Actual and potential production of agricultural crops[1]

TH. ALBERDA

Institute of Biological and Chemical Research on Field Crops and Herbage, Wageningen, Netherlands

Summary

The upper level of dry-matter production of a crop is determined by the photosynthetic efficiency of its green surface.
In evergreen and tropical forests a closed green surface may be present throughout the year but for other crops there is usually a period in which such a closed green crop surface is not present and, consequently, a part of the incoming light energy is absorbed by the soil.
Solar energy-conversion values of around 2 per cent, often found in older literature, were derived from calculations on growth periods from emergence up to harvest and, therefore, include periods without a closed green crop surface. Such calculations cannot give an insight into the photosynthetic capacity of the green tissue of these crops, nor can they be used in comparing different crops.
It is better, therefore, to estimate photosynthetic efficiency during periods in which no light energy is reaching the soil. Recent experiments, in which a grass and a sugar-beet crop were provided with ample supplies of water and nutrients, have given efficiency values ranging between 5 and 6 per cent of the incoming light energy (calsulated for wave lengths between 400 and 700 m μ).
These values are in fairly close agreement with the calculated potential production rates of a closed green crop surface. In agricultural practice it is not likely that higher efficiency values can be reached. Attention should, therefore, be focussed on extending the period during which a closed green crop surface is present.

1. Introduction

The dry-matter production of a crop is the result of the net photosynthesis of the individual plants and once the photosynthetic efficiency of a green leaf has been estimated it is possible to calculate the upper level of potential crop production. In the following article some calculations of potential production will be compared with figures for actual production without a complete survey of the literature on this point being attempted. In this respect the reader is referred to a recent article in the *Annual Review of Plant Physiology* (TALLING, 1961).
It has been assumed (VAN DER PAAUW, 1956) that factors like carbon dioxide concentration, light intensity and temperature do not contribute very much to yield fluctuations in agricultural practice, these being in fact more or less determined by other factors, such as mineral nutrition and water supply.
To go somewhat further into this matter, I should like to compare two identical plants one of which has an ample supply of water and nutrients, while the other

[1] Lecture held at the course "Fundamentals of dry-matter production and distribution" organized by the Royal Netherlands Society for Agricultural Sciences, Wageningen, 9th January, 1962.

has a somewhat suboptimal nitrogen supply. Such a shortage of nitrogen does not alter the photosynthetic capacity of the green tissue (unpublished data), but simply changes the distribution of dry matter in such a way that the plant with the suboptimal nitrogen supply makes relatively less leaf tissue than the other one, which results in a lower growth rate. At the same time it can be assumed that the leaves of both plants shade each other in such a way that under the given light conditions some leaves receive a light intensity above saturation point, whereas other leaves lie distinctly below it. Consequently, the rate of dry-matter production of the plant with the suboptimal nitrogen supply can simultaneously be increased by:

1. a better nitrogen supply, since this will increase the leaf area,
2. a higher light intensity, since it will increase the rate of photosynthesis of the leaves below saturation point,
3. a higher carbon dioxide concentration, since it will increase the rate of photosynthesis of the leaves above saturation point.

Besides these three factors there are, of course, other external factors which influence dry-matter production, like temperature and water supply. The example is only given to show that the growth rate of a plant is the result of processes influencing dry-matter production and distribution and that, even if growth is limited by a deficiency in minerals or water, radiation, temperature and carbon dioxide concentration can still influence production.

2. Radiation as a determining factor

If actual and potential production are to be compared the supply of water and minerals should be at an optimal level. Of the remaining factors temperature is not supposed to have a distinct influence on the rate of photosynthesis, except at the beginning and the end of the growing season (DE WIT, 1958) and the carbon dioxide concentration is thought to be 300 ppm everywhere in the crop. These conditions will therefore be regarded as representing the optimum in practice (although strictly speaking carbon dioxide is still partly limiting) and dry-matter production can be considered to be determined by the incoming radiation.

The production of a crop is usually expressed per unit area. Under optimal conditions this production will be determined by the amount of light energy[1] that is absorbed by the plants in this area. If all incoming light energy is either absorbed or reflected by fully green plant tissue, so that no light reaches the soil, one may speak of a closed crop surface (DE WIT, 1959).

Such a closed crop surface is not, however, always present during the whole growth period which in an annual crop can be divided into three phases. At the beginning (phase 1, FIG. 1 A) a considerable portion of the incoming light is absorbed by the soil. This portion decreases gradually and is zero when a closed crop surface is reached (phase 2). At the end of the growth period, when maturity begins, the leaves turn yellow, the photosynthetic capacity is reduced and thus the definition of a closed crop surface no longer holds (phase 3).

With a perennial fodder crop which can be grazed or mown the kind of situation illustrated in FIG. 1 B arises. After mowing or grazing usually so much of the assimilating tissue is taken away that a part of the incoming radiation reaches the soil.

[1] In this paper light energy means the visible light energy, *i.e.* between 400 and 700 mμ amounting to 40 per cent of the total short-wave radiation of the sun.

Thereafter the closed crop surface is gradually restored until the grass is cut for the second time.

It is only in sylviculture (evergreen forest or tropical forest) that a closed crop surface is present throughout the year (FIG. 1 C).

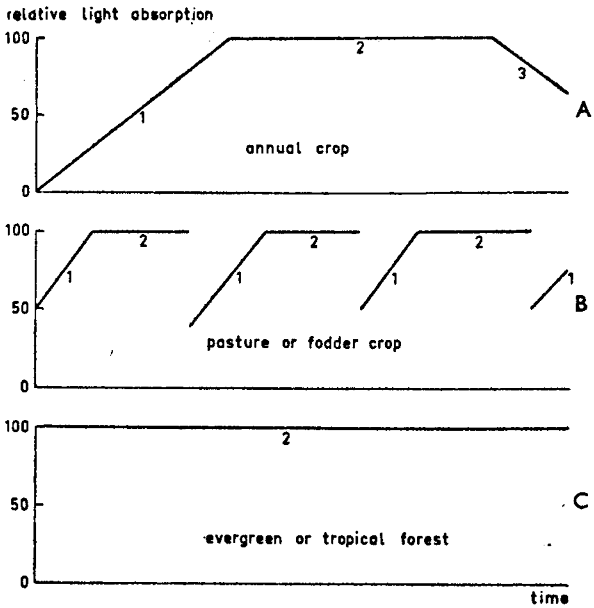

FIG. 1
Schematic representation of growth stages in different kinds of crop

1. Stage in which part of the incoming light energy reaches the soil
2. Stage of closed green crop surface
3. Stage of senescence (leaf discoloration or leaf dropping)

In calculating the light-energy utilization of a crop the whole growth period from sowing to harvest has often been taken into consideration. This does not make much sense, since the values thus obtained are not characteristic for the photosynthetic capacity of the green tissue of the given crop, but include also the light energy that is absorbed by the soil instead of by the plant. In small scale experiments it may be possible to determine the leaf area, but then it is difficult to decide which part of the total area has been active in photosynthesis. Therefore, in comparing the light utilization of a given crop with the utilization of a separate leaf of the same crop below the saturation value, or alternatively, the utilization of different crops it is better to take a period of growth when a closed crop surface is present.

Attempts to calculate the potential production of such a closed crop surface have been made by DE WIT (1959). Using the relationship between light intensity and rate of photosynthesis of leaves of crop plants given by GAASTRA, DE WIT calculated a mean efficiency value for light intensities below saturation point. In this range of light intensities a quantity of $6{,}7 \times 10^{-13}$ g dry matter is formed for each erg absorbed and when no leaves are irradiated with a light intensity above the saturation value, the dry-matter production of a closed crop surface can easily be calculated by multiplying the incoming radiation by this factor. However, in most cases a part of the leaves will absorb light above saturation point, *i.e.* light which is not efficient in photosynthesis. By assuming that the leaves adopt no specific position in relation to the sun, DE WIT was able to calculate the portion of the incoming light that is absorbed above the saturation level for a given altitude of

the sun. With the aid of the diagrams in his publication it is possible to calculate the potential dry-matter production during a given time when the incoming light energy is known. The data in TABLE 1 represent the daily growth rates as a mean for each month, calculated by DE WIT from ten years mean light-energy data for the Netherlands (column 1). Column 3 of the same table gives the corresponding photosynthetic efficiencies as a percentage of the incoming radiation. Both kinds of figures are based on true assimilation. To compare these values with real growth rates, they have to be corrected for dissimilation. DE WIT assumes a correction of 20 per cent of the true assimilation rate.
The growth rates and efficiency values corrected in this way are given in the columns 2 and 4 of TABLE 1.

TABLE 1. True and apparent potential photosynthesis (20 % dissimilation) and its efficiency, calculated from data of DE WIT, *Neth. J. agric. Sci.* 7 (1959), 148

Months	Potential photosynthesis ($kg\ CH_2O\ ha^{-1}.\ day^{-1}$)		Efficiency of photosynthesis (%)	
	true	apparent	true	apparent
Jan.	50	40	9,1	7,3
Febr.	86	69	8,1	6,5
March	142	114	6,9	5,6
April	212	170	6,3	5,0
May	258	206	6,1	4,9
June	290	232	6,2	4,9
July	276	221	6,6	5,3
Aug.	262	210	6,6	5,3
Sep.	196	157	7,6	6,1
Oct.	134	107	8,6	6,9
Nov.	60	48	9,4	7,5
Dec.	40	32	9,1	7,3

TABLE 2 refers to some data on actual total dry-matter production of several crops collected by WASSINK (1948), together with the efficiency values calculated by him. A comparison with the efficiency figures for the potential production during the same growth periods shows that the latter is around 4 to 5 times higher. That the low values given by WASSINK are indeed a result of the fact that the light energy

TABLE 2. Dry-matter production and light-efficiency values for several agricultural crops (after WASSINK, *Meded. Dir. Tuinb. 11* (1948), 509)

Crop	Vegetation period	Total yield ($tons\ ha^{-1}$)	Actual efficiency (%)	Potential efficiency (%)
Potatoes	April—Sep.	9,60	1,23	5,2
Winter wheat	Nov.—Aug.	10,45	1,26	5,3
Sugar beet	May—Oct.	16,00	2,2	5,3
Fodder beet	May—Oct.	16,00	2,2	5,3
Swedes	May—Oct.	11,00	1,5	5,3
Carrots	May—Oct.	6,86	0,94	5,3
Chicory	May—Oct.	9,00	1,32	5,3
Turnips	Aug.—Nov.	3,60	1,24	5,9

falling on the soil is included, is apparent from data given by GAASTRA (1958), who showed — using figures for the rate of dry-matter production of sugar beet — that the efficiency during the period before a closed crop surface was reached is only around 0,30—0,40 per cent, whereas thereafter values between 4 and 6 per cent could be calculated.

The light-efficiency figures given by WASSINK will also tend to lie below the potential value on account of the fact that it is usually rather difficult to estimate the actual total dry-matter production of a crop. Parts of the root system and older leaves may easily get lost at harvest, not to mention the possibility that leaves may have been shed before that time. Perhaps this may explain why the highest efficiency values were found for sugar beet, where losses in harvest are expected to be small. The values calculated by GAASTRA for a closed sugarbeet crop surface are quite in line with the potential values.

3. Results of experiments carried out by the author

In the following section the results of two experiments will be discussed; one involving sugar beet (hitherto unpublished) and one on grass (ALBERDA and DE WIT, 1961; ALBERDA and SIBMA, 1962). With grass a closed crop surface can be present during the greater part of the growing season, but it is difficult to measure the total dry-weight increment during a given period, and for this reason only above-ground growth was determined. With sugar beet it is relatively easy to obtain the total dry weight but the period during which a closed crop surface is present is rather short.

In both experiments harvests were taken every ten days and the rate of dry-matter production was calculated for each ten days period. For sugar beet the data for five successive harvests during the period when a closed crop surface was present is given in TABLE 3, together with the potential values, based on 20 per cent respiration. There was a close agreement between actual and potential production. The light-energy utilization figure over the whole period was 5,6 per cent, and was thus of the same magnitude as that obtained by GAASTRA (1958) for a comparable growth period.

TABLE 3. Rate of dry-matter production in kg $ha^{-1} . day^{-1}$ of a sugar beet crop during 4 successive growth periods as compared with the calculated potential production

Period	1	2	3	4
Growth rate of sugar beet	219	193	196	186
Potential growth rate	196	201	206	210

The experiment with grass was performed in order to compare actual and potential production over the whole growing season. To this end a grass field was divided into several plots. In early spring one of these plots was fertilized in order to start a rapid growth as soon as weather conditions would permit it. When a closed crop surface was reached the daily growth rate was established for each ten day period by mowing a strip of the plot. The second plot was similarly started off when the first was well under way and here again the first harvest was taken as soon as a closed crop surface was established. In 1960 four plots were taken without scarcely any overlapping of data; in 1961 there were six plots with much more overlapping. For the sake of clarity the design for 1961 is given in TABLE 4. Before a plot was used the grass only received a very low nitrogen dressing and was frequently cut without removing the cut grass. By this "lawn treatment" a very dense sward could be established until the experiment proper. The experimental field was sprinkled with water when necessary and the mineral nutrition was checked by regular analysis. In this way the growth rate could be calculated as a mean for each ten day period throughout the growing season.

TABLE 4. Schematic representation of the mowing dates for the six different plots

Plots					
1	2	3	4	5	6
10-IV	1-V	20-V	10-VI	1-VII	20-VII
20-IV	10-V	1-VI	20-VI	10-VII	1-VIII
1-V	20-V	10-VI	1-VII	20-VII	10-VIII
10-V	1-VI	20-VI	10-VII	1-VIII	20-VIII
20-V	10-VI	1-VII	20-VII	10-VIII	1-IX
1-VI	20-VI	10-VII	1-VIII	20-VIII	10-IX
10-VI	1-VII	20-VII	10-VIII	1-IX	20-IX

The results for both years are given in FIG. 2. Except for the first plot in 1960, the growth rate was highest when the grass was short; it tended to decrease as the sward became taller and at the end of a 70 day growth period it was usually around zero. The same pattern of growth was found by DAVIDSON and DONALD (1958), who assumed that as the length of the grass increased the proportion of photosynthetic to non-photosynthetic tissue decreased, causing the rate of growth to fall. It may in fact be reasonably presumed that at the end of the growth period of each plot the rates of net assimilation and dissimilation are of the same order of magnitude. For cut grass values have been found for losses in dry weight during 24 hours, which are of a magnitude comparable to assimilation figures for that period (DEIJS and HARBERTS, 1949).

After a correction for the fluctuations in growth rate the maximum grass growth values for each ten days period were multiplied with a factor 1,67, assuming that the leaf production is 60 per cent of the total dry-matter production. In FIG. 3 the actual growth rate for both seasons thus obtained is compared with the potential values. The fluctuations in both curves show an unmistakable correlation which proves that the rate of dry-matter production is principally determined by the incoming radiation.

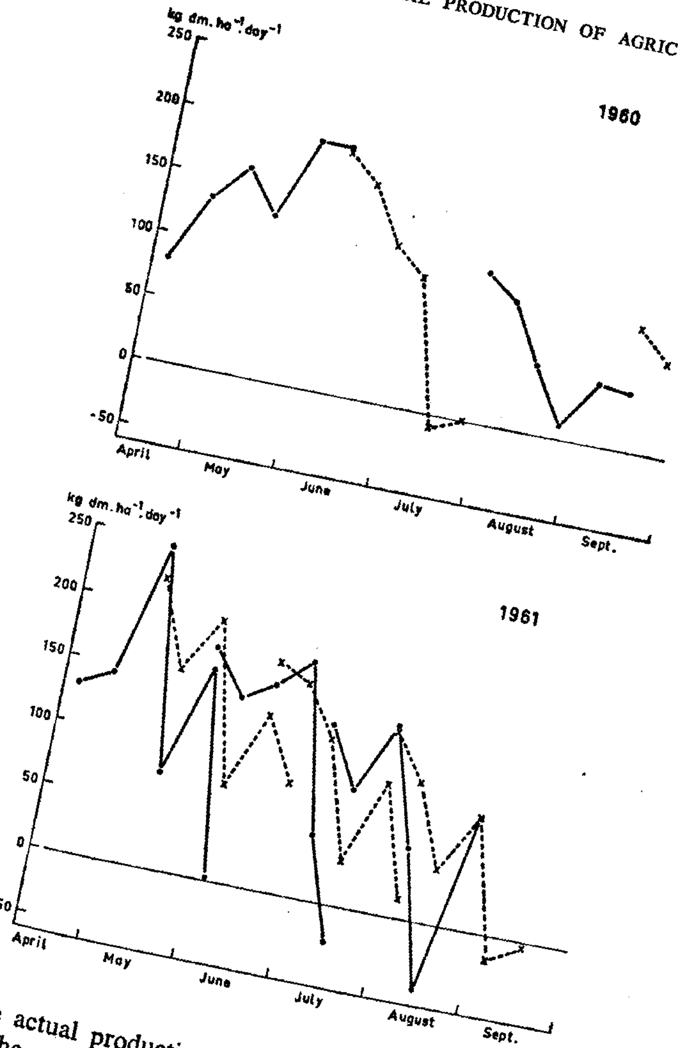

FIG. 2
Leaf-growth rates of the different plots during 1960 and 1961
Solid lines: plots 1, 3 and 5
Broken lines: plots 2, 4 and 6

The actual production in both years shows the same general trend. In the first half of the growing season the actual growth rate was around or even above the potential rate. After June, however, the actual rate dropped below the potential, the difference gradually increasing in the course of the season. Up to now a reasonable explanation has not been found for this gradual reduction in growth rate. It is known that the carbohydrate reserves in grass increase during the winter to reach very high values early in the spring. However, this large amount of carbohydrates is only sufficient for one or two days of growth at the observed rates and certainly cannot account for the differences in growth rate between the beginning and the end of the growing season.

That the actual production was higher than the potential value is not of much significance. In the first place leaf production was assumed to be 60 per cent of the total dry-matter production, a value which has been derived from a great number of experiments with nutrient solution, but which may be incorrect under field conditions. In the second place the potential production as calculated by DE WIT is an

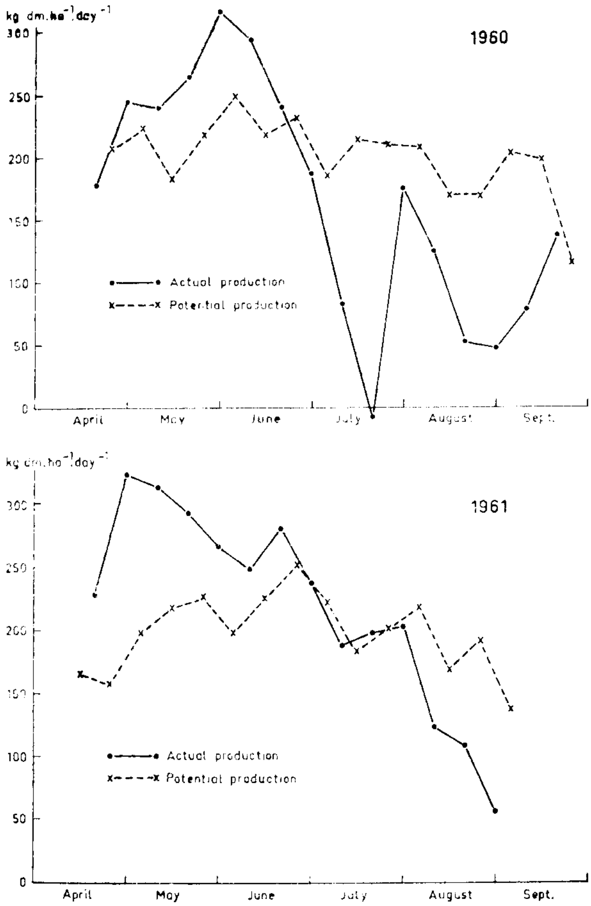

FIG. 3
Actual and potential growth rates during 1960 and 1961; in calculating the potential growth rate a dissimilation rate of 20 % has been used

approximate value and not a maximum value which cannot be surpassed. For the period with these high growth rates a light-energy utilization between 6 and 7 per cent could be calculated. For the herbage production between 10 April and 1 June the value calculated was only 4 per cent.

4. Conclusions

Taking everything into account it can be stated that light utilization values obtained recently for several agricultural crops have tended to lie between 5 and 6 per cent of the incoming light energy provided that growing conditions were optimal and a closed green crop surface was present. This value is about the same as that calculated by DE WIT for the spring and summer months. With grass it has been shown that the increasing bulk of tissue not taking part in the process of photosynthesis diminishes the rate of dry-matter production. There is a slight indication that this was also the case with sugar beet (TABLE 3).

As it is not likely that a higher efficiency value can be reached in agricultural practice, an attempt should be made to keep the closed green-surface stage as long as possible. In this respect the effect of a late nitrogen supply on the leaf discoloration of small grain crops should be mentioned (VAN DOBBEN, 1959). Furthermore, attention should be given to the rates of dissimilation under field conditions, values of which given in the literature are not only rather scanty but vary enormously.

ACKNOWLEDGEMENTS

The author is very much indebted to Miss ALISON G. DAVIES, Welsh Plant Breeding Station, Aberystwyth, for correcting the text.

REFERENCES

ALBERDA, TH., and C. T. DE WIT 1961 Dry matter production and light interception of crop surfaces. Uninterrupted growth of a grass sward. *Jaarb. I.B.S. 1961*, 37—44.

ALBERDA, TH., and L. SIBMA 1962 Dry matter production and light interception of crop surfaces II. Relation between rate of growth and length of grass. *Jaarb. I.B.S. 1962*, 47—58.

DAVIDSON, J. L., and C. M. DONALD 1958 The growth of swards of subterranian clover with particular reference to leaf area. *Australian J. Agric. Res. 9*, 53—72.

DEIJS, W. B., and C. L. HARBERTS 1949 Ademhaling van afgesneden gras. *Verslag C.I.L.O. 1949*, 130—134.

DOBBEN, W. H. VAN 1959 Enige waarnemingen over de stikstofhuishouding van tarwe en maanzaad. *Jaarb. I.B.S. 1959*, 93—105.

GAASTRA, P. 1958 Light energy conversion in field crops in comparison with the photosynthetic efficiency under laboratory conditions. *Meded. Landb.hogesch. Wageningen. 58* (4), 1—12.

PAAUW, F. VAN DER 1956 De plaats van de fotosynthese in het produktieproces. *Landbouwk. Tijdschr. 68*, 635—646.

TALLING, J. F. 1961 Photosynthesis under natural conditions. *Ann. Rev. Plant Physiol. 12*, 133—154.

WASSINK, E. C. 1948 De lichtfactor in de photosynthese en zijn relatie tot andere milieufactoren. *Meded. Dir. Tuinb. 11*, 503—513.

WIT, C. T. DE 1958 Transpiration and crop yields. *Versl. Landb. Onderz.* No. 64.6, 88 pp.

—— 1959 Potential photosynthesis of crop surfaces. *Neth. J. agric. Sci. 7*, 141—149.