

Quantum requirement in photosynthesis.

A new method for its estimation

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For the determination of the quantum requirement in photosynthesis it is necessary (1) to express in quanta the luminous energy E absorbed by the assimilating cells and utilized for the synthesis of carbohydrates, (2) to calculate from the rate of photosynthesis F the number of decomposed carbon dioxide molecules. While the latter point presents no difficulties and ambiguity, some precisions concerning the energy used in photosynthesis are necessary. It has long been realised (W a r b u r g 1922) that in researches on the quantum yield all the photosynthetically inactive radiations must be eliminated and that a good yield can be expected only if the radiant energy is the factor limiting the rate of photosynthesis. If it is supplied to the plant in excess and above its photosynthetic capacities, a great part of this energy will be dissipated as heat and a low yield will ensue. On the other hand, in low light intensities the assimilation rate is small and the intensity of respiration comparatively great, sometimes even greater than the rate of photosynthesis. In these conditions the quantum requirement becomes uncertain because its value depends upon an assimilation rate which is chiefly determined by an uncertain correction for respiration.

The method described below is free from the limitation imposed by the light conditions. It allows the evaluation of the quantum requirement for high light intensities for which the correction for respiration plays only a minor rôle, its value being only a small fraction of the assimilation rate. The method is based on the results presented in a preceding contribution to the theory of limiting factors in photosynthesis (1953).

The starting point of our considerations is again an algal suspension of the thickness d contained in a cylindrical vessel and illuminated from below with light active in photosynthesis ($\lambda = 400 - 700 \text{ m}\mu$). Owing to the absorption of the luminous energy by the cell pigments the light

intensity diminishes in the suspension, and according to Beer's law at the level z it has the intensity

$$I_z = I_e^{-kz}, \quad (1)$$

where I is the intensity of the incident light, I_z — its intensity at the level z , k — the absorption constant, e — the basis of natural logarithms.

As long as the light intensity I is feeble light is the limiting factor in the whole suspension. In these conditions the intensity of photosynthesis F increases proportionally to I . However, when of sufficiently high intensity, light ceases to be the limiting agent in the lower layers of the suspension, while it retains this rôle in the upper layers. It is then possible to divide the whole suspension in two layers: in the first or lower the luminous energy is supplied to the cells in excess, while in the second or upper layer light is the factor limiting the assimilation rate. The level separating the two layers is the transition level with a corresponding (constant) light intensity I_l . The height h of the transition level, measured from the bottom of the suspension, increases as the light intensity is augmented, for it is obvious that the greater is I the greater is the height to which light of the intensity I_l can penetrate. Finally, for a given sufficiently high light intensity I_B the transition level will reach the surface of the suspension ($h = d$). Then the upper layer vanishes and light becomes the factor in excess throughout the suspension. Simultaneously, the intensity of photosynthesis attains its maximum value: $F = F_B = F_{max}$. Now the whole suspension is supersaturated with radiant energy and any increase in the light intensity should remain (and actually remains) without effect on the assimilation rate.

Let us denote by E_a the quantity of luminous energy (photosynthetically active) which penetrates into the suspension and is absorbed by the assimilating cells. If light is the limiting factor we can assume that all the absorbed energy is available for the reduction of carbon dioxide. In reality a part of E_a is lost in absorption by other plant constituents than the chloroplasts or is dissipated as heat, fluorescent light etc., but nevertheless we may assume that in principle the whole of E_a can be utilized for the synthesis of carbohydrates. On the contrary, if light is the factor supplied in excess to the assimilating cells, then it is obvious that only a part of it (which we will denote by E_u) can be used for photosynthetic purposes, the rest $E_a - E_u$ being necessarily wasted in the form of heat etc.

Our next step is to calculate E_u ; for this purpose we will first find a function $E_a(z)$ expressing the quantity of radiant energy absorbed by a suspension of the thickness z . Let us consider a very thin layer dz of the

suspension on the level z . According to (1) the light intensities on the levels z and $z + dz$ are:

$$I_z = Ie^{-kz} \quad I_{z+dz} = Ie^{-k(z+dz)}.$$

The difference $dE_a = I_z - I_{z+dz}$ is equal to the light energy absorbed in a unit of time by the layer of the thickness dz on the level z :

$$dE_a = I[e^{-kz} - e^{-k(z+dz)}] = Ie^{-kz}(1 - e^{-k dz}), \quad (2)$$

but $e^{-k dz} = 1 - k dz + \frac{k^2 d^2 z}{1.2} - \text{etc.}$ However dz being very small, all the terms of this expansion from the third one can be neglected, hence $e^{-k dz} = 1 - k dz$. Substituting this value in (2) we obtain:

$$dE_a = Ike^{-kz} dz. \quad (3)$$

Let us now represent graphically the function $J(z) = Ike^{-kz}$ for a given light intensity I (fig. 1). If through the points z and $z + dz$ on the z -axis the corresponding ordinates be drawn, then the area of the very thin strip contained between them is equal dE_a . Similarly the area delimited by the curve, the two axes and the ordinate corresponding to the abscissa z represents the energy $E_a(z)$ absorbed by a suspension of the thickness z . It follows from the graph that:

$$E_a(z) = \int_0^z Ike^{-kz} dz = Ik \int_0^z e^{-kz} dz = -Ie^{-kz} + I = (1 - e^{-kz})I, \quad (4)$$

in particular, the energy absorbed by the whole suspension ($z = d$) is:

$$E_a(d) = (1 - e^{-kd})I. \quad (5)$$

As we have already stated, only the part E_u of $E_a(d)$ is available for the synthesis of carbohydrates. To calculate E_u let us draw on the graph representing $J = Ike^{-kz}$ (fig. 1) the ordinate for $z = h$, i. e. the ordinate corresponding to the height of the transition level in the suspension, it cuts the curve at H . A line drawn through H parallel to the z -axis meets in L the other axis. We shall show that the area limited by the line $OhdDHLO$ represents E_u . The ordinate hH divides this area into two parts, I and II, corresponding respectively to the lower and the upper layer of the suspension. Now, ex definitione, in the upper layer light is the limiting factor, and therefore its energy can be adequately utilized in photosynthesis. It follows from the graph that this energy is:

$$E_u(II) = \int_h^d Ike^{-kz} dz = Ie^{-kz} \Big|_d^h = (e^{-kh} - e^{-kd})I. \quad (6)$$

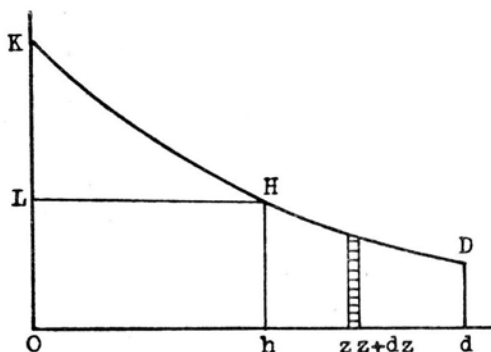


Fig. 1. Graphical representation of function $J(z) = I_0 k e^{-kz}$. The function is represented by the line KHD, h = abscissa corresponding to the transition level for which $I = I_1$; d = thickness of the suspension. The stripped area represents $d E_a$. Area OhdDHKLO = $E_a(d)$, area OhHLO = E_u (I), area hdDHh = E_u (II).

In the lower layer, on the contrary, where light is supplied in excess, only a part, E_u (I), of the radiant energy absorbed by the suspension can be utilized for the synthesis of sugars. E_u (I) can be easily found from the fact that, owing to the uniformity of the experimental conditions (the light excepted), the assimilation rate dF of the very thin layer dz is constant and independent of z :

$$dF = \text{const. } dz. \quad (0 \leq z \leq h)$$

From this relation it follows also that

$$dE_u = \text{const. } dz. \quad (0 \leq z \leq h) \quad (7)$$

if by dE_u we denote the energy utilized in photosynthesis by a layer of the thickness dz on the level z ($z \leq h$). The integration of (7) gives:

$$E_u(I) = \int_0^h \text{const. } dz = \text{const. } h. \quad (8)$$

On the transition level ($z = h$) the quantity of the absorbed energy is equal to the amount of the energy utilized in photosynthesis, hence, from (3):

$$dE_a = dE_u = I k e^{-kh} dz. \quad (9)$$

From a comparison of (7) and (9) it follows that $\text{const} = I k e^{-kh}$, hence, from (8):

$$E_u(I) = I k e^{-kh} \cdot h. \quad (10)$$

The energy E_u utilized in photosynthesis by the whole suspension is the sum $E_u(I) + E_u(II)$:

$$E_u = I k h e^{-kh} + I(e^{-kh} - e^{-kd}) = I[e^{-kh}(1 + kh) - e^{-kd}],$$

but as, from (1), $h = 1/k \cdot \lg I/I_t$:

$$E_u = I [\exp(-\lg I/I_t)(1 + \lg I/I_t) - e^{-kd}],$$

and as $e^{-\lg X} = 1/X$:

$$E_u = I \left[\frac{I_t}{I} (1 + \lg \frac{I}{I_t}) - e^{-kd} \right],$$

and finally:

$$E_u = I_t (1 + \lg \frac{I}{I_t}) - I e^{-kd}. \quad (11)$$

In this expression only I is directly measurable and known, the two other constants, I_t and kd , are hardly to be found experimentally. We will see, however, that it is possible to calculate them, provided that the relation $F = f(I)$ between the assimilation rate and the light intensity is known. In a preceding paper (1953) we have shown that this relation can be expressed by the following functions:

$$1^0 F = \frac{a}{k} (1 - e^{-kd}) I, \quad (12)$$

valid only for feeble light intensities: $0 \leq I \leq I_t$,

$$2^0 F = \frac{a I_t}{k} \lg \text{nat} \frac{I}{I_t} + \frac{a}{k} (I_t - I e^{-kd}), \quad (13)$$

valid only for middle light intensities: $I_t \leq I \leq I_t e^{kd}$,

$$3^0 F = F_{\max} = a I_t d = \text{const.}, \quad (14)$$

valid only for strong light intensities: $I \geq I_t e^{kd}$.

In these formulas a is a proportionality factor and k , d , I_t are constants for a given set of experimental conditions. On a graph (fig. 2) the curve representing F in relation to I is composed of three parts, viz, of two segments (functions (12) and (14)) connected by an arch AB , the equation of which is given by (13). The coordinates of the endpoints of the first segment are 0,0, and $I_t, \frac{a}{k} (1 - e^{-kd}) I_t$. The second segment is parallel to the I -axis and begins at the point $B: I_t e^{kd}, a I_t d$.

The constants a , k , I_t , and d appearing in (12) — (14) are neither given by nor calculable from the experimental data which usually consist of pairs of corresponding values of I and F . We have shown that if the following substitutions are made:

$$\frac{k}{aI_t} = p, \quad \frac{1}{I_t e^{kd}} = q, \quad \lg n I_t = M \log I_t = Mr, \quad \lg n I = M \log I, \quad (15)$$

($\lg n = \log_{\text{nat}}$, $M = \text{logarithmic modulus}$, 2,302585...)

then the function (13) takes the form:

$$pF + qI + Mr - M \log I - 1 = 0 \quad (16)$$

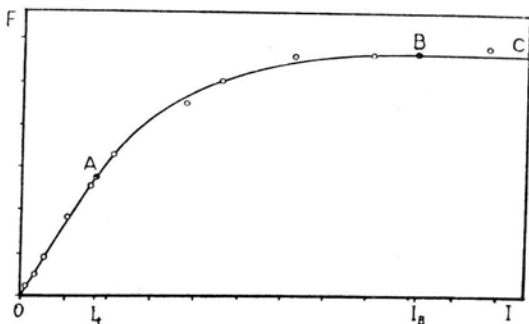


Fig. 2. Graphical representation of the relation between the assimilation rate F (ordinates) and the light intensity I (abscissae). To functions (12), (13) and (14) correspond the segment OA , the arch AB and the segment BC respectively. $I_t = \text{abscissa of point A}$, $I_b = I_t e^{kd} = \text{abscissa of point B}$. The circles represent the data obtained by Gabrielsen (1940, table III, pag. 176, leaf of *Sinapis alba*, yellow-green light).

with three constants only. We have also shown that their values are calculable from the experimental data, provided that they contain values corresponding to the part AB of the curve. In the simplest case these data consist of three pairs of values of I and F : $I_1, F_1; I_2, F_2; I_3, F_3$. Inserting them in (16) we obtain three linear equations from which it is easy to calculate the values of p, q, r .

The function (16) was the object of a detailed study presented in the preceding paper (1953) already mentioned. Using the experimental evidence accumulated by different plant physiologists working with several species, we have checked its validity and found a good agreement between the theory and the experimental results. We will therefore assume the validity of (16) and suppose that the constants $p, q, I_t = e^{Mr}$ are known and proceed to show the way they can be used for calculating the quantum requirement R_q . If the relations (15) are taken into account, the function (11) takes the form:

$$E_u = I_t (1 + M \log I - Mr - qI). \quad (17)$$

For calculating R_q the energy must be expressed in quanta, to this effect E_u is multiplied by λf , where λ is the wave length (in $\text{m}\mu$) of the inci-

dent light and f_1 a factor, the value of which depends on the unit used for the measurements of the radiant energy (ergs or calories, more details in the appendix), We have:

$$E_u \text{ (in quanta)} = \lambda f_1 \cdot I_t (1 + M \log I - Mr - qI). \quad (17a)$$

Similarly the rate of photosynthesis must be expressed as the number of decomposed carbon dioxide molecules. This is done by multiplying F by a conversion factor f_2 ; it follows from (16) that

$$F \text{ (in molecules)} = f_2 \cdot \frac{1}{p} (1 + M \log I - Mr - qI). \quad (16a)$$

Then the quantum requirement is the ratio of (17a) and (16a):

$$R_q = \frac{E_u}{F} = \lambda \cdot f \cdot I_t p, \quad (18)$$

where $f = f_1/f_2$. Table I indicates the values of factor f according to the units used for measurements of F and I . They were calculated on the assumption that photosynthesis proceeds in conformity with the equation:



and hence that the ratio $\text{CO}_2/\text{O}_2 = 1$ (by volume). If this ratio is different from unity and has the value γ , the factor f is to be multiplied by an additional coefficient whose value must be deduced from γ . In the simplest case, when F is measured in cmm O_2 , f ought be multiplied by γ .

It follows from (15) that $I_t p = k/a$ and from (12) that $\frac{a}{k}(1 - e^{-kd})$ is the angular coefficient m of the straight line representing

TABLE I
Values of the conversion factor f

| F measured in | The intensity I of the incident light is measured in | |
|------------------------------------|---|------------|
| | ergs | g-calories |
| mg CO_2 | $3,68 \times 10^{-11}$ | 0,00154 |
| mg O_2 | $2,675 \times 10^{-11}$ | 0,00112 |
| cmm O_2 (CO_2) | $1,874 \times 10^{-8}$ | 0,784 |

(The wave length of the light in $\text{m}\mu$)

the function (12), $F = f(I)$, for low light intensities. For dense or thick suspensions the term e^{-kd} can be neglected and then the angular coefficient has the value $m = a/k$, hence:

$$I_l p = \frac{1}{m} \quad \text{and} \quad R_q = \frac{\lambda f}{m}. \quad (20)$$

In the next section of this paper the reader will find a few examples explaining the application of formulas (18) and (20).

When E_a and E_u are known it is possible to calculate not only the quantum requirement but also other characteristics of the energy relations in photosynthesis.

1. The energy yield of photosynthesis is the ratio E_{as}/E_u of the energy stored in the carbohydrates and the energy available for the assimilation of carbon dioxide. F must be expressed in terms of energy (ergs or calories), this is done by multiplying F by a convenient factor g , the value of which depends on the units used to measure I and F . Some values of g (assuming the validity of equation (19)) are tabulated in table II. If the yield is expressed in percentages we have:

$$\% w = \frac{100 F \cdot g}{E_u} = \frac{100 g}{I_l p} \quad (21)$$

TABLE II

Conversion factors g

| F measured in | The intensity I of the incident light is measured in | |
|---------------------------------------|---|------------|
| | ergs | g-calories |
| mg CO ₂ | $1,068 \times 10^8$ | 2,5525 |
| mg O ₂ | $1,469 \times 10^8$ | 3,5104 |
| cmm O ₂ (CO ₂) | $2,097 \times 10^5$ | 0,005012 |

If the application of formula (20) is admissible the above relation becomes

$$\% w = 100 g m. \quad (21a)$$

2. Sometimes the yield is defined as the ratio E_{as}/E_a of the energy stored in the carbohydrates and the energy absorbed by the assimilating cells; it follows from (16) and (5) that

$$w = \frac{E_{as}}{E_a} = \frac{gF}{E_a} = \frac{g(1 + M \log I - Mr - qI)}{p(1 - e^{-kd})I}, \quad (22)$$

the value of the product kd appearing in the denominator is calculated from (15):

$$kd = -(\log_{\text{nat}} I_l + \log_{\text{nat}} q) = -M(r + \log q). \quad (23)$$

3. It is also possible to calculate the ratio E_u/E_a of the energy available for photosynthesis and the total absorbed energy, in %:

$$\% E_u = \frac{100 E_u}{E_a} = \frac{[I_t (1 + \lg I/I_t) - I e^{-kd}] 100}{(1 - e^{-kd}) I} \quad (24)$$

The value of $\% E_u$ is not constant, but as in the preceding case diminishes with the increase of I . The value of kd is given by formula (23).

II

A few examples may illustrate the way the quantum requirement and the energy yield are calculated from the experimental data. Unfortunately there are only very few papers with results which can be used for this purpose. The reason is that in the vast majority of investigations on the relation $F = f(I)$ the light intensity is measured not in energy units (ergs or calories) but in lux. As an exception the results obtained by Gabrielsen (1934, 1940) can be quoted, who employed approximately monochromatic light and expressed its intensity in g-cal. per hour and 50 cm². The fact that in his experiments the assimilating object was not an algal suspension but a leaf (*Sinapis alba*) is of no real importance, since a leaf blade can be considered with permissible approximation as a very thin suspension. As for the calculation of R_q measurements based on a great range of light intensities are preferable, we have selected for this purpose the longest series OR₁, and OR₂ and GG (table III, pag. 154), from Gabrielsen's ample experimental data. Using methods presented in detail in a preceding paper (1953) the values of the constants p , q , I_t have been calculated¹⁾. By comparing the observed with the calculated values (table IV) the agreement between theory and experimental results can be judged²⁾. Table III contains the values of the constants and the

TABLE III

| series | λ (m μ) mean | | p | q | Mr | I_t |
|-----------------|------------------------------|--------------|---------|----------|--------|-------|
| GG | 545 | yellow-green | 0,1465 | 0,001093 | 5,1494 | 172,3 |
| OR ₂ | 640 | orange-red | 0,1405 | 0,001804 | 4,7302 | 113,2 |
| OR ₁ | 660 | „ „ | 0,18097 | 0,001597 | 4,3766 | 80,8 |

mean wave lengths. As light intensities are expressed in g-calories and the assimilation rate in mg CO₂ the value 0,00154 for the factor f (table I)

¹⁾ The method based on F_{max} and two points situated on the arch AB was used for calculating p , q , r .

²⁾ The data for yellow-green light are plotted in graph 2.

TABLE IV

- I — intensity of the incident light, *Sinapis*: g-cal/hour x 50 cm²; *Nitschia*: ergs/sec x cm².
 I_t — transition value of the light intensity.
 I_B — saturation value of the light intensity.
 I_{red} — light intensity expressed in ergs/hour x 5,8 cm².
 F_{obs} — assimilation rate, *Sinapis*: mg CO₂/hour x 50 cm²; *Nitschia*: cmm O₂ per hour.
 F_{cal} — assimilation rates calculated from equations (12), (13) and (14) of the text.

Sinapis alba
 Gabrielsen, 1940
 GG, yellow—green light

| | I | F _{obs} | F _{cal} |
|----------------|-------|------------------|------------------|
| | 11 | 0,5 | 0,35 |
| | 32 | 1,0 | 1,03 |
| | 53 | 1,8 | 1,7 |
| | 106 | 3,7 | 3,4 |
| | 162 | 5,2 | 5,2 |
| I _t | 172,3 | — | 5,54 |
| | 212 | 6,6 | 6,6 |
| | 380 | 9,0 | 9,4 |
| | 460 | 10,1 | 10,1 |
| | 640 | 11,3 | 11,0 |
| | 810 | 11,4 | 11,35 |
| I _B | 914,6 | — | 11,4 |
| | 1080 | 11,7 | „ |

Sinapis alba
 Gabrielsen, 1940
 OR, orange—red light

| | I | F _{obs} | F _{cal} |
|----------------|-------|------------------|------------------|
| | 9 | 0,6 | 0,45 |
| | 19 | 1,2 | 0,95 |
| | 37 | 2,1 | 1,85 |
| | 68 | 4,1 | 3,4 |
| I _t | 113,3 | — | 5,66 |
| | 136 | 6,8 | 6,7 |
| | 159 | 7,4 | 7,5 |
| | 270 | 9,5 | 9,8 |
| | 350 | 11,1 | 10,65 |
| | 530 | 11,0 | 11,3 |
| I _B | 554,4 | — | 11,3 |
| | 750 | 11,3 | „ |
| | 1050 | 11,7 | „ |

Sinapis alba
 Gabrielsen, 1940
 Or₁, orange—red light

| | I | F _{obs} | F _{cal} |
|-----------------|-------|------------------|------------------|
| | 9 | 0,7 | 0,54 |
| | 35 | 2,2 | 2,1 |
| | 70 | 4,2 | 4,2 |
| I _t | 80,8 | — | 4,8 |
| | 130 | 7,0 | 7,1 |
| | 208 | 9,0 | 9,0 |
| | 278 | 9,9 | 10,0 |
| | 340 | 11,3 | 10,55 |
| | 440 | 11,5 | 11,1 |
| II _B | 626,2 | — | 11,4 |
| | 670 | 11,3 | „ |

Nitschia dissipata
 Wassink & Kersten, 1944
 white light

| | I | I _{red} | F _{obs} | F _{cal} |
|----------------|------|------------------|------------------|------------------|
| | 0,24 | 5011 | 27 | 24 |
| | 0,35 | 7358 | 35 | 35,5 |
| | 0,85 | 17748 | 89 | 86 |
| I _t | 1,13 | 23587 | — | 114,7 |
| | 1,45 | 30276 | 142 | 142 |
| | 2,20 | 45936 | 180 | 180 |
| | 3,00 | 62640 | 200 | 200 |
| I _B | 4,42 | 92313 | — | 210 |

must be used. The substitution of the values of p , I_t f and γ in (18) gives:

$$\text{GG } R_q = 545 \times 0,00154 \times 172,33 \times 0,1465 = 21,2$$

$$\text{OR}_2 R_q = 645 \times 0,00154 \times 113,3 \times 0,1405 = 15,8$$

$$\text{OR}_1 R_q = 660 \times 0,00154 \times 80,8 \times 0,181 = 14,9$$

These values are of the same magnitude as those found by many American physiologists (vide R a b i n o v i t c h, 1951, chapt. 30).

In a similar way the energy yield can be calculated from (21):

$$\text{GG } \% w = \frac{100 \times 2,552}{172,33 \times 0,1465} = 10,1$$

$$\text{OR}_2 \% w = \frac{255,2}{113,32 \times 0,1405} = 16,0$$

$$\text{OR}_1 \% w = \frac{255,2}{80,8 \times 0,181} = 17,2$$

The values show good agreement with those found by G a b r i e l s e n with a different method.

If only an approximate value of the quantum requirement is needed even results obtained in experiments with white light may be utilized. W a s s i n k's and K e r s t e n's data (1944) referring to the CO_2 assimilation of the diatom *Nitzschia dissipata* may be cited as an example. The light intensity was measured in ergs/sec/cm², the assimilation rate in cmm oxygen per hour (manometric technique, table IV). The bottom area of the assimilation vessels is not indicated in Wassink's paper of 1944, but it may be assumed to be equal to 5,8 cm², as this is the value mentioned in a later paper (1946). By multiplying the light intensities by $3600 \times 5,80 = 20880$ we reduce them to the hour as the time unit and to 5,8 cm² as the area unit. The values of the constants $p = 0,00649$, $q = 0,2262$, $Mr = 0,1219$ and $I_t = 1,13$ were calculated by the method mentioned on page 6¹⁾. The radiant energy being expressed in ergs and the assimilation rate in cmm oxygen the factor $f = 1,874 \times 10^{-8}$ (table I) must be inserted in equation (18). Assuming that the mean wave length is 550 m μ the quantum requirement and the energy yield are:

$$Rq = 550 \times 1,874 \times 10^{-8} \times 235875100 \times 0,00649 = 15,8,$$

$$\% w = \frac{2,097 \times 10^5 \times 10^2}{235875100 \times 0,00649} = 13,7\%$$

As the last example let us calculate the quantum requirement of *Chlorella* by applying equation (20) to the data obtained by W a r b u r g in 1922. This is permissible since in his experiments a complete absorption of the radiant energy ($\lambda = 570 - 645 \text{ m}\mu$, mean, $609 \text{ m}\mu$) was assured by the use of very dense suspensions. The light intensities and the

¹⁾ In calculations it is much simpler to use the original data and to multiply the values of p , q , r and I_t by convenient factors.

assimilation rates of Warburg's table I are graphically summarised in fig. 3, from which it is apparent that the data for higher light intensities present too much scatter to be of any use; on the contrary from the data corresponding to feeble light intensities the angular coefficient of the

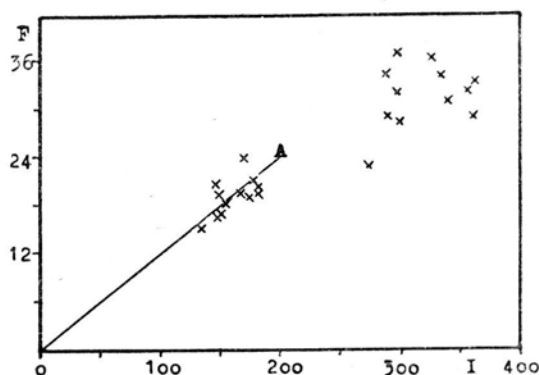


Fig. 3. Chlorella, Warburg's and Negelein's data (1922). The light intensity I is measured in $\text{g-cal}/(10 \text{ minutes})/14 \text{ cm}^2$, the assimilation rate F in $\text{cmm oxygen per 10 minutes}$. Wave length 570—645 $\text{m}\mu$. The value of the angular coefficient of the line OA is $m = 119,6$.

line of best fit can be evaluated and is found to be $m = 119,6$ ($m = S(IF)/S(I^2)$). The light energy being expressed in g-calories and the assimilation rate in cmm oxygen , the factor $f = 0,784$ from table I must be inserted in (20):

$$Rq = \frac{0,784 \times 609}{119,6} = 4.$$

The application of formula (21a) gives:

$$\%ow = 100 \times 0,005012 \times 119,6 = 60\%.$$

Appendix

Factor f appearing in (18) is the ratio of two factors f_1 and f_2 which when they are multiplied by the absorbed energy E_u and the assimilation rate F respectively express the energy in quanta and the rate as the number of decomposed carbon dioxide molecules. By definition the energy quantum is

$$\varepsilon = h\nu = \frac{hc}{\lambda},$$

where h is Planck's constant, ν — the frequency of the light, λ — its wave length and c — the velocity of light. To express the energy in quanta E_u must be divided by ε :

$$E_u \text{ in quanta} = \frac{E_u}{\varepsilon} = \frac{\lambda E_u}{hc}.$$

In this expression $f_1 = 1/hc$.

To calculate f_2 let us first assume that F is measured in mg CO₂ or O₂. Let m be the molecular weight (in milligrams) and N the Avogadro number (number of molecules in one mol). Then the ratio $N:m$ i.e. the number of molecules in 1 mg of CO₂ or O₂ is f_2 , and:

$$f = \frac{f_1}{f_2} = \frac{1}{hc} \cdot \frac{m}{M}. \quad (25)$$

The value of f depends upon the units used to measure E_u , F and λ . Let us suppose that λ is always expressed in m μ then $c = 299793 \times 10^{12}$ m μ /sec. Besides $N = 6,023 \times 10^{23}$.

1. E_u in ergs, F in mg CO₂, then $h = 6,624 \times 10^{-27}$ ergsec, $m = 44010$ mg. Inserting these values in (25) we have:

$$f = \frac{44010}{6,624 \times 10^{-27} \times 299793 \times 10^{12} \times 6,023 \times 10^{23}} = 3,68 \times 10^{-11}.$$

2. E_u in ergs, F in mg O₂, then $m = 32000$ mg and

$$f = \frac{32000}{\text{the same denominator as in 1.}} = 2,675 \times 10^{-11}.$$

3. E_u in calories, F in mg CO₂, then $h = 6,624 \times 10^{-27} \times 2,389 \times 10^{-8} = 1,5825 \times 10^{-34}$ calsec, because 1 erg = $2,389 \times 10^{-8}$ cal; $m = 44010$ mg.

$$f = \frac{4410}{1,5825 \times 10^{-34} \times 299793 \times 10^{12} \times 6,023 \times 10^{23}} = 0,00154.$$

4. E_u in cal., F in mg O₂, then $m = 32000$ mg and

$$f = \frac{32000}{\text{the same denominator as in 3.}} = 0,00112.$$

The formula (25) is inapplicable if the assimilation rate is expressed in cmm O₂ or CO₂. In this case $f_2 = N/22412000$, because 22.412 liters or 22412000 cmm gas at N.T.P. correspond to 1 mol or N molecules.

5. If the energy is measured in ergs then

$$f = \frac{f_1}{f_2} = \frac{1}{hc} \cdot \frac{22412000}{N} = \frac{22412000}{6,624 \times 299793 \times 6,023 \times 10^{-8}} = 1,874 \times 10^{-8}.$$

6. E_u in cal., then $h = 1,5825 \times 10^{-34}$ (vide p. 3) and:

$$f = \frac{22412000}{1,5825 \times 10^{-34} \times 299793 \times 6,023 \times 10^{23}} = 0,784.$$

The factors tabulated in table II serve to express the assimilation rate in energy units.

1. If the energy is measured in ergs and F in mg CO₂ then it follows from (19) that 6×44010 mg CO₂ correspond to $674000 \times 4,184 \times 10^7$ ergs, hence

$$g = \frac{674000 \times 4,184 \times 10^7}{6 \times 44010} = 1,068 \times 10^8.$$

2. If the energy is expressed in g-calories then

$$g = \frac{674000}{6 \times 44010} = 2,552.$$

3. and 4. If the energy is expressed in ergs or g-calories and F in mg O₂ then:

$$g = \frac{674 \times 4,184 \times 10^{10}}{6 \times 32000} = 1,469 \times 10^8, \quad g = \frac{674000}{6 \times 32000} = 3,510.$$

5. E in ergs, F in cmm O₂ or CO₂ (N.T.P.). In this case $6 \times 22,412$ liters or 6×22412000 cmm of gas correspond to $674000 \times 4,184 \times 10^7$ ergs, hence

$$g = \frac{674 \times 4,184 \times 10^{10}}{6 \times 22412000} = 2,097 \times 10^5.$$

6. E in calories, F in cmm O₂ or CO₂:

$$g = \frac{674000}{6 \times 22412000} = 0,005012.$$

SUMMARY

The quantum requirement in photosynthesis is defined as the number of quanta of radiant energy necessary for the decomposition of one carbon dioxide molecule. However, in an assimilating plant not the whole energy of the incident light I , or even the energy absorbed by the assimilating cells E_a but only the energy E_u that is really used in photosynthesis is relevant for the estimation of the quantum requirement R_q . The present paper is principally concerned with the calculation of E_u , because when it is known it can be expressed in terms of quanta and compared with the number of decomposed CO₂ molecules derived from the assimilation rate.

The argument is developed on a model formed by an algal suspension illuminated from below (manometric vessel). Owing to the decrease of the intensity of light pervading through the suspension, this suspension

can be divided in two layers. In the lower the light energy is supplied in excess, while in the upper it is the factor limiting the assimilation rate. On the level separating the two layers (transition level) the light intensity is I_t . In the lower layer, where light is in excess, only a part of the absorbed energy can be utilized for the reduction of carbon dioxide; on the contrary in the upper layer, with the light as the limiting factor, its total energy can (at least in principle) be used for assimilation purposes. The author shows, that the energy really used in photosynthesis by the whole suspension is $E_u = E_t (1 + \lg \text{nat } I/I_t - e^{-kd})$, where k is the absorption constant of the suspension and d its thickness. It is further shown that the above expression can be reduced to the form $E_u = I_t \cdot pF$ in which p is a constant, the value of which can be calculated from the experimental data, provided that a sufficient number of simultaneous determinations of the light intensity I and the assimilation rate F is at hand. E_u expressed in quanta takes the form $E_u = \lambda f_1 \cdot I_t pF$, where λ is the wave length of the incident light and f_1 a factor, the value of which depends on the units used to measure I and F . Once E_u is expressed in quanta the formula for R_q is easily found as follows: by multiplying the assimilation rate by a convenient factor f_2 the number of decomposed CO_2 molecules is calculated: $f_2 \times F$. The ratio

$$R_q = \frac{E_u}{f_2 F} = \frac{\lambda f_1 \cdot I_t p F}{f_2 F} = \lambda f \cdot I_t p \quad (f = f_1/f_2)$$

gives the quantum requirement.

The first section of the paper ends with some additional formulas for the estimation of the energy yield in photosynthesis. In the second section on a few examples drawn from the papers of E. K. Gabrielsen, O. Warburg, E. C. Wassink and J. A. H. Kersten the application of the method in question is illustrated. In the appendix the numerical values of some factors appearing in the formulas of the text are calculated.

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