POTENTIAL PHOTOSYNTHESIS OF CROP SURFACES ¹)

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SUMMARY

A formula is arrived at for the calculation of the photosynthesis of a closed crop surface, it being assumed that the leaves of a crop surface are arranged without any preference as to direction, and that the photosynthesis curve of single leaves may be represented by a simple "BLACKMAN" curve.

The course of photosynthesis during the day is calculated by means of this formula. The potential photosynthesis of a crop surface in the Netherlands appears to vary from about 290 kg CH_2O ha^{-1} day^{-1} in June to about 50 kg ha^{-1} day^{-1} in December.

Actual photosynthesis is lower because dissimilation has to be subtracted a closed crop surface assimilating at its full leaf capacity is not obtained in many cases, translocation of sugars may be a limiting factor, and the carbon dioxide content of the atmosphere may be less than the normal 0.03 %.

INTRODUCTION

The relation between the photosynthesis rate of leaves and the light intensity at *normal carbon dioxide concentrations of the air* (0.03 %) has been determined by several investigators (THOMAS and HILL, 1950; BOEHNIG and BURNSIDE, 1956; GAASTRA, 1958). The present author (DE WIT, 1958) has collected evidence to show that within the normal temperature range this relation is largely unaffected by temperature and is substantially the same for several agricultural crops. The photosynthesis of a crop surface depends not only on the photosynthesis curve of the leaves but also on the position of the leaves with respect to the direction of the incident light, the direct and diffuse light intensity, the mutual shading of the leaves, the soil coverage and the carbon dioxide content of the atmosphere.

When estimating the photosynthesis of crop surfaces it is sometimes assumed that such a surface consists of several layers of horizontally arranged leaves, or that the light of the sun is evenly distributed over the foliage of the crop surface (GAASTRA, 1958). The photosynthesis of crop surfaces is underestimated in the first and overestimated in the second case.

The present author based certain calculations on the hypothesis that the leaves of a crop surface are so arranged that there is no preference as to direction. Some results of these calculations were given in a previous paper (DE WIT, 1958). MAKKINK (1959, in press) compared these results of calculations with actual yield data and showed that the present method was a good basis for comparing yield data. The basic hypothesis, mathematical treatment and some results relating to the Netherlands are given here.

THE PHOTOSYNTHESIS CURVE

The relation between the photosynthesis rate of a sugar beet leaf and the incident light intensity as determined by GAASTRA (1958) is shown by curve a

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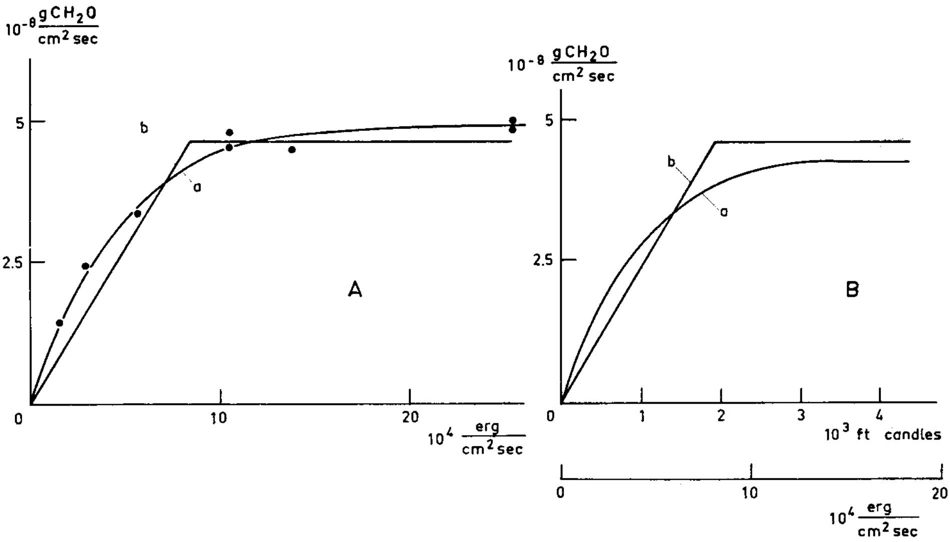

FIG. 1 THE RELATION BETWEEN PHOTOSYNTHESIS IN LEAVES AND THE INCIDENT LIGHT INTENSITY.
A : Sugar beet leaves (GAASTRA, 1958).
B : Average for leaves of castor bean, sunflower, soybean, tomato, tobacco, cotton and bean (BOEHNIG and BURNSIDE, 1956).

in figure 1 A. The photosynthesis rate is expressed in g CH_2O cm^{-2} sec^{-1} and the light intensity in erg cm^{-2} sec^{-1} within the range 400–700 m μ. The average relation between the photosynthesis rate of seven agricultural and horticultural crops and the incident light intensity of Mazda electric flood lamps as determined by BOEHNIG and BURNSIDE (1956) is shown by curve a in figure 1 B. The photosynthesis rate is again expressed in g CH_2O cm^{-2} sec^{-1} and the light intensity in foot-candles ; an auxiliary scale gives the estimated light intensity in erg cm^{-2} sec^{-1}. The photosynthesis rates in figure 1 B are corrected for dissimilation which was found to be about 15% of the saturation value. The original article showed that the photosynthesis of the individual species does not differ by more than 15% of the saturation value on either side of the average curve.

GAASTRA's data are also smoothed in figure 1 A by the expressly simplified curve b (a BLACKMAN curve) consisting of two straight lines ; the same curve is shown in figure 1 B in order to demonstrate that the photosynthesis as determined by GAASTRA on one hand and BOEHNIG and BURNSIDE on the other do not greatly differ.

The saturation rate is found to be $4.7 \cdot 10^{-8}$ g CH_2O cm^{-2} sec^{-1} and is reached at an incident light intensity of $8.5 \cdot 10^4$ erg cm^{-2} sec^{-1} or an absorbed light intensity of about $7 \cdot 10^4$ erg cm^{-2} sec^{-1}. Hence inside the range in which light is a limiting factor, $\frac{4.7 \cdot 10^{-8}}{7 \cdot 10^4} = 6.7 \cdot 10^{-13}$ g CH_2O is formed for each erg absorbed by the leaf inside the range 400–700 m μ.

The above simplified relation between photosynthesis and light intensity is used in this paper as a standard photosynthesis curve of leaves. It is appreciated that there are plant species, e.g. "shade plants", for which the photosynthesis curve differs so greatly from this standard curve that any numerical calculations based thereon are of no value. The mathematical treatment is, however, presented in such a way that similar calculations can be made using other curves as a basis.

ESTIMATING POTENTIAL PHOTOSYNTHESIS

Besides the photosynthesis curve of single leaves, the photosynthesis of crop surfaces depends on the position of the leaves with respect to the horizontal surface, the position of the sun, the amount of cloud and the carbon dioxide content of the atmosphere.

Assuming the photosynthesis curve of single leaves to be as in figure 1, curve b, it is possible to estimate the portion of incoming light which is neither reflected nor absorbed by leaves already at their saturation light intensity. This portion is represented by the symbol r and expressed in erg cm^{-2} sec^{-1}. To obtain the potential assimilation rate in g CH_2O cm^{-2} sec^{-1} of a closed crop surface, represented by the symbol a_p |, the value of r in erg cm^{-2} sec^{-1} should be multiplied by the value $6.7 \cdot 10^{-13}$ g CH_2O erg^{-1}, i.e. the gradient of the straight line through the origin in figure 1.

Actual assimilation is always lower than this potential assimilation because dissimilation has to be subtracted. Moreover, under field conditions a part of the light may be absorbed by the bare soil or by leaves which owing to water shortage, low mineral level, subnormal carbon dioxide concentrations, age, etc., are unable to assimilate at their normal rate.

The intensity of the direct sunlight, diffuse skylight and the sum of both are denoted by the symbols h_s , h_d and h respectively. These values are again expressed in erg cm^{-2} sec^{-1}; only the light energy inside the range 400–700 mμ is considered. The values of h_s , h_d , h, r and a_p integrated over the whole day are denoted by the capitals H_s , H_d , H, R, and A_p and expressed in erg cm^{-2} day^{-1}, respectively kg CH_2O ha^{-1} day^{-1}.

In order to simplify the calculations required for estimating r the following assumptions are made:

a A saturation value h_l exists of the absorbed light intensity. Below this value assimilation is assumed to be proportionate to the absorbed light intensity and above this value independent of the light intensity (figure 1, curve b).

b The reflection coefficient (ϱ) and the transmission coefficient (τ) of the leaves are independent of the direction of the incoming light. In subsequent calculations both are assumed to be equal to 0.1 (cf. MOSS and LOOMIS, 1952).

c There is no preferred direction in the arrangement of the leaves. This hypothesis is possibly not very wide of the mark, considering the constantly changing position of the sun and leaf fluttering due to wind. At any rate it is a great improvement on the hypothesis that a crop surface consists of horizontally arranged leaves, or that the light is evenly distributed over the whole leaf surface.

d The crop surface is so dense that only a negligible amount of light reaches the soil. This is the definition of a closed crop surface used in this paper.

At first it is also assumed that there is only direct light from the sun, i.e. that $h_d = 0$. Let $h_s^{(p)}$ be the light intensity from the sun measured at right-angles to the rays of the sun, β the height of the sun above the horizon, O the leaf surface per unit soil surface directly exposed to the rays of the sun, and α the angle between a particular leaf and the rays of the sun.

The projection of O in the direction of the rays of the sun is then

$$\int_{0}^{\pi/2} \frac{O}{\pi/2} \sin \alpha \, \mathrm{d}\, \alpha = \frac{O}{\pi/2}$$

and on the other hand equal to the projection of the unit soil surface in the direction of the rays of the sun, or $\sin \beta$ times the unit soil, surface, so that

$$O = \frac{\pi}{2} \sin \beta$$

Hence the surface of the directly exposed leaves making an angle of between α and $\alpha + \mathrm{d}\,\alpha$ with the rays of the sun is $\sin \beta \, \mathrm{d}\, \alpha$ and the projection of this surface in the direction of the rays of the sun $\sin \beta \sin \alpha \, \mathrm{d}\, \alpha$.

Leaves for which α is between $\pi/2$ and $\arcsin \dfrac{h_l}{(1-\varrho-\tau)\, h_s^{(p)}} = \arcsin s'$ (with $s' = \dfrac{h_l}{(1-\varrho-\tau)\, h_s^{(p)}}$) are saturated with light. The portion of light absorbed by these leaves is

$$(1-\varrho-\tau)\, h_s^{(p)} \int_{\alpha = \arcsin s'}^{\pi/2} \sin \beta \sin \alpha \, \mathrm{d}\, \alpha = (1-\varrho-\tau)\, h_s^{(p)} \sin \beta \sqrt{1-s'^{\,2}} \qquad (1)$$

The portion of this light contributing to assimilation is

$$h_l \int_{\alpha = \arcsin s'}^{\pi/2} \sin \beta \, \mathrm{d}\, \alpha = h_l \sin \beta \left(\frac{\pi}{2} - \arcsin s'\right) \qquad (2)$$

The portion of light absorbed by these saturated leaves but not contributing to assimilation is the difference between (2) and (1).

Apart from reflection, all other radiation is either absorbed by leaves exposed to direct sunlight but not saturated with light, or by leaves in the shade of other leaves. Since h_l is about $7 \cdot 10^4$, $h_s^{(p)}$ not more than $46 \cdot 10^4$ erg cm^{-2} sec^{-1} and the transmission coefficient (τ) below $7/46 = 0.15$ for the leaves of most plant species, these shaded leaves are never saturated with light.

The light intensity r' contributing to assimilation is therefore

$$r' = (1-\varrho)\, h_s^{(p)} \sin \beta - \left\{(1-\varrho-\tau)\, h_s^{(p)} \sin \beta \sqrt{1-s'^{\,2}} - h_l \sin \beta \left(\frac{\pi}{2} - \arcsin s'\right)\right\}$$

and since $h_s^{(p)} = \dfrac{h_s}{\sin \beta}$ and $h_l = (1-\varrho-\tau)\, h_s^{(p)} s'$

$$r' = (1- \quad)\, h_s \left\{ 1 - (1-\tau) \left[\sqrt{1-s'^{\,2}} - s' \left(\frac{\pi}{2} - \arcsin s'\right)\right]\right\} \qquad (3)$$

with $$s' = \frac{h_l \sin \beta}{(1-\varrho-\tau)\, h_s}$$

The diffuse radiation is not taken into account in the above treatment. The intensity of diffuse skylight measured on a horizontal surface is below $7 \cdot 10^4$ erg cm^{-2} sec^{-1} and, except for reflection, this light contributes fully to assimilation under conditions in which direct light is absent.

The contribution of direct sunlight may now be superimposed on the contribution of diffuse skylight. The light intensity r contributing to assimilation in the presence of diffuse skylight is found to be with some approximation:

$$r \simeq (1-\varrho)\,\left(h_d + h_s \left\{ 1 - (1-\tau)\, \left[\sqrt{1-s^2} - s\left(\frac{\pi}{2} - \arcsin s\right)\right]\right\}\right) \quad (4)$$

with $$s = \frac{h_l - \frac{2}{\pi}(1-\varrho-\tau)\, h_d \sin \beta}{(1-\varrho-\tau)\, h_s}$$

The fraction $\frac{2}{\pi}(1-\varrho-\tau)\, h_d$ in s is due to the received diffuse light; the factor $2/\pi$ is due to the assumption that the diffuse light is evenly distributed over a leaf surface which is equal to the surface visible from a vertical direction. The potential assimilation a_p in g CH_2O cm^{-2} sec^{-1} may now be calculated by multiplying the above value of r, expressed in erg cm^{-2} sec^{-1} by the constant $6.7 \cdot 10^{-13}$ g CH_2O erg^{-1}.

POTENTIAL PHOTOSYNTHESIS ON PERFECTLY CLEAR DAYS

Table 1 shows the light intensity of the sun on days without clouds and dust and with only 10 mm precipitable water in the atmosphere. The data are found by means of tables 137 and 149 of the METEOROLOGICAL TABLES (1951), assuming 40% of the energy to be inside the range 400–700 mμ. The index c of h indicates that these values only apply to days with perfectly clear skies. The fractions h_s and h_d in the table are estimated by means of table 819 of the PHYSICAL TABLES (1956). Values of r_c (c again denoting perfectly clear skies), calculated by means of formula (4) and the assumptions that

Table 1 Intensity of total (h_c), direct (h_s) and diffuse light (h_d) inside the range 400-700 mμ on a perfectly clear day at different heights of the sun (β degrees) and the value of r_c calculated from equation (4), expressed in 10^5 erg cm^{-2} sec^{-1}.

β °	h_c	h_s	h_d	r_c
10	0.70	0.39	0.31	0.45
20	1.42	1.06	0.36	0.70
30	2.16	1.74	0.42	0.92
40	2.86	2.39	0.47	1.12
50	3.48	2.95	0.53	1.26
60	3.97	3.41	0.56	1.37
70	4.34	3.76	0.58	1.46
80	4.53	3.92	0.61	1.48
90	4.58	3.97	0.61	1.48

$h_l = 7 \cdot 10^4$ erg cm^{-2} sec^{-1}, $\varrho = 0.1$ and $\tau = 0.1$, are also given.

The values of h_c and r_c during the course of the day on, for instance, 1st June in latitude 52° N (the Netherlands) are estimated as follows. The height of the sun at each full hour is obtained from table 170 of the METEOROLOGICAL TABLES (1951) or a similar nomogram. The values of h_c and r_c are then read from graphs with the height of the sun along the horizontal axis and h_c or r_c along the vertical axis (table 1) and plotted against the time of the day as in figure 2. In this figure the scales of h_c and r_c are such that the maximum noon values are the same.

It is found that there is no value of h_c beyond which r_c does not increase with increasing h_c. Such a value cannot exist because the portion of leaves of a plant cover exposed to direct sunlight increases with increasing height of the sun. In the case of single plants, the portion of leaves exposed to direct sunlight is much less dependent on the height of the sun. Hence the curve of r_c against time of the day is found to be much flatter for single plants than for crop covers. This striking difference was found experimentally (cf. DE WIT, 1958).

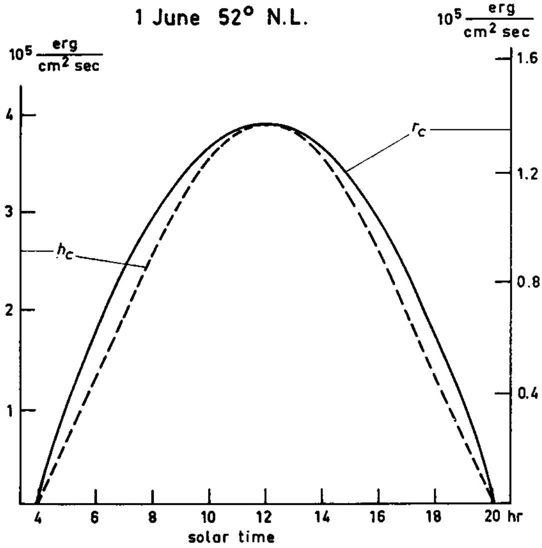

Fig. 2 Values of h_c and r_c on a perfectly clear day on 1st June at latitude 52°.

Curves similar to those in figure 2 were calculated for the first of each month at latitude 52° and then numerically integrated. The integrated values, H_c and R_c, are expressed in erg cm^{-2} day^{-1}.

The relation between H_c and the time of the year is shown in figure 3 A, and that between R_c and the time of the year in figure 3 B. Both curves relate to perfectly clear days and therefore represent the maximum values to be found.

REESINCK and DE VRIES (1942) calculated from radiation measurements the total daily radiation to be found on days on which the relative sunshine percentage, as measured by the CAMPBELL-STOKES recorder, is 100 percent. The maximum daily amount of light (Q) as calculated from their data is shown

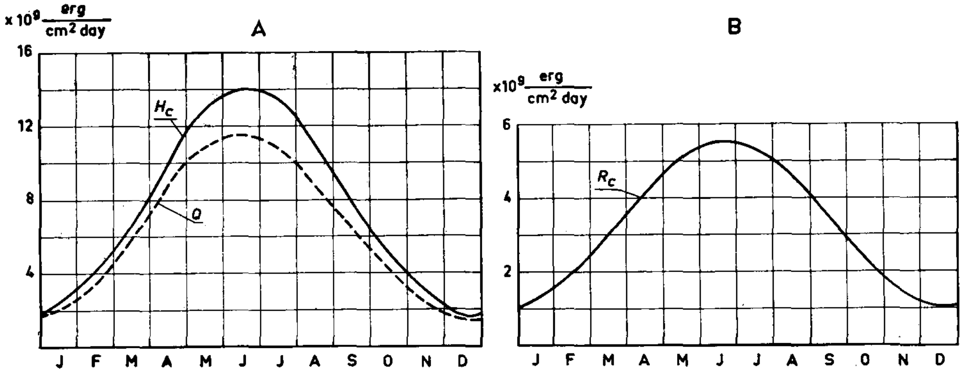

FIG. 3 VALUES OF H_c (FIGURE A) AND R_c (FIGURE B) DURING THE COURSE OF THE YEAR AT LATITUDE 52°.
Q is the daily light total in the Netherlands provided the relative sunshine percentage is 100 percent.

by the dotted curve in figure 3 A and in the Netherlands is found to be about 15% lower than the maximum to be expected on perfectly clear days (no dust, no transparent clouds, etc.).

The potential photosynthesis on a perfectly clear day in June is apparently $5.5 \cdot 10^9$ erg $cm^{-2} sec^{-1} \times 6.7 \cdot 10^{-13}$ g CH_2O $erg^{-1} \times 10^8$ cm^2 $ha^{-1} \times 10^{-3}$ kg $g^{-1} = 370$ kg CH_2O ha^{-1} day^{-1} and on a perfectly clear day in December 67 kg ha^{-1} day^{-1}.

THE INFLUENCE OF CLOUDS

To account for the effect of clouds it is assumed that where the daily total of light is reduced to $x\ H_c$ (x less than one), H_d (the diffuse light) remains the same but direct light is reduced to $H_s - (1 - x)\ H_c$. This is certainly not the case with overcast skies, but under such conditions the value of s in equation (4) is close to one and any assumption will do.

By substituting actual values in equation (4) it is found that irrespective of date and latitude below 60° the relation between H and R is fairly well represented by curve a in figure 4 which shows the relation between H and R expressed as fractions of H_c and R_c . However, this estimate of R on cloudy days tends to be too high owing to the use of light intensity values integrated over one day or more.

Another assumption is that periods of bright sunshine alternate with periods of overcast skies. During the bright periods the average light intensity is about 0.85 times the intensity with perfectly clear skies, and during the periods with overcast skies about $0.3 \times 0.85 = 0.25$ times the intensity with perfectly clear skies (cf. REESINCK and DE VRIES (1942) for the numerical value 0.3). On this assumption the relation between $H\ H_c^{\ -1}$ and $R\ R_c^{\ -1}$ is represented by the straight line b inside the range $0.25 < H\ H_c^{\ -1} < 0.85$.

It will be readily understood that the actual relation between the relative values of H and R lies inside the range defined by curves a and b ; it is assumed to be represented by the average curve c in figure 4.

The value of R is now calculated as follows. We can see from figure 3 A

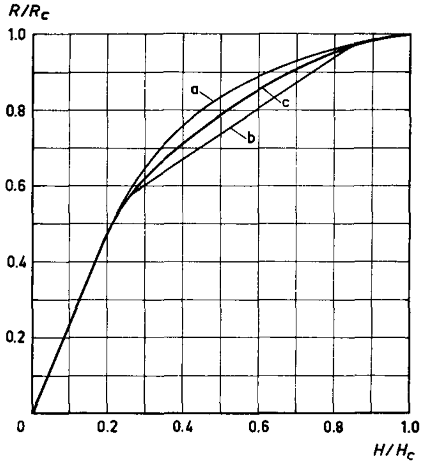

FIG. 4 THE RELATION BETWEEN H AND R, BOTH EXPRESSED AS RELATIVE VALUES WITH RESPECT TO H_c AND R_c ; CURVE c REPRESENTS THE BEST APPROXIMATION.

that on 21st June $H_c = 14 \cdot 10^9$ erg cm^{-2} sec^{-1}. The value of $H\ H_c^{\ -1}$ is 0.5 when the actual light total is $7 \cdot 10^9$ erg cm^{-2} day^{-1}. We can now see from figure 4 that $R\ R_c^{\ -1}$ is 0.78, so that, when $R_c = 5.5 \cdot 10^9$ erg cm^{-2} day^{-1} (figure 3 B), R is found to be $0.78 \times 5.5 \cdot 10^9 = 4.3 \cdot 10^9$ erg cm^{-2} day^{-1}.

THE AVERAGE POTENTIAL PHOTOSYNTHESIS (A_p) IN THE NETHERLANDS

The daily light total, averaged over the years 1943—1953 (DE VRIES, 1955) is shown in the first column of table 2. The average value of R calculated by means of these data and those in figures 3 and 4 are shown in the second column. The potential photosynthesis A_p in the third column is calculated by multiplying the value of R by $6.7 \cdot 10^{-13}$ g CH_2O erg^{-1}. It was found that the average potential photosynthesis varied from 50 kg CH_2O ha^{-1} day^{-1} in December to 290 kg ha^{-1} day^{-1} in June.

Table 2 The daily light total (H) averaged over the years 1943—1953, the value of (R) and the potential photosynthesis (A_p) in the Netherlands.

	H	R	A_p
	in 10^9 erg	cm^{-2} day^{-1}	kg CH_2O ha^{-1} day^{-1}
Jan.	0.85	0.75	54
Feb.	1.64	1.29	86
March	3.17	2.12	142
April	5.23	3.17	212
May	6.53	3.85	258
June	7.30	4.33	290
July	6.46	4.12	276
Aug.	6.15	3.91	262
Sept.	4.01	2.93	196
Oct.	2.42	2.00	134
Nov.	0.99	0.90	72
Dec.	0.68	0.60	50

This potential photosynthesis is the photosynthesis which may be reached by a closed green crop cover with healthy leaves not short of water under such conditions that translocation of sugars is not a limiting factor and the carbondioxyde concentration of the air is normal. Moreover, dissimilation should be subtracted in order to obtain the apparent photosynthesis. It was nevertheless found (MAKKINK, 1959 in press) that under favourable conditions actual photosynthesis is close to the potential photosynthesis as calculated in this paper.

The potential photosynthesis from April to September inclusive is 44.8 tons per hectare, so that subtracting 20 percent for dissimilation, the maximum possible production during this period is about 36 tons per hectare. This is much more than the maximum seasonal grass production of about 15 tons per hectare reached at present. The present maximum production is probably so much lower than potential production owing to water shortage, the fact that practical management methods do not ensure a closed green crop surface, throughout the season and the carbon dioxide concentration of the atmosphere may be lower than 0.03%. Field and greenhouse experiments are in progress in order to obtain yields which are as close as possible to potential production.

Potential photosynthesis is found to be appreciable higher in the spring than in the autumn. This agrees with the experience in greenhouses that plants grow much better in the spring than in the autumn.

Calculations similar to those given in this paper may be carried out for other latitudes and countries. A nomogram with values of H_c and R_c at different dates and latitudes has been published in another paper (DE WIT, 1958). The values in this nomogram are expressed in cal cm^{-2} day^{-1} and include infrared radiation. They should be multiplied by $1.67 \cdot 10^7$ erg cal^{-1} to obtain the light total in erg cm^{-2} day^{-1} inside the range 400–700 μ.

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