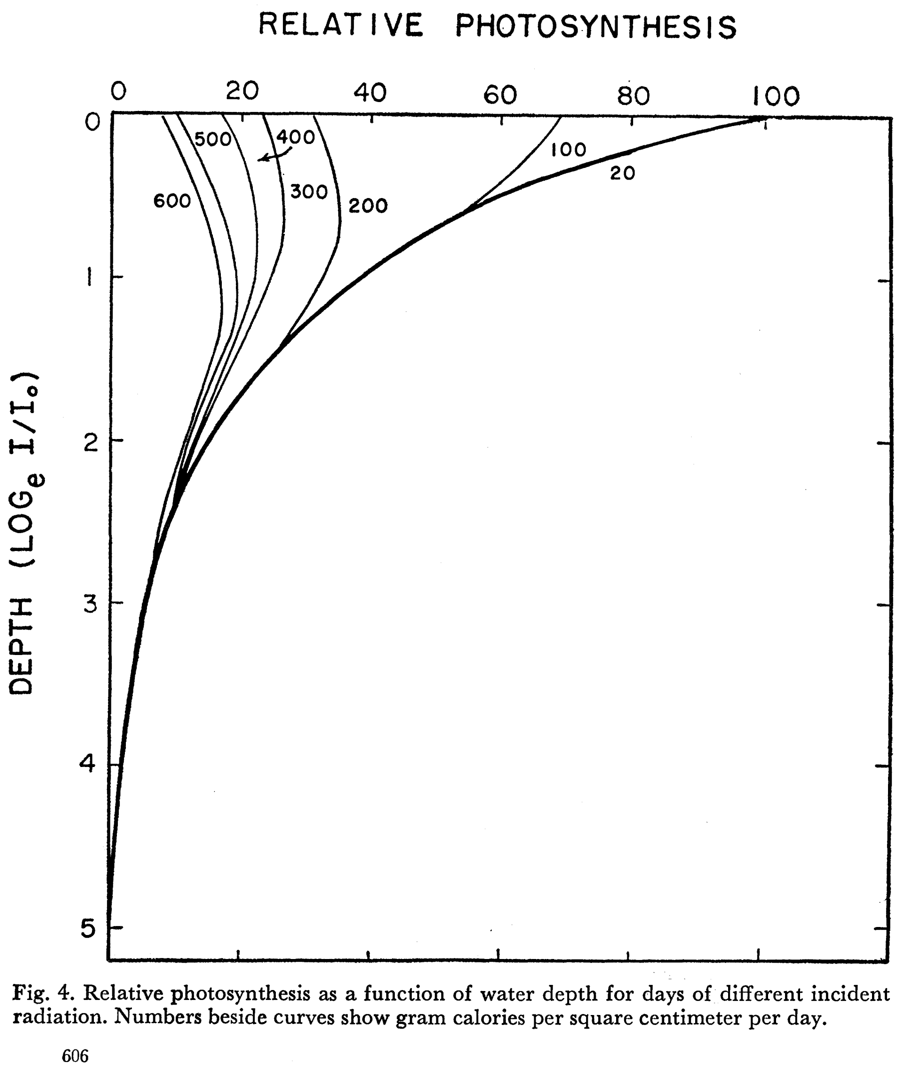

Fig. 4. Relative photosynthesis as a function of water depth for days of different incident radiation. Numbers beside curves show gram calories per square centimeter per day.

Although the annual range of daily incident radiation is extremely wide, even for a given latitude, this short-term variability is probably not very significant in affecting the general level of organic production of a given area. If one examines the tables compiled by Kimball (*17*) showing mean monthly radiation for different latitudes, it appears that over 80 percent of the data (including all latitudes and seasons) fall within a range of 200 to 400 g cal/cm$^2$ day. Thus, over most of the earth for most of the year a potential production of organic matter of some 10 to 20 g/m$^2$ day may be expected, while for shorter periods of fine summer weather, a net production of 25 g/m$^2$ day or slightly more may occur.

## Comparison of Theoretical and Observed Production Rates

We may now compare the production rates which were calculated in the preceding sections with some values which have been observed empirically. Since the former are based on hypothetical situations in which all light entering the water is absorbed by plants, the observational data, to be comparable, must be restricted to natural environments in which these conditions are at least closely approximated (for example, in dense plankton blooms, thick stands of benthic algae and rooted plants). In addition to these maximal values, the theoretical potential may be contrasted with average oceanic productivity rates.

We may also extend this comparison to the terrestrial environment, including some of the better agricultural yields, bearing in mind, however, that the physiology and hence, perhaps, the biotic potential of land plants may differ significantly from those of algae.

Finally, we may include the yields of *Chlorella* grown in outdoor mass culture, drawing here upon the excellent, continuing studies of H. Tamiya and his collaborators. These are of particular interest, since the conditions of these experiments were as optimal as possible and since the physiology of *Chlorella* is identical or closely similar to that of the organisms upon which our calculations are based. Thus the *Chlorella* yields will serve as a check for the theoretical production rates.

It is important, in making these comparisons, to keep in mind the distinction between gross and net production as defined above. Some of the data refer to true photosynthesis measurements (gross production) while others, such as the *Chlorella* experiments and the agricultural yields, are based on the actual harvest of organic matter (net production). In those cases in which only gross production values are available and where radiation data are given, net production has been obtained from Figure 5 and is shown in parentheses.

The theoretical production potential for average and maximal radiation, and the observational data for both marine and terrestrial environments, are given in Table 1. In each case the original source is given, except for the land values, where reference is made to the recent compilation by Odum (*18*). The various methods by which the values were obtained will not be discussed here except in the case of the unpublished data, in which gross production was calculated from chlorophyll and light, according to the method of Ryther and Yentsch (*19*) and net production was measured by the $C^{14}$ method, uncorrected for respiration as this method is interpreted by Ryther (*20*). Where gross production (photosynthesis) was originally reported as oxygen evolution, this has been converted to carbon assimilation, using an assimilatory quotient

$$\left(\Delta \frac{+O_2}{-CO_2}\right)$$

of 1.25 (see Ryther, *20*). Carbon uptake, in turn, has been converted to total organic production by assuming that the latter is 50 percent carbon by weight.

The maximal values for the marine environment represent the seven highest such values known to me. In addition to these, data are given for three regions (one inshore, one coastal, and one offshore) which have been studied over long enough periods of time to justify the calculation of annual means.

## Discussion

The mean yield of *Chlorella* obtained by the Japanese workers is almost identical to the mean theoretical production for days of average radiation (12.4 versus 13.5 g/m² day). These yields of *Chlorella* were produced only during the warmer part of the year, presumably owing to the poor growth of *Chlorella* at low temperatures. The highest yields of *Chlorella* (up to 28 g/m² day) were, according to Tamiya, "obtained on fair days in the warmer months." This maximum is approximately the same as the theoretical net production for days of maximum radiation. Thus, the *Chlorella* yields agree very well with the theoretical productive potential of the sea.

The land values for net production quoted from Odum's tables range from 18.4 g/m² day for the highest yields of sugar cane to 0.2 g/m² day for deserts. The best agricultural yields are generally of the same order of magnitude as the theoretical net production of the sea, as are the values for the salt marsh and the pine forest (during its years of best growth). Uncultivated grasslands range from 3.0 for tall prairie to 0.2 for desert

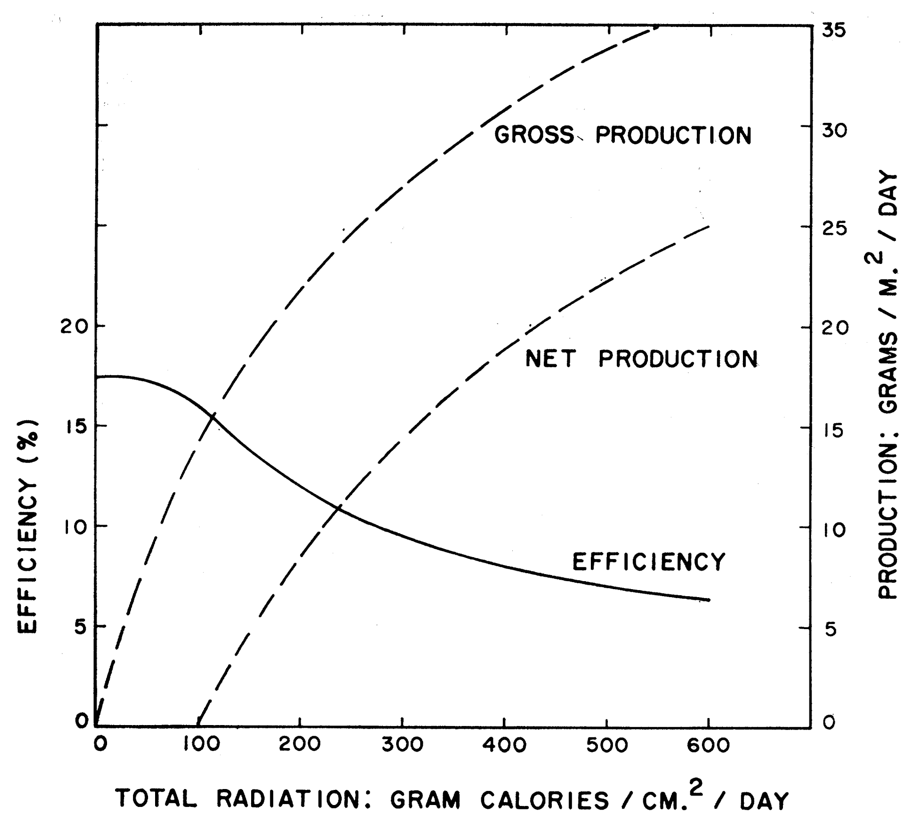

Fig. 5. Photosynthetic efficiency and theoretical maximum potential gross and net production as a function of incident radiation.

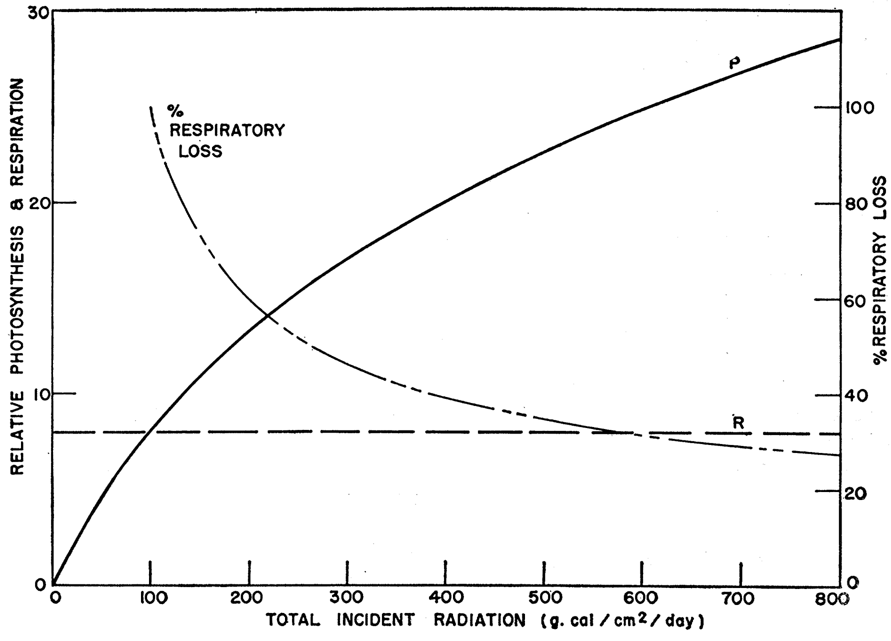

Fig. 6. Relative photosynthesis, respiration, and percentage of respiratory loss as a function of incident radiation.

conditions. Because of the extreme contrasts among terrestrial environments, mean values for the land as a whole are difficult to determine and would have little meaning. It is interesting, however, that Schroeder's estimate (*21*) of the annual production of all the land is equivalent to a mean daily production of 0.55 $g/m^2$, roughly the same as the value given in Table 1 for short prairie grass.

With regard to the marine data, it is perhaps surprising that net production rates differ by less than a factor of 2 in such diverse environments as a coral reef, a turtle grass flat, a polluted creek, and the Grand Banks. This alone would indicate that production in each case is limited by the same basic factor, the photosynthetic potential of the plants, and indeed these and the other high values in *D* in Table 1 all closely approach the theoretical potential.

Seasonal studies have been made of three marine areas, Long Island Sound, the continental shelf off New York, and the Sargasso Sea off Bermuda. In each case temporary rates of production were observed during the spring flowering which approached the theoretical maximum, but the annual means were more than an order of magnitude lower (*E* in Table 1). True, these regions do not, throughout the year, satisfy the postulated conditions necessary to obtain this maximum, namely, that all light entering the water be absorbed by plants. For example, in his Long Island Sound studies, Riley (*22*) found that no more than one-third of the incident radiation was utilized by plants, the remainder presumably being absorbed by nonliving particulate and dissolved materials. Using Riley's techniques, I estimated that only 25 to 40 percent of the light penetrating the continental shelf waters was absorbed by the phytoplankton. This alone, however, is insufficient to account for the discrepancy between observed and potential production rates. In the clear waters of the Sargasso Sea only 10 to 20 percent of the light is absorbed by the phytoplankton during most of the year. But there is little if any other particulate matter present; the remainder of the light is absorbed by the water itself. This is not a cause but an effect of low production. The underlying reason for low production rates here and in most parts of the ocean is the limitation of essential nutrients in the upper, euphotic layers and the inadequacy of vertical mixing processes in bringing deep, nutrient-rich water to the surface.

With the exception of the three planktonic communities which have been discussed, the seasonal cycles of marine production are largely unknown and can only be surmised. Probably high levels may be maintained throughout the year in benthic populations such as the coral reef, the turtle grass flats (see *D* in Table 1) and in thick beds of seaweeds, provided that seasonal temperature extremes do not impair growth. While the concentrations of nutrients in the surrounding waters may be very low, the fact that they are continually being replenished as the water moves over the plants probably prevents their ever being limiting. Plankton organisms, on the other hand, suspended as they are in their milieu, can probably never maintain high production rates in a given parcel of water, for their growth rapidly exhausts the nutrients from their surrounding environment and any mixing process which enriches the water must, at the same time, dilute the organisms. However, high plankton production may be sustained in a given geographic area (a polluted estuary, a region of permanent upwelling of deep water, and so forth), which is continually replenished with enriched water. In these situations, the productive capacity of the sea may be sustained for long periods, perhaps permanently.

For most of the ocean, as stated above, no such mechanism for nutrient replenishment is available. The combined meteorological and hydrographic conditions which produce the typical spring flowering of the phytoplankton over much of the oceans have been adequately described elsewhere and need not be discussed here. Suffice it to say that, in the oceans as a whole, as seasonal studies have demonstrated, high production approaching the theoretical maximum under optimal conditions is restricted to periods of a few days or, at most, weeks, per year.

Steemann Nielsen (*23*) has recently estimated the net production of the entire hydrosphere as 1.2 to $1.5 \times 10^{10}$ tons of carbon per year, roughly one-tenth the earlier estimates made by Riley (*24*) and others, and about comparable to Schroeder's figure (*21*) for the land. Our production estimates are somewhat higher than those of Steemann Nielsen, the annual mean net production of organic matter for the Sargasso Sea (0.40 $g/m^2$ day) being about 6 times as great as his value for the same area, and twice his average for the oceans as a whole. This discrepancy appears to be largely due to the fact that Steemann Nielsen's values are based on single observations which probably seldom included seasonal maxima. His observations in the Sargasso Sea, for example, were made in June and did not differ greatly from our June values, which were the seasonal minima. If the Sargasso Sea is one of the less fertile parts of the ocean, as is generally believed, then our data would indicate that the seas are more than twice as productive as the land (*25*).

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