581.132

MEDEDELINGEN VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN/NEDERLAND
58 (4), 1-12 (1958)

LIGHT ENERGY CONVERSION IN FIELD CROPS IN COMPARISON WITH THE PHOTOSYNTHETIC EFFICIENCY UNDER LABORATORY CONDITIONS

by

P. GAASTRA

Laboratory of Plant Physiological Research, Agricultural University, Wageningen, Netherlands, 180th Communication; 64th Communication on Photosynthesis

(*Received 7.7.'58*)

1. INTRODUCTION

Photosynthesis is one of the important processes, governing the production of agricultural crops. Up to now, rather little and in many cases conflicting information is available on quantitative aspects of the photosynthetic process in crop plants, *e.g.* regarding differences in the photosynthetic activity in different species or in different varieties of the same species. Such data may be important in connection with plant selection, for the estimation of CO_2, light and temperature requirements in glasshouse culture, and for considerations regarding the optimum production capacity of crop plants.

The main reason why we do not yet have an abundance of such data is of technical nature. The study of photosynthesis in higher plants is much more difficult than that using suspensions of micro-organisms.

During the last years we have built an equipment enabling a thorough study of several factors involved in higher plant photosynthesis. Our apparatus allows the simultaneous recording of the rate of photosynthesis, the transpiration rate and the leaf temperature of intact plants as well as of a leaf, attached to the plant. The light intensity, the CO_2-concentration, the leaf temperature, and the humidity of the air can be varied over a wide range.

Some questions we are considering and on which we have collected a number of data with our apparatus are the following: The situation of the compensation point; the efficiency of light energy conversion in the light limiting range; the light intensity at which saturation is reached and the photosynthetic rate at saturating intensities; the influence of the CO_2-concentration and of the leaf temperature upon the photosynthetic rate; the effect of age and of stomatal aperture; the phenomenon of the "midday-depression"; the relation between transpiration and photosynthesis.

A complete description of the technique employed and of the results obtained so far will be dealt with in a forthcoming, extensive publication.

Photosynthesis curves obtained so far with our technique, moreover, provide a basis for the interpretation of data on solar energy conversion in field crops, derived from harvest data and simultaneous records of incident solar radiation. The present paper gives an example of such a case for beets. The underlying harvest data were published by BOONSTRA (2). Records of solar radiation, also obtained at Wageningen, are available for the greater part of the experimental period (22). Data on photosynthesis have been derived from detailed photosynthesis curves as obtained with the apparatus mentioned above.

2. STATEMENT OF THE PROBLEM

In the photosynthetic process part of the absorbed light energy is converted into the chemical energy of carbohydrates. Schematically:

$$CO_2 + H_2O + \text{light} \rightarrow (CH_2O) + O_2 \qquad (1),$$

$$x \quad \rightarrow \quad y \qquad + z \qquad (1a),$$

in which x, y and z symbolize the light energy absorbed, the chemical energy of the carbohydrates formed and the light energy not utilized in photosynthesis, respectively. The efficiency of the light energy conversion (ε) is represented by the ratio y/x.

One can also consider efficiency values based upon the incident light energy and/or upon the apparent photosynthetic rate (no correction for respiratory activity being applied) instead of the true photosynthetic rate. In order to distinguish between the various possibilities, the following notations will be used:

$$\varepsilon_{true/a}, \quad \varepsilon_{true/i}, \quad \varepsilon_{app/a}, \quad \varepsilon_{app/i}, \qquad (2)$$

where the suffixes "true" and "app" refer to true and apparent photosynthetic rates, "a" and "i" to absorbed and incident light energy, respectively.

The efficiency of light utilization can also be expressed by the quantum yield Φ:

$$\Phi = \frac{\text{Moles converted}}{\text{Einsteins absorbed}} \qquad (3)$$

We will consider Φ only in connection with true photosynthesis and absorbed light, hence no suffixes will be used for this symbol.

For a given wave length, λ, the relationship between Φ and $\varepsilon_{true/a}$ is given by

$$\varepsilon_{true/a,\,\lambda} = \Phi_\lambda \cdot \frac{\Delta H}{Nhc/\lambda} \qquad (4)$$

where

ΔH = heat of combustion of 1 mole CH_2O (4.7×10^{12} ergs);
Nhc/λ = energy content (ergs) of 1 Einstein at wave length λ;
N = AVOGADRO's number (6.03×10^{23});
h = PLANCK's constant (6.60×10^{-27} ergs sec);
c = velocity of light (3×10^{10} cm sec^{-1});
λ = wave length (cm).

Expressing the energy content of 1 Einstein in cal, (4) becomes

$$\varepsilon_{true/a,\,\lambda} = \frac{\Phi_\lambda \cdot 112000}{2.85\,/\,\lambda} \qquad (4a)$$

Most work on quantum yield is done with unicellular algae; most workers in this field have obtained maximum values of Φ between 0.125 and 0.1. (*cf.* reviews on this subject *e.g.* by RABINOWITCH (12, 13), DANIELS (3), and KOK (5).

With higher plants only few experiments are available in which measurements of the photosynthetic rate are combined with measurements of light absorption by the same plant material (WASSINK, 19). Besides, for a number of leaf types, reliable and mutually well corresponding spectral absorption curves have been determined by SEYBOLD und WEISSWEILER (14, 15), RABIDEAU, FRENCH and HOLT (11), and MOSS and LOOMIS (8). GABRIELSEN (4) and the present author (*cf.* section 3) estimated Φ by combining those data with their curves of photosynthetic rate *versus* incident light intensity.

For most plants, WASSINK (19) found maximum quantum yields between 0.1 and 0.05. For *Sinapis alba, Corylus maxima* and *Fraxinus excelsior*, GABRIELSEN obtained Φ values of 0.076, 0,072 and 0.076 respectively. Also in the experiments of the author Φ values of the same order of magnitude were obtained (section 3).

From these experiments it seems safe to assume that maximum quantum yields also for higher plants are in the order of 0.1. Assuming the quantum efficiency to be constant over the range of 400–700 mμ, according to formula 4a the energy efficiency, $\varepsilon_{\text{true/a}}$, for $\Phi = 0.1$ is 15.7 and 27.5 % respectively for the extreme wave lengths. For non-monochromatic light sources the ε values are intermediate.

It is of interest to compare the maximum photosynthetic efficiency with the efficiency of light energy conversion of growing plants as calculated from the caloric value of the organic matter produced. In literature some data are available for the entire growing season of field crops. The caloric value of the organic matter produced per unit of cultivated area is compared with the irradiated light energy on the same area during the same period. No measurements of respiratory activity being available, the values obtained represent $\varepsilon_{\text{app/i}}$. Most values of $\varepsilon_{\text{app/i}}$ are between 1 and 2 % (400–700 mμ), *cf.* PÜTTER (10) as commented by RABINOWITCH (12), TRANSEAU (18), WASSINK (20), BERNARD (1).

It is to be expected *a priori* that these values should be lower than the maximum true photosynthetic efficiencies, because of the following reasons, from which 1–3 refer to the individual plants and 4 is especially inhaerent to field conditions:

1. Incident energy instead of absorbed energy is considered and no correction for respiratory losses is made.
2. Some leaves may be less active, due to age effects, stomatal closure, *etc.*
3. The incident light intensity to which part of the leaves are exposed, may represent light saturation or nearly so.
4. During part of the growing season the soil surface is not completely covered by the crop.

The surprisingly large difference between the maximum value of $\varepsilon_{\text{true/a}}$ of the photosynthetic process proper and $\varepsilon_{\text{app/i}}$ as calculated from the production of a field crop, (20 % and 1 to 2 %), induced us to analize the energy efficiencies of field crops in somewhat greater detail.

3. ESTIMATION OF THE MAXIMUM QUANTUM YIELD AND ENERGY EFFICIENCY IN SUNLIGHT IN SUGAR BEET LEAVES, BASED UPON DIRECT MEASUREMENTS OF THE PHOTOSYNTHETIC RATE

A curve representing the rate of photosynthesis against the incident light intensity on a sugar beet leaf (variety Kuhn P) is given in figure 1. (Leaf temperature 20°C; 0.03 % CO_2; relative humidity 80 %; light source: high pressure mercury lamps Philips HO–450W). From an intensity of 1.7×10^4 ergs sec^{-1} cm^{-2} upwards the slope of the curve decreases steadily until light saturation is reached.

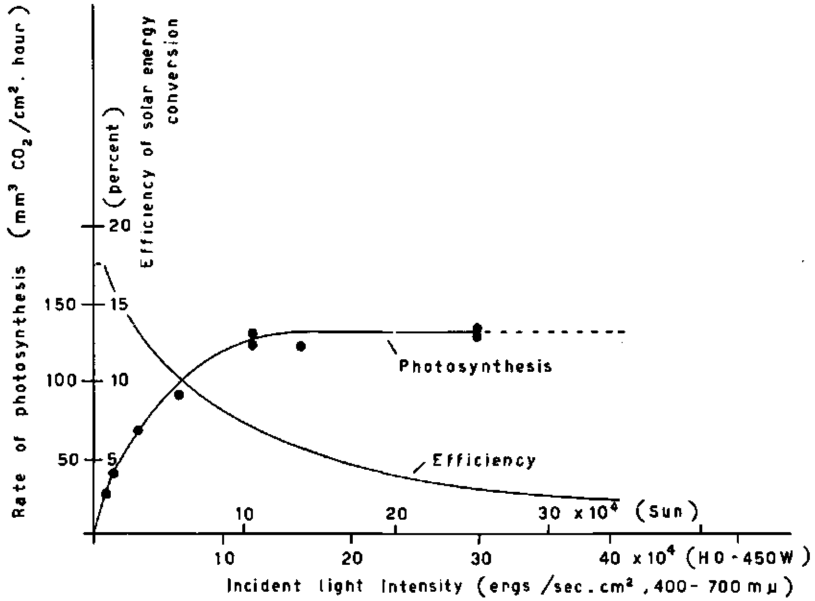

FIG. 1. (*a*) Rate of photosynthesis in a leaf of sugar beet, var. Kuhn P, measured with a mercury lamp (Philips HO-450W) as a light source, and calculated for sunlight. (*b*) Efficiency of solar energy conversion. (20 °C; 0.03 % CO_2; rel. humidity 80 %).

For the calculation of the maximum quantum yield Φ, the number of Einsteins absorbed has to be estimated. For this purpose the emission spectrum of the light source between 400 and 700 mμ as well as the absorption spectrum of the leaf in the same spectral region should be known. Data on the emission spectrum of the light source are supplied by the manufacturer. Furthermore, we have assumed that the mean absorption curve for leaves of four crop plants (bean, spinach, Swiss chard, tobacco) as given by MOSS and LOOMIS (8) is valid for sugar beet leaves.

At the incident intensity E_λ, the number of Einsteins absorbed is:

$$E_\lambda \cdot a_\lambda \;/\; Nhc/\lambda \qquad (5)$$

in which E_λ = incident energy (ergs sec^{-1} cm^{-2}) and a_λ = the absorbed fraction of the incident light at wave length λ ($O \leqslant a \leqslant 1$), while N, h, c, and λ have the same meaning as in formula 4.

The continuous emission spectrum of the mercury lamp used is negligible, hence λ stands for each wave length of the mercury lines. For the spectral region 400–700 mμ the ratio $R_{mercury}$ (Einsteins absorbed/incident ergs) is calculated according to

$$R_{mercury} = \frac{\Sigma\,(E_\lambda \cdot a_\lambda \;/\; Nhc/\lambda)}{\Sigma\, E_\lambda} \qquad (6)$$

and amounts to 3.20×10^{-13}. The maximum quantum yield was calculated from the photosynthetic rate at an incident light intensity of 10^4 ergs sec^{-1} cm^{-2}. This rate amounts to 26 mm^3 CO_2 $cm^{-2}hour^{-1}$, corresponding to 3.22×10^{-10}

moles CO_2 cm^{-2} sec^{-1}. Hence $\Phi = \frac{3.22 \times 10^{-10}}{10^4 \times 3.20 \times 10^{-13}} = 0.10$, in good agreement with the data referred to above.

In connection with the calculation of the energy conversion by a field crop of sugar beet (*cf.* section 4), it is of interest to be informed on the approximate photosynthetic rate of a sugar beet leaf in sunlight. This rate can be derived from our curve in mercury light, assuming that the relationship photosynthetic rate/Einsteins absorbed is the same for both light sources in the spectral region 400–700 mμ (which may not be completely valid for several reasons).

Symbolizing the solar energy emission at any wavelength λ by E'_λ and applying MOON's spectral emission curve of the sun (7), the number of Einsteins absorbed per incident erg of sunlight (R_{sun}) is calculated according to formula 6, E'_λ and a_λ being mean values from 10 mμ intervals; R_{sun} thus calculated is 3.76×10^{-13}. The incident intensity in mercury light now can be converted into incident intensity in sunlight by multiplication with

$$\frac{R_{merc}}{R_{sun}} = \frac{3.20 \times 10^{-13}}{3.76 \times 10^{-13}} = 0.85$$

The result of this computation has been introduced into figure 1 as a conversion of the abscissa.

For our present purpose we want to be informed also about $\varepsilon_{true/i}$ at different intensities of sunlight which now can be easily derived from the data of figure 1. This relation is also given in figure 1. At increasing light intensities, before complete light saturation is reached, $\varepsilon_{true/i}$ decreases from 17.8 % until 7.4 %. At maximum sunlight (approximately 35×10^4 ergs sec^{-1} cm^{-2} between 400 and 700 mμ) $\varepsilon_{true/i}$ is 2.2 %. This value is of the same order of magnitude as the efficiency of energy conversion by field crops for the entire season. Since maximum sunlight in the Netherlands rarely obtains and, moreover, leaves may shade each other and thus be exposed to light intensities considerably below the maximum available, it is evident that higher efficiencies should be expected. This proves that, in field crops, other factors operate to depress the efficiency of light energy conversion. An analysis of the situation is attempted in the next section.

4. THE SOLAR ENERGY CONVERSION BY FIELD CROPS OF SUGAR AND FODDER BEETS DURING DIFFERENT PERIODS OF THE GROWING SEASON

An analysis of the energy conversion in a field crop should consider possible variation of this conversion during the season. In the beginning for instance, a particularly low value may be expected, owing to insufficient covering of the soil. Further analysis would require periodic harvests and the relative radiation data. On the basis of the considerations presented in the preceeding section, we have made an attempt in this direction by combining data on periodic harvests for sugar beet and fodder beet collected by BOONSTRA (2), with measurements of the daily solar irradiation by ZUIDHOF and DE VRIES (22). Both sets of data have been obtained at Wageningen.

Some of our results have been put at Professor THIMANN's disposal and have been communicated at the World Symposium on Applied Solar Energy at Phoenix, Arizona (18).

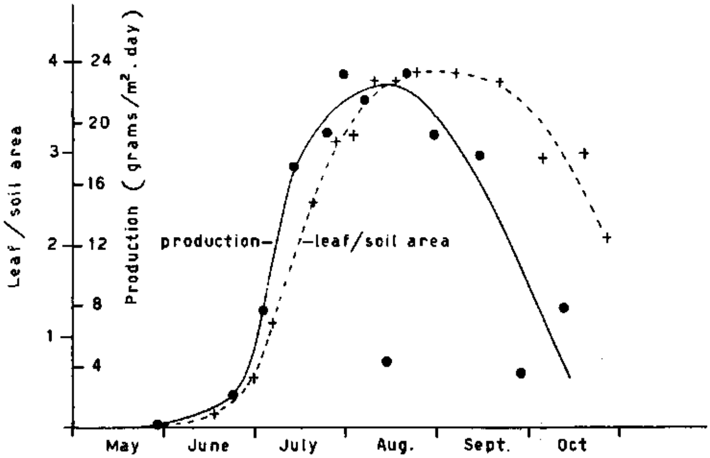

FIG. 2. Leaf/soil area ratio and organic matter production (grams/ m^2 soil · day) in a field crop of sugar beet. From data by BOONSTRA (2).

BOONSTRA used seven varieties of beets, *viz.* strain Z, Kuhn P, strain A, Friso, Eureka, Hautana, Productiva (in the order of decreasing dry matter content of the beet); all were sown on the 8th of May, 1937. The first harvest was made June 17. The following harvests were made every 7 or 14 days. An extensive analysis of plant growth was made by BOONSTRA, based upon many plant properties, determined at each harvest.

For our purpose, the organic matter content and the leaf area per plant are of interest. From the plant density, the production and mean leaf area per unit soil surface during every period is calculated. We suppose the organic matter in its average composition to correspond to carbohydrates, with a heat of combustion of 3700 cal/gram.

We have calculated the leaf/soil area ratio and the mean production of organic matter in grams per day and per m^2 soil area for each period. The data for Kuhn P are given in figure 2. It appears that in this case the leaf area equaled the soil area in the beginning of July. Maximum leaf area was reached in the beginning of August. The area ratio then amounted to 3.9. For the other varieties this ratio varied between 2.6 and 4.0. In May and June, the production of organic matter was very low. Corresponding with the strong increase in leaf area the production increased sharply in July. The decrease in production at the end of the season proceeded more quickly than the decrease in leaf area. The maximum production amounted to 23.2 grams per m^2 soil area per day. For the other varieties the maximum production was between 19 and 22 g m^{-2} day^{-1}.

The daily irradiance data (cal/day/horizontal cm^2) have been obtained by a recording thermopile galvanometer system. The original data include the infrared. We have assumed 40 % of the total radiation to belong to the region 400–700 $m\mu$. The actual day totals vary strongly within short periods. Hence the mean daily irradiance per experimental period is based upon strongly scattering values. Occasionally the mean daily irradiance deviated from the time trend to be expected, *e.g.* the irradiance was low at the end of July and the middle of August and high in the beginning of August. Unfortunately, no irradiance was measured after October 10, while the experiments lasted until the end of that month.

The calculated energy efficiencies $\varepsilon_{app/i}$ are presented in figure 3A. During the first two months the efficiencies were very low, due to poor covering of the soil surface. In the middle of the season the highest efficiencies were obtained, reaching maximum values between 7 and 9 %. At the end of September, the efficiencies again were lower.

On the basis of leaf development, dry matter production, and energy efficiency, the growing season may be divided into three main periods which lasted until July 7, September 21, and October 26, respectively. For these periods, as well as for the entire growing season, the figures for production and efficiency are compiled in table I. The mean energy efficiency during the period of 2.5 months in the middle of the season was between 5 and 6 % for several varieties. Between 80 and 90 % of the total organic matter was produced in this period, covering only 44.5 % of the total growing season. The production of organic matter per unit soil surface in this period was 9 to 16 times as high as that in the first period, and 2 to 9 times as high as that in the last one.

In figures 3A and 3B the data for the beet variety Kuhn P are compared with VAN OORSCHOT's data for *Chlorella* in mass cultures on a semi-technical scale, obtained at Wageningen in 1952 (9). It appears that in the middle of the season both the organic matter production and the efficiency of solar energy conversion for this beet crop are higher than those obtained with the algae. This result is especially remarkable, because the algae were supplied with excess CO_2, whereas the photosynthetic rate of the beets at high light intensities was certainly limited by insufficient CO_2-supply.

More recently, however, KOK and VAN OORSCHOT (6) have obtained higher yields in algal cultures, corresponding with yields recently obtained by other authors, *cf.* (16). Thus, the average daily production per unit area and the

TABLE I. Production and efficiency of energy conversion in beet crops under field conditions, during different periods of the season. (Data derived from BOONSTRA (2)).

I	II	III	IV	V	VI	VII	VIII	IX	X
	Period	Days	Varieties of beets						
			Z	Kuhn P	A	Friso	Eureka	Productiva	Hautana
Production (grams/period/ m² soil surface)	8/5–26/10	171	1215	1635	1515	1490	1560	1318	1182
	8/5– 7/7	60	68	76	66	73	72	91	76
	7/7–21/9	76	1092	1414	1294	1327	1163	1057	937
	21/9–26/10	35	55	145	155	90	325	170	169
Production per period per m² soil surface (relative values)	8/5–26/10	100	100	100	100	100	100	100	100
	8/5– 7/7	35.0	5.5	4.5	4.5	5.0	4.5	7.0	6.5
	7/7–21/9	44.5	90.0	86.5	85.5	89.0	75.0	80.0	79.0
	21/9–26/10	20.5	4.5	9.0	10.0	6.0	20.5	13.0	14.5
Production (grams/day/m² soil surface)	8/5–26/10	171	7.2	9.6	9.1	8.6	9.1	7.6	6.8
	8/5– 7/7	60	1.2	1.3	1.1	1.2	1.2	1.5	1.2
	7/7–21/9	76	14.1	18.3	17.4	17.2	15.0	13.7	12.2
	21/9–26/10	35	1.6	4.2	4.4	2.6	9.3	4.8	4.8
Energy efficiency (400–700 mμ) (%)	8/5– 7/7	60	0.29	0.32	0.28	0.30	0.30	0.37	0.31
	7/7–21/9	76	4.6	6.1	5.6	5.7	5.0	4.6	4.0

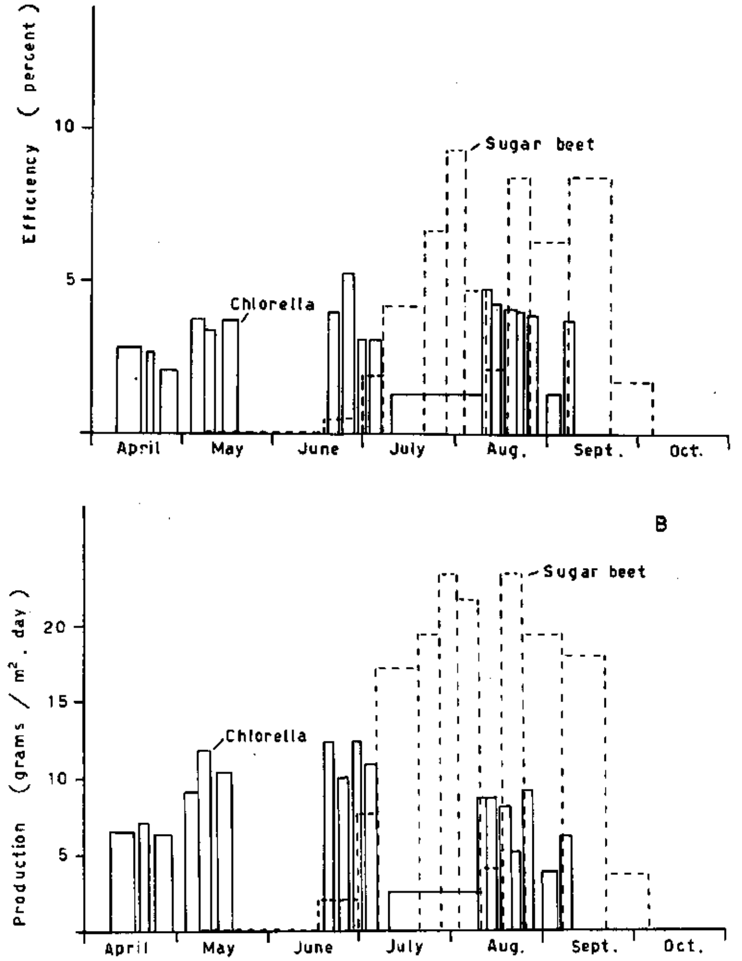

FIG. 3. A. Efficiency of solar energy conversion in a field crop of sugar beet and in mass-cultured algae (*Chlorella*).
B. Dry matter production (grams/m^2 · day) in a field crop of sugar beet and in mass-cultured algae.
Data for sugar beet (var. Kuhn P) calculated from data by BOONSTRA (2) and ZUIDHOF & DE VRIES (22), data for *Chlorella* taken from VAN OORSCHOT (9).

average efficiency of energy conversion in algae during the most favourable part of the year are of the same order of magnitude as in field crops of beets in the middle of the season. It seems, therefore, that, contrary to the opinion frequently expressed, higher plants may be as efficient solar energy converters as algae.

Another aim of algal culture, *viz.* better light utilisation during a longer period of the year may be reached also with higher plants, provided the leaf apparatus is well developed during the greater part of the season. Methods tending to such purpose are not uncommon in agricultural practice, *viz.* early sowing, sowing of a second crop under the first one, sowing of the second crop on a

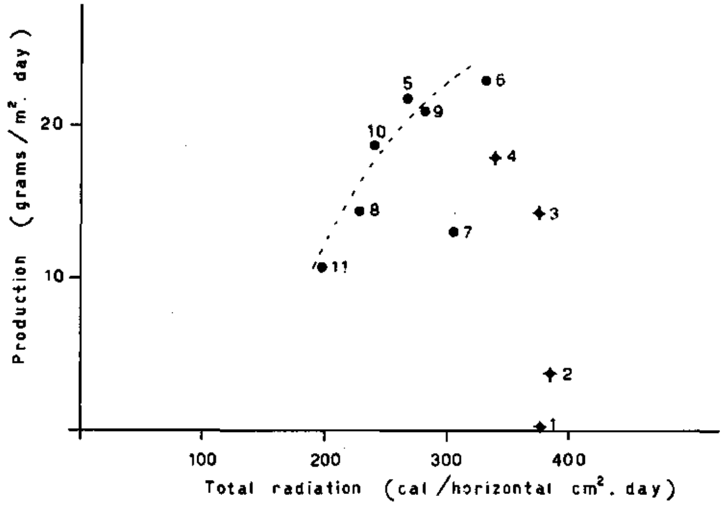

FIG. 4. Organic matter production (grams/m² · day) in a field crop of sugar beet, in relation with the daily irradiation (cal/day · cm², horizontal surface). From data by BOONSTRA (2) and ZUIDHOF & DE VRIES (22).

seperate seedbed and transplanting it to the field after the harvest of the first crop, *etc.*

Although higher plants appear to be as efficient in the production of total dry matter as algae, the latter seem to offer greater possibilities with respect to the production of proteins and the production of a high percentage of utilizable organic matter. Perhaps these aims may be reached with higher plants also, by the introduction of new crops, or by selection.

In figure 4 the mean daily irradiance is plotted against the daily organic matter production of Kuhn P. In order to eliminate the influence of sampling errors, the production and the irradiation values of two successive periods have been averaged. Thus, in the figure the mean of the first and second period is represented by point number 1, *etc.* The relative values of the efficiencies of light energy conversion are expressed by the slopes of straight lines connecting the origin with each separate point. For points 1, 2, 3, and 4 (indicated by +) the efficiencies are low, owing to the insufficient covering of the soil surface. Once the soil is covered there is a trend of increasing production and increasing efficiency of light energy conversion with increasing irradiance. This relationship need not be a direct one, since irradiance and temperature are closely linked while, moreover, age effects may interfere. The latter may act by changes of the activity of the photosynthetic apparatus, but also by the increase with age of photosynthetically inactive tissues as compared with the amount of leaf tissues, thus enhancing respiratory losses. In BOONSTRA's data *e.g.* the dry matter content of the entire plant per gram dry matter of leaves, increased from 3.1 (g/g) in the beginning of July until 16.0 at the end of October.

Field experiments of the type under discussion do not allow an analysis of the influence of separate factors (*cf.* WATSON (21)). However, an impression may be gained about the actual photosynthetic activity of leaves under field conditions in comparison with the optimum rate as measured under laboratory conditions. We feel sure that in our experiments (*cf.* figure 1) optimum photosynthetic rates are well approached (high maximum quantum efficiency and high rate at light saturation). In order to compare the rate under field conditions with the optimum rate, the actual incident intensity and the uptake of CO_2 per cm^2 leaf surface and per unit time of irradiation should be estimated. The latter can be derived from the daily organic production, assuming the organic matter to be represented by carbohydrates. The estimation of the incident intensity is complicated, because different leaves are exposed to different intensities while, moreover, the intensity incident on a leaf changes during the day. For our calculation we will make the simplifying assumption of an equal distribution of the incident radiation over the leaves and during the light period.

The outcome of this calculation is presented in table II. The mean incident intensities for the successive periods (column I) are given in column II. In column III, the calculated mean apparent photosynthetic rates of Kuhn P under field conditions are given. If we estimate the daily respiration of the entire plant to be 20 % of the apparent rate of photosynthesis, we arrive at the true rates under field conditions as given in column IV. The optimum rates as obtained for Kuhn P in the laboratory experiment at the computed average light intensities are given in column V. The ratio (column VI) of the true rate under field conditions over the optimum rate was about 0.60 in most cases.

It has to be taken into account that this value is to be considered as a minimum since our simplified assumption of equal distribution of the incident light energy over the leaves and during the day is not strictly valid. In reality, several leaves will be under light saturation during part of the day, while the average light intensity computed as discussed above, is well below light saturation in most cases. The values of column V are those of our laboratory experiment, observed at the mean light intensities. They are, therefore, higher than those that would have been obtained in the laboratory experiment if, *e.g.*, fractions of the leaf had been exposed to various light intensities corresponding to those actually incident in the various leaves in the field crop.

TABLE II. Photosynthetic rates in sugar beet leaves, derived from production data in a field crop, as compared with optimum rates, based upon actually measured rates under laboratory conditions.

I	II	III	IV	V	VI
Period	Mean irradiance per leaf ergs sec^{-1} cm^{-2} (400–700 mμ)	Mean photos. rate, field conditions (mm^3 CO_2/cm^2 leaf/hour)		Optimum photos. rate, laboratory conditions (mm^3 CO_2/cm^2 leaf/hour)	Relative photos. rate under field conditions $\left\{\frac{(IV)}{(V)}\right\}$
		apparent	true (estimated)		
6/7–20/7	6.00×10^4	49.5	59.5	102	0.58
20/7–27/7	2.86×10^4	32.0	38.5	67	0.57
27/7– 3/8	2.30×10^4	34.5	41.5	57	0.72
3/8–10/8	3.70×10^4	29.4	35.5	78	0.46
10/8–17/8	1.53×10^4	5.6	6.8	41	0.17
17/8–24/8	2.37×10^4	31.5	38.0	58	0.65
24/8– 7/9	2.55×10^4	26.8	32.3	60	0.54
7/9–21/9	1.95×10^4	27.3	32.8	50	0.65

Occasionally, severe depressions of the photosynthetic rate occur, *cf.* in the period 3/8–17/8, probably due to a decrease of the photosynthetic activity of the leaf.

5. SUMMARY

1. An equipment has been built enabling the simultaneous recording of the rate of photosynthesis, the transpiration rate and the leaf temperature at a widely varying range of light intensities, CO_2-concentrations, leaf temperatures and air humidities.

2. For leaves of sugar beet, the relation between the incident light intensity and the rate of photosynthesis has been determined with this technique. The maximum quantum yield was found to be 0.10.

3. In these experiments, the efficiency of solar energy conversion in sugar beet leaves varies between 17.6 % at low light intensities and 2.2 % at full sunlight (considering the spectral region 400–700 mμ).

4. Combining published data on the production of organic matter in field crops of beets, and on solar irradiance, shows that the efficiency of these crops reaches 7–9 % in the middle of the season (considering the spectral region 400–700 mμ).

5. The analysis, moreover, shows that between 80 and 90 % of the total organic matter was produced in only 44.5 % of the growing season. During this part of the season (2.5 months) beets are at least as efficient in solar energy conversion as mass-cultured algae.

6. Comparison of the estimated photosynthetic rates in sugar beet leaves under field conditions with the actually measured optimum rates at comparable intensities under laboratory conditions, revealed that the photosynthetic rate in the field crop was at least 60 % of the optimum rate during a great part of the season. This value has to be considered as a minimum, because some simplifying assumptions lead to overestimate the optimum rate at the actual light intensities.

7. Occasionally, very low photosynthetic rates occur, most probably due to a decrease in the photosynthetic activity of the leaf.

ACKNOWLEDGEMENT

This work is being sponsored by the Organization for Applied Scientific Research (T.N.O.). The work is carried out under the direction of Professor E. C. WASSINK whom I wish to thank for initiating the problem and for his continued interest.

REFERENCES

1. BERNARD, E. A., Public. Inst. National pour l'Étude Agronomique du Congo Belge (INEAC), Série scientifique No. 68 (1956).
2. BOONSTRA, A. E. H. R., Meded. Inst. Suikerbietenteelt **12**, 13–95 (1942).
3. DANIELS, F., In: Radiation Biology, Vol. III (Ed.: A. Hollaender), New York (1956).
4. GABRIELSEN, E. K., Experientia **3**, 439–442 (1947).
5. KOK, B., In: Handbuch der Pflanzenphysiologie, Band V (Ed.: W. Ruhland), Berlin (1958, in press).
6. KOK, B. and J. L. P. VAN OORSCHOT, Acta Botanica Neerl. **3**, 533–546 (1954).
7. MOON, P., J. Franklin Inst. **230**, 583–617 (1940).
8. MOSS, R. A. and W. E. LOOMIS, Plant Physiol. **27**, 370–391 (1952).
9. OORSCHOT, J. L. P. VAN, Meded. Landbouwhogeschool Wageningen **55**, 225–276 (1955).
10. PÜTTER, A., Naturwiss. **2**, 169–174 (1914).
11. RABIDEAU, G. S., C. S. FRENCH and A. S. HOLT, Am. J. Bot. **33**, 769–777 (1946).

12. RABINOWITCH, E. I., Photosynthesis and related processes. Vol. II, Part 1. New York. 600–1208 (1951).
13. RABINOWITCH, E. I., Photosynthesis and related processes. Vol. II, Part 2. New York. 1209–2088 (1956).
14. SEYBOLD, A. und A. WEISSWEILER, Botan. Archiv **43**, 252–290 (1942).
15. SEYBOLD, A. und A. WEISSWEILER, Botan. Archiv **44**, 102–153 (1943).
16. TAMIYA, H., Ann. Rev. Plant Physiol. **8**, 309–334 (1957).
17. THIMANN, K. V., In: Proc. World Symp. on Applied Solar Energy. Phoenix, Arizona, p. 255–259 (1955).
18. TRANSEAU, E. N., Ohio J. Science **26**, 1–10 (1926).
19. WASSINK, E. C., Enzymol. **12**, 33–55 (1946).
20. WASSINK, E. C., Meded. Dir. Tuinb. **11**, 503–513 (1948).
21. WATSON, D. J., Adv. Agronomy **4**, 101–145 (1952).
22. ZUIDHOF, G. and D. A. DE VRIES, Meded. Landbouwhogeschool Wageningen **44**, 3–18 (1940).