Th. Alberda et al.

Centre for Agrobiological Research (CABO), Wageningen

Crop photosynthesis:
methods and compilation of data
obtained with a mobile field equipment

136576

Abstract

Preliminary measurements of the daily course of photosynthesis, respir-
ation and transpiration of a number of crops are presented in relation to
some factors influencing these processes. After a description of the
measuring equipment the influence of age and postion of leaves in a grass
sward is studied as well as that of nitrogen fertilization. Next a short
description of the basic crop simulator (BACROS) is given together with meas-
ured rates of photosynthesis, respiration and transpiration of a maize crop
with varying temperature and CO_2 concentrations. With wheat photosynthesis
is studied in the post-flowering stage to measure the effect of ageing with
and without the prevention of fungal diseases. The effect of some growth re-
tardents was studied with potatoes, flax and sugar beet and finally late
autumn photosynthesis was measured with three varieties of stubble turnips.

Free descriptors: photosynthesis, respiration, transpiration, measuring
equipment, crop growth simulation, leaf age, leaf position, leaf temperature,
crop structure, fungicides, growth retardants, nitrogen fertilization, grass,
maize, wheat, potatoes, flax, sugar beet, stubble turnips

Contents

1. Centre for Agrobiological Research (CABO), Wageningen
2. Department of Theoretical Production Ecology, Agricultural University,
Wageningen
3. Foundation for Agricultural Plant Breeding 'De Haaff' (SVP), Wageningen.

1 Introduction

Th. Alberda

Laboratory equipment for measuring net photosynthesis, respiration and transpiration of separate leaves and individual plants has been in use for several years.

A similar piece of equipment has been constructed as a mobile unit for measurements on closed crops growing in the field. This mobile equipment has been in use for four consecutive years, but only a small part of the data obtained so far has been published, mainly because additional information is needed before the problem can be solved.

As this kind of equipment is rare and the demand for data on photosynthetic performance of crops rather large, it was decided to publish the data obtained so far in a rather condensed form. For each crop examined a short description of the objective and the lay-out of the experiment is given, followed by the photosynthesis data obtained under the prevailing situations. When there is doubt whether the data are reliable, comment is made.

2 Methods

W. Louwerse

2.1 LABORATORY EQUIPMENT

Separate leaves and individual plants are put into specially constructed plant chambers to measure net photosynthesis and respiration. These plant chambers are part of an open system; to determine photosynthesis and respiration, the uptake or relase of carbon dioxide by the plants is measured by infrared gas analysis. Transpiration is determined by measuring the humidity of the air with thermocouple psychrometers. Measurements can be made over a wide range of experimental conditions. CO_2 concentrations in the plant chamber of 0-2000 cm^3/m^3 are obtained by mixing fixed quantitites of CO_2-free air and pure carbon dioxide. Temperature can be controlled between 10 and 40 $^{\circ}C$ by regulating the surrounding room temperature and by using specially constructed plant chambers.

The humidity in the plant chamber can be controlled between 30-100 % RH. The radiation intensity is varied with perforated metal screens between the lamps and the plant chamber. The maximum radiation intensity is 2.0 J cm^{-2} min^{-1} (400-700 nm).

For more details see Louwerse & van Oorschot (1969).

2.2 FIELD EQUIPMENT

The mobile equipment can be used for measurements on crops growing in the field. A fixed area of the crop is enclosed. Net photosynthesis and respiration are determined in an open system by measuring the CO_2 concentration of the ingoing and outgoing air of the enclosure by infrared gas analysis. Transpiration is determined by measuring the humidity of the ingoing and outgoing air by LiCl sensors and by collecting the water, condensed on the cooling body, in a rain gauge. The temperature in the enclosure can be controlled either by following the ambient temperature (from 8 $^{\circ}C$ below up to 15 $^{\circ}C$ above) or by keeping it constant.

The controlling and monitoring units can handle two enclosures simulta-

neously, in this way one can act as a reference for the other, when the experimental conditions are changed in the latter.

Initially (1971) for grass a perspex enclosure of 0.5 m x 0.5 m x 0.5 m was used. For maize, potato and wheat the enclosure consisted of different units which could be mounted one on top of the other, the number being dependent on the length of the plants (max. length 2.20 m, area 0.76 m x 0.67 m).

During experimentation, however, several problems arose: especially crops with severe lodging like potatoes and grass, cause considerable border effects. To decrease these effects the area of the plant enclosure for grass and potatoes has been increased from 0.25 m^2 to 2.0 m^2. For a good heat exchange with the environment these enclosures consist of a perspex rim (0.20 m high) with a cover of PVC film (0.15 mm thick), held in position by a small metal wire frame. The dimensions of the enclosures are: for grass 1.5 m x 1.33 m x 0.5 m and for potatoes 1.5 m x 1.33 m x 1.2 m. Increasing the area of the enclosures, without increasing the fresh air supply, caused a considerable CO_2 depletion of the air in the plant chambers at high irradiance. This was prevented by adding pure CO_2 to the system in such a way that the CO_2 concentration in the enclosure was nearly ambient. Up to now this is handled manually, so that the CO_2 concentration in the enclosure may fluctuate slightly with changes in irradiance. The time constants of the different chambers are (at maximum air supply): for wheat 2 min, for grass and maize 3 min, and for potatoes 4 min, giving equilibration times (3-4 time constants) of about 7, 10 and 14 min, respectively. With rapidly changing environmental conditions (mainly radiation) giving rapidly changing CO_2 concentrations in the enclosures, only values obtained under conditions that have been constant for 3-4 time constants, are used. Because of the long response time of the measurement of transpiration rate, this rate is integrated over 1-hour periods.

The radiation is measured with a Kipp solarimeter outside the chamber. Radiation interception by the perspex (3 mm) and the PVC (0.15 mm) is 15 % and 12 %, respectively. The values given in the publication have not been corrected for this interception. For more details see Louwerse & Eikhoudt (1975).

3 Perennial ryegrass

Th. Alberda

Measurements on herbage production under conditions of optimal supply with water and minerals have shown that the rate of dry herbage production decreases with the age of the sward and, for a given age, as the growing season proceeds (Alberda & Sibma, 1968). As it is very difficult to measure accurately enough the dry matter production of stubble and roots of a perennial sward, it could not be decided whether such a decrease in herbage production was caused by a change in photosynthetic performance or by a change in dry matter distribution above and below the cutting level. Therefore photosynthesis was measured of swards of different age at the same time and of swards of the same age at different times during the growing season.

For the measurements enclosures of 2 m^2 were used. The cover consisted of a thin polythene sheet, kept rigid by the slight overpressure in the enclosure. Only where the airstream entered the enclosure the grass was slightly blown out of its normal position over an area of 0.02 to 0.03 m^2. Inside and around the enclosure the sward was virtually undisturbed. Inside the enclosure the wind speed through the sward is usually higher than outside. As a result the wet decaying leaves in the lower part of the sward dry out gradually so that the respiration rate decreases gradually with time. By wetting these leaves again a distinct increase in repiration was achieved.

Because a kind of lodging occurs both with older swards and later in the season, it was thought necessary to study the effect of leaf position on sward photosynthesis. A wide-meshed iron screen was used to bring the leaves into a more horizontal position to simulate lodging by laying it over a non-lodging sward, and also to prevent lodging by placing it, directly after cutting, on the spot to be measured. The tillers then grow through the meshes and the leaves can be kept in an upright position by pulling the screen up as the grass grows.

Since this is the first crop to be presented in this paper, the way in which the primary data were used is described in Fig. 1. In the upper half of the figure the trend of light intensity and temperature are given for a 24-hour period on a sunny day. In the lower half the photosynthesis data are
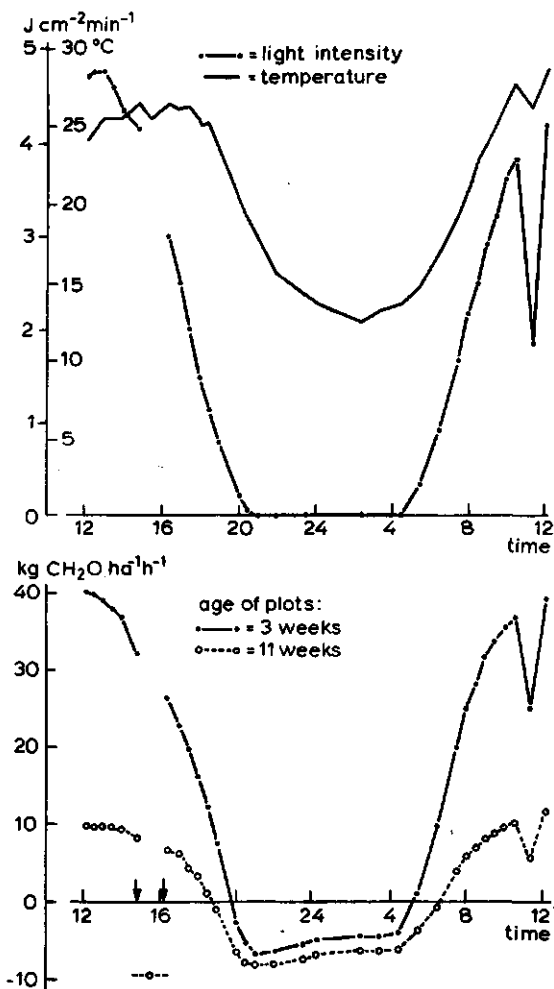
4

Fig. 1. Light intensity and temperature top and net photosynthesis and res-
piration (bottom) of two perennial ryegrass swards (3 and 11 weeks old),
4 July 1973. Between arrows: dark respiration during the day. Total radi-
ation: 562 J cm^{-2} day^{-1}, total net production:
3-week-old sward: 367.0 - 45.6 = 321.4 kg CH_2O ha^{-1} day^{-1}
11-week-old sward: 111.0 - 72.0 = 39.0 kg CH_2O ha^{-1} day^{-1}.

presented as calculated from the difference in CO_2 concentration in the in-
going and outgoing airstream. By relating the photosynthesis values to the
corresponding light intensities a light response curve can be constructed as
presented in Fig. 2 and following. On cloudy days short time changes in light
intensity were followed by comparable changes in photosynthesis rate. On such
days periods of constant light intensity of sufficient length were selected
to be sure that the corresponding photosynthesis rate could be found.
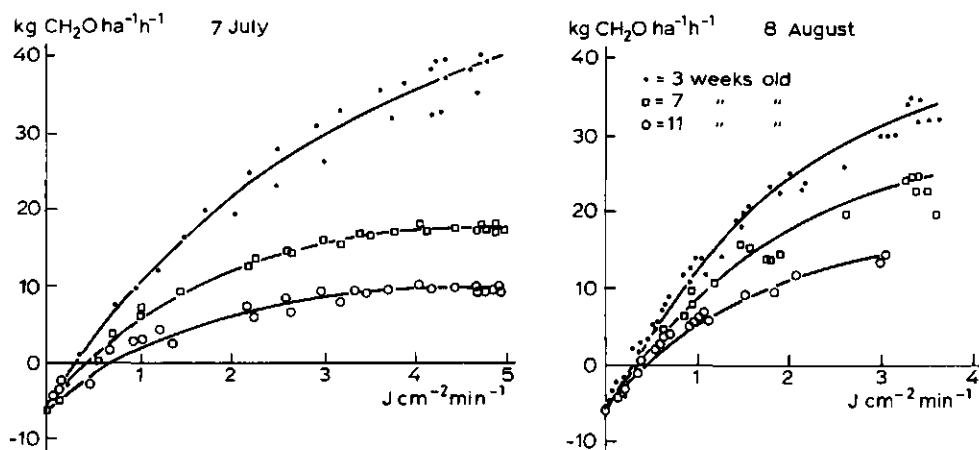
5

Fig. 2. Light response curves of three perennial ryegrass swards on two dates in 1973.

To study the influence of the age of the sward on the rate of photosynthesis, rapid growth was initiated at different times in the spring by applying nitrogen fertilizer on different plots in such a way that plots which were 3, 7 and 11 weeks old, respectively, could be compared two by two during one measuring week. It turned out that during the whole growing season the photosynthesis rate of a sward diminished with age. Two examples are given in Fig. 2, one at the beginning of July and the other at the beginning of August. Although there is always a considerable reduction in photosynthesis with the age of the sward, the absolute values vary from month to month. In this particular case the relation between light intensity and photosynthesis was about the same for the youngest sward; no light saturation was obtained over the range of light intensities examined. For the two older swards light saturation was practically reached at 5 J cm^{-2} min^{-1}, but in July the absolute values were lower than in August. In July the saturation value of the 11-week-old sward was only somewhat greater than the respiration, and the daily gain in dry matter was found to be negligible, which is in accordance with the herbage production measurements (Alberda & Sibma, 1968).

The influence of the growing season on the rate of photosynthesis is presented in Fig. 3a and 3b for the data found in 1972 and 1973, respectively. In both years young swards were compared. It can be seen that in both years there was a rather small but consistent decrease in photosynthesis rate with the advancement of the season.

To see whether the changes in photosynthesis with age of the sward and
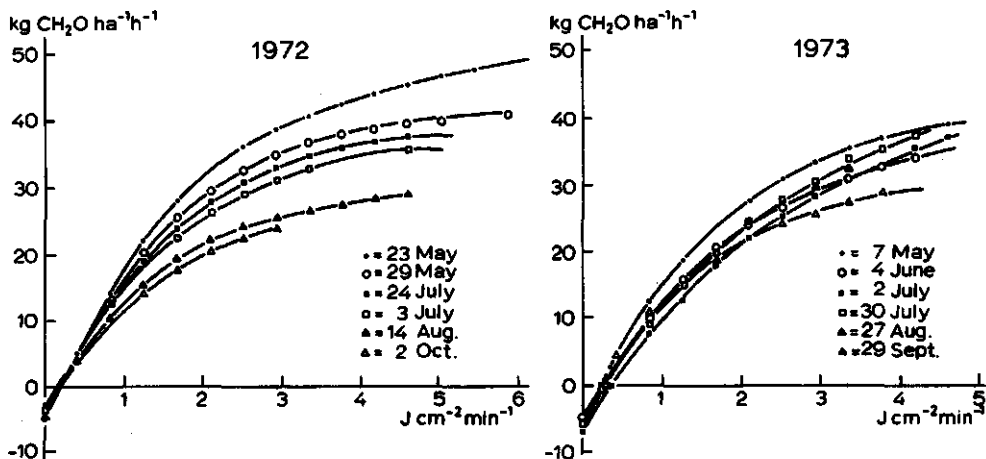
6

Fig. 3. Light response curves of perennial ryegrass swards on several dates in 1972 and 1973.
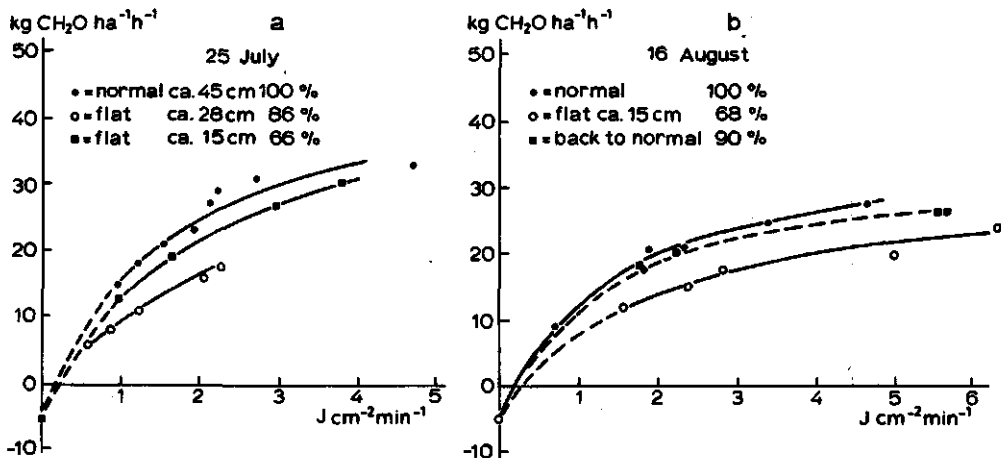

Fig. 4. Light response curves of perennial ryegrass swards with different leaf position, on two dates in 1973.

the advancement of the season might be related to changes in leaf position due to lodging, an artificial change in leaf position was brought about with the wide-meshed iron screen. This was first used to change the position of the leaves of an erect sward into a virtually horizontal one by laying the screen on top of the sward and pressing it slightly down. The results are presented in Fig. 4a and 4b. In Fig. 4a the light response curves are given for a normal sward with the leaf tips at a height of 45 cm and for the same sward with the leaves pressed down to a more horizontal position at a height

of 28 and 15 cm, respectively. This led to reductions in photosynthetic per-
formance of 14 and 34 %, respectively. Fig. 4b shows that when the screen is
removed and the leaves are put into a more upright position by hand, the pho-
tosynthesis rate is restored for the greater part. Of course it is nearly im-
possible to put the leaves back into their original position completely and
therefore a 100 % recovery cannot be expected. This restoration of photosyn-
thesis shows that the reduction in net photosynthesis by bringing the leaves
into a more horizontal position is not due to increased respiration caused
by some sward damage, but that there is some influence of leaf position on
true sward photosynthesis. Attempts were also made to bring the leaves of a
lodging sward into a more upright position. The frame was laid on the stubble
shortly after cutting so that the tillers could grow through it. As soon as
severe lodging occurred the photosynthesis was measured and then the leaves
were brought into a more vertical position by pulling the frame upwards. This
never had any positive influence on the rate of photosynthesis, which remained
either the same or was slightly suppressed. When, however, lodging was sup-
pressed by pulling the frame upwards with the growth of the grass, there was
a distinct improvement in the photosynthesis rate compared with that of a
sward with severe lodging (Fig. 5).

The rate of photosynthesis is measured in an 'open' system, which implies
that the concentration of CO_2 in the enclosure depends on the rate of photo-
synthesis of the sward. Consequently, the concentration will always be lower
inside the enclosure than outside. If the concentration drops very much below
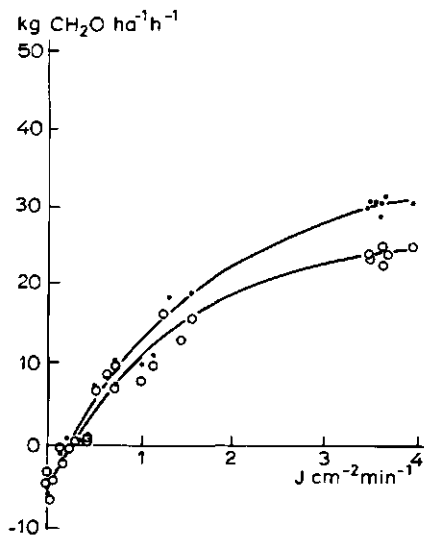

Fig. 5. Light response curves of two
6-week-old perennial ryegrass swards.
(● kept upright with a metal frame,
height 42 cm; O severe lodging, height
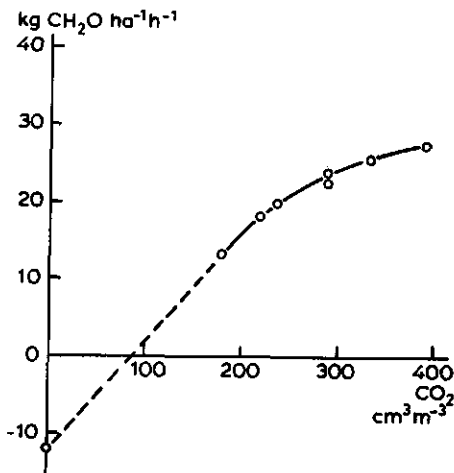18 cm), 26 August 1974.

8

Fig. 6. The relation between the rate of net photosynthesis (and respiration?) of a perennial ryegrass sward and the CO_2 concentration.

the outside value extra CO_2 can be added to the ingoing airstream. During the photosynthesis measurements of a grass sward, so many data with varying CO_2-concentrations were obtained that it is possible to establish the relation between the rate of photosynthesis and the CO_2 concentration. This is seen in Fig. 6 over a concentration range from 200 to 400 cm^3 CO_2/m^3. Over this range an increase in external CO_2 concentration leads to an increase in net photosynthesis, but the effect is gradually diminishing.

Nitrogen fertilizer is necessary to obtain high grass yields. On the experimental site there is hardly any production of herbage without nitrogen. It was thought worthwhile to study the effect of fertilization on photosynthesis. It is, however, difficult to obtain two swards with high and low nitrogen application and with comparable sward height and density, leaf position and chlorophyll content. For the nearest possible approach one plot was fertilized with a little nitrogen to stimulate some growth, and another plot was fertilized with a large amount of nitrogen when the first one had attained the closed sward situation. When both were approximately the same height the measurements were carried out. There was a small difference in colour, the low N plot being light green and the high N plot dark green. It does not seem likely, however, that a difference in photosynthesis was caused by a difference in chlorophyll content. The results are given in Fig. 7. The low N plot shows a lower rate of respiration in the dark and a lower rate of photosynthesis than the high N plot at all light intensities. The reduction in photosynthesis amounts to approximately 30 % at the highest light intensity, gradually decreasing at lower light intensities. However, even at the highest
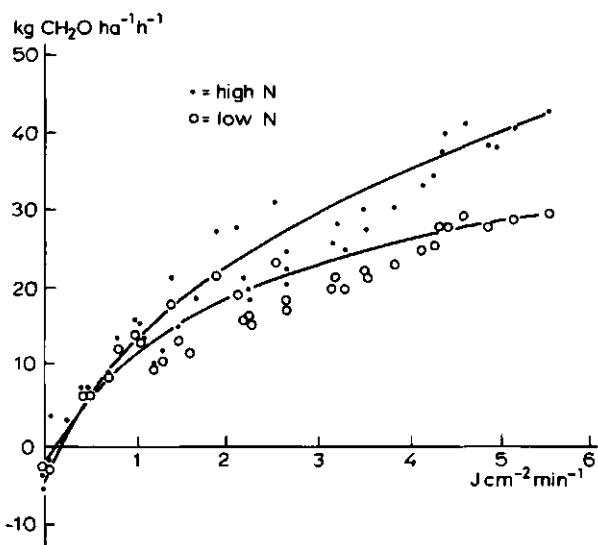
Fig. 7. Light response curves of two perennial ryegrass swards with high nitrogen (dark green, height 20 cm) and low nitrogen (light green, height 14 cm) fertilization, 5 August 1974.

light intensity the difference in photosynthesis rate is much smaller than the difference in the rate of dry herbage production. This result indicates that with low nitrogen fertilization a relatively greater part of the photosynthesis products is used below the cutting level. This conclusion is in agreement with the general observation that a shortage in essential elements promotes root formation.

The data of grass sward photosynthesis can be related to a photosynthesis simulation program. In this simulation program the photosynthesis function of the individual leaf is one of the essential parameters. When the light response curve that was obtained from leaves of plants grown on nutrient solution in a climate room was taken for this function, there was good agreement between the daily net photosynthesis measured of a sward in the field under optimal conditions and the calculated value of the simulation program. When swards were taken from the field and the light response curve of individual leaves was measured in the laboratory, much lower values were obtained than with plants cultivated in the climate rooms. A decrease in the photosynthesis rate with the age of the sward or with the season could not be detected. A better method was to grow plants in pots dug in at sward level and to lift them periodically for laboratory measurements. The light response curves then obtained from leaves of a young sward in spring agreed better with those found of plants cultivated in growth rooms. Also a decrease in maximum photosynthesis rate was found with the age of the sward and the advancement of the season. It can be concluded that the decrease in sward photosynthesis under

10

such conditions is at least partly caused by a decrease in photosynthesis function of the individual leaf. Whether this explains the phenomenon fully has to be calculated with the simulation program, when the actual and calculated photosynthesis rates are compared for the swards with the appropriate leaf functions.

When the effect of leaf position in the canopy on photosynthesis is calculated for the most vertical and most horizontal leaf positions measured in the field, the outcome is that there is hardly any difference; only when the leaves are completely parallel, forming one closed layer, are reductions in photosynthesis of the order of 30 %.

From the results it can be concluded that the changes in photosynthesis rates of closed green ryegrass swards with age are due to lodging. According to the simulation program these changes are not caused by changes in leaf position as such, since also in a sward with severe lodging the canopy does not consist of one closed layer of parallel leaves. This is corroborated by the fact that it is not possible to increase the rate of photosynthesis by artificially bringing the leaves into a more vertical position. Only when lodging was prevented throughout the growing period, was the rate of photosynthesis higher than that of a control with several lodging. It is suggested that preventing the penetration of light into the deeper layers of the canopy has an adverse effect on the photosynthesis of the lower positioned leaves.

The reduction in the rate of photosynthesis with the advancement of the season is correlated with a reduction in photosynthesis of the individual leaves. The cause of this reduction is difficult to establish. As new leaves are formed at regular intervals it cannot be an age effect; on the contrary, at the flowering stage, when no new leaves are formed on the reproductive tillers and the life-span of the existing leaves is longer, the photosynthesis rate is at its top level.

The effect of nitrogen shortage on sward photosynthesis is comparable with that on individual plants and separate leaves. The shortage in nitrogen must be rather severe before any effect on the photosynthesis rate can be observed. In an experiment with plants on nutrient solution the photosynthesis rate of leaves after 17 days of starvation from nitrogen was still 60 % of the normal value. It seems that changes in dry matter distribution occur before the rate of photosynthesis diminishes.

These results and conclusions have to be considered as provisional. Further research on grass sward photosynthesis will be concentrated on the performance of individual leaves under various artificially changed conditions.

4 Maize

H.H. van Laar, D. Kremer and C.T. de Wit

Assimilation and transpiration of maize in the field are being measured and compared with simulated results under the same conditions. Another publication (de Wit & Penning de Vries, 1977) will treat this evaluation in detail, while this paper presents some typical examples.

A short description of the Basic Crop Simulator (BACROS) is given first.

A crop in the vegetative phase of growth, well supplied with water and nutrients, is considered. Growth of this crop is defined as increase in dry weight of the structural plant material, so that those organic substances that may be classified as reserves are excluded. The model is based on physical, chemical and physiological processes, and may be applied under any condition.

The CO_2 assimilation is calculated by adding the assimilation rates of the variously exposed leaves in successive leaf layers. These rates are dependent on the light intensity, the CO_2 concentration in the ambient air and the resistance to CO_2 diffusion from the atmosphere towards the active sites. Transpiration and CO_2 assimilation interact closely, not only because a relatively large transpiration may lead to a low plant water status and subsequent closure of stomata, but also because a low assimilation rate may lead to closure of stomata and low transpiration, through regulation of the CO_2 concentration in the stomatal cavity.

One of the main problems is the introduction of the assimilatory properties of the leaves, which depend on past exposure to light and temperature and on age. As yet this subject has been insufficiently investigated. Assimilation of energy through the reduction of CO_2, as well as that through the reduction of NO_3^- in the leaves in the light are considered.

The respiration is the sum of maintenance respiration and growth respiration. The growth respiration is caused by the conversion of reserves into structural material and is therefore proportional to the growth rate and dependent on the chemical composition of the plant. Apart from the dependence of the rate of growth on temperature, growth respiration is independent of

temperature. CO_2 evolution resulting from active loading and unloading of the phloem with organic substances is usually included in the growth respiration term. The rate of maintenance respiration depends on the turnover rates of proteins and the maintenance of ionic gradients between cells and between cells and their surrounding. This respiration process is largely proportional to the amount of proteins in the biomass and sensitive to the temperature of the tissues.

The level of reserves is increased by the assimilation rate and decreased by growth and respiration. No distinction is made between different pools of reserves in different organs, but some discrimination is made with regard to their availability for growth of various parts of the plant.

The growth rate of the organs is dependent on the amount of reserves and temperature. Under water stress, the growth of the shoots is retarded so that accumulation of reserves is favoured and thus, the roots grow. By this mechanism a functional balance is obtained between root and shoot growth.

The maintenance of the functional balance between root and shoot growth is a first attempt to simulate some aspects of the development of form and function of the plant. Up to now, no satisfactory solution has been found for the simulation of the growth of leaf surface in relation to the growth of leaf or shoot weight, so that these aspects are mimicked rather than simulated, that is, described on the basis of information obtained from field experiments and not derived from knowledge of the underlying processes.

The plant water status is determined by the balance between transpiration and water uptake from the soil. The transpiration rate of the crop is found by adding the transpiration rates of the variously exposed leaves in successive leaf layers of the crop.

These rates are calculated from the absorbed radiation, the resistance of the laminar layer, the humidity and temperature of the ambient air and the stomatal resistance. The calculation also provides leaf temperatures, which are used in the photosynthesis section and also averaged to give the crop temperature that affects growth and respiration. The water uptake is determined by the conductivity of the root system and the plant and soil water status. The latter is assumed to be optimal ('field capacity'), so that the transport of water within the soil does not play an important part. The conductivity of the root system is proportional to the amount of roots and dependent on their degree of suberization and the temperature. The growth of the roots is governed by the soil temperature and the amount of reserves.

The micro-weather is calculated from the weather measured at screen

13

height, taking into account the extinction of radiant energy from sun and sky within the crop. The thermal radiation from the canopy is also computed. A calculation of the distribution of radiation over the leaves is necessary for computation of assimilation and transpiration. The extinction of turbulence in the canopy is also considered so that transfer of heat, vapour and CO_2 can be computed. The ratio of latent and sensible heat exchange governs to a large extent the micro-weather, and this ratio is governed largely by stomatal behaviour. Basically, temperatures of leaf and soil surface are simulated. For the latter, transfer of heat within the soil has also to be taken into account so that the temperature profile in the soil is also computed.

The output of this model is evaluated by comparison of simulated daily courses of CO_2 assimilation and transpiration with measured courses within enclosures. The influence of the enclosure on the radiation climate, and that of the ventilation speed on the turbulence within the crop is taken into account and time lags introduced by the measuring method are simulated.

The measurements were in general carried out in a maize field with rows spaced at 80 cm and the plants in the rows spaced at 10-12 cm. The surface of the enclosure is 0.64 m^2 and it contains about 7 plants of one row. Even if there is no lodging in the experimental fields, some disturbance of leaf position is unavoidable because the leaves of plants of adjacent rows overlap. The height of the perspex enclosure may be adjusted to plant height between 120 cm and 300 cm. Even within the highest enclosure the turbulence is large enough to ensure a uniform distribution of temperature, humidity and CO_2. The evaporation of the soil is suppressed by a gravel layer of a few centimeters.

Considerable attention was paid to the measurement of leaf temperatures within the enclosure, but the overall accuracy of the Heimann's radiation meter used for this purpose was too small to allow evaluation of computed leaf temperatures for various reasonable assumptions with respect to stomatal behaviour. A daily course of air and leaf temperature is given in Fig. 9a. The measured leaf temperature at night was found to be higher than the air temperature but this is probably due to inaccuracies in the method.

Daily courses of net assimilation are given in Fig. 8a and 9a. The negative CO_2 assimilation during daytime is achieved by complete shading and is in general larger than the respiration during the night. This difference is attributed to the larger growth rate, one of the assumptions that is evaluated by simulation. The relation between CO_2 assimilation and light intensity measured throughout the day are given in Fig. 8b and 9b. Fig. 8b concerns a
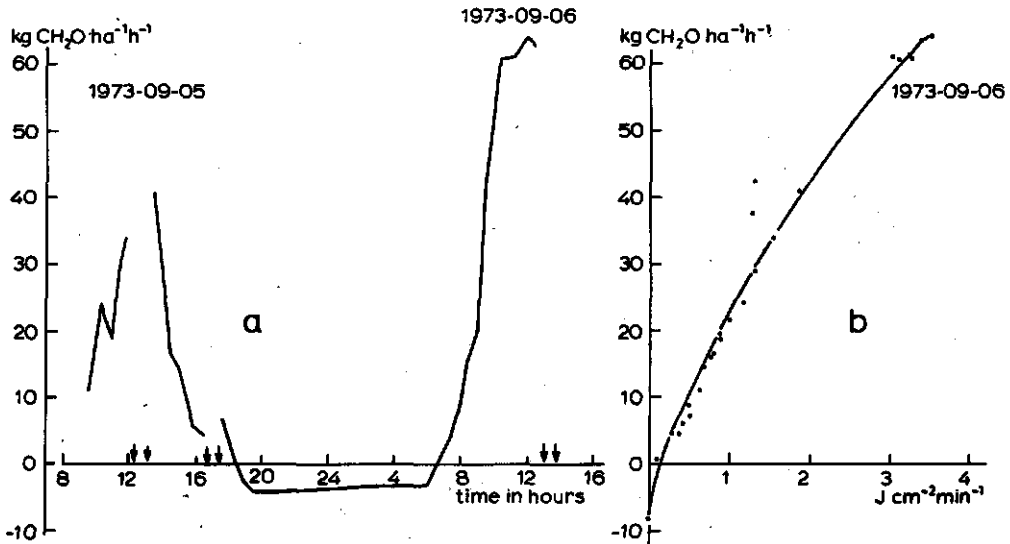
14

Fig. 8. CO_2 assimilation expressed in kg CH_2O ha^{-1} h^{-1} as a function of time
(a) and as a function of light (b) of a maize crop.
    Species: *Zea mays* cv. Caldera 535; density: 10 plants m^{-2}; measuring
date: 1973-09-06; sowing date: 1973-08-06; location: Born-Zuid, Wageningen;
leaf area index: about 10 m^2 m^{-2}; dry weight shoot: about 3600 kg ha^{-1};
stage: 0.5 - 1.0 (Hanway, 1966); height: 50 cm.
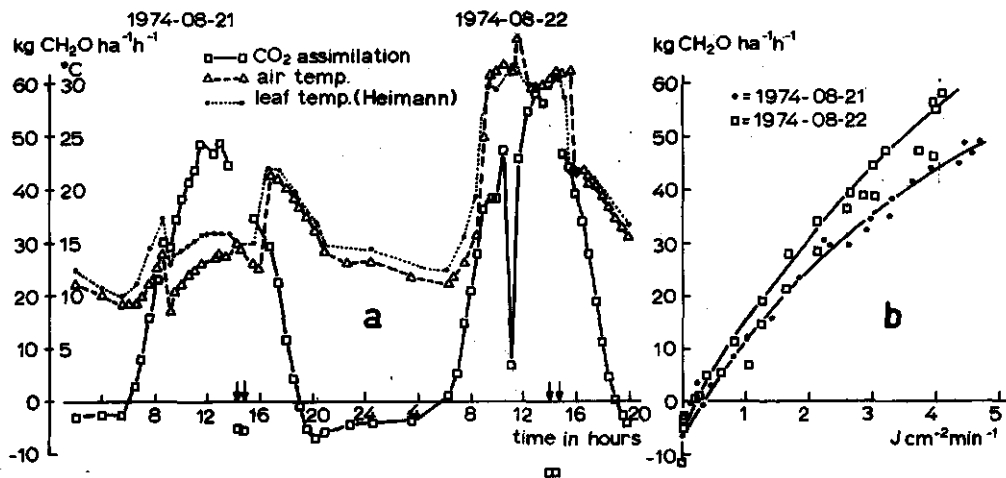   Between arrows: dark respiration during the day.

Fig. 9. CO_2 assimilation expressed in kg CH_2O ha^{-1} h^{-1} as a function of time
(a) and as a function of light (b) of a maize crop. Also leaf and air tem-
perature as a function of time (a).
    Species: *Zea mays* cv. Caldera 535; density: 10 plants m^{-2}; measuring
date: 1974-08-21; sowing date: 1974-04-25; location: Oost-Flevoland, Lely-
stad; leaf area index: 5.14 m^2 m^{-2}; dry weight shoot: 10 678 kg ha^{-1}; stage:
4.5 (Hanway, 1966); height: 280 cm.
    Between arrows: dark respiration during the day.

15

young crop in the stage 0.5-1 (after Hanway, 1966), and its CO_2 assimilation at a radiation of 3 J cm^{-2} min^{-1} is about 30 % higher than that of the older crop in Fig. 9 which is in the grain filling stage. The increase in assimilation of the crop surface in successive days in the enclosure is not fully understood.

The CO_2 assimilation of a closed crop surface of maize in the period of 31 July to 18 September is given in Fig. 10a and 10b for two replicates. The assimilation drops considerably with age. One of the objectives of the simulation was to analyse to what extent such a decrease may be attributed to a
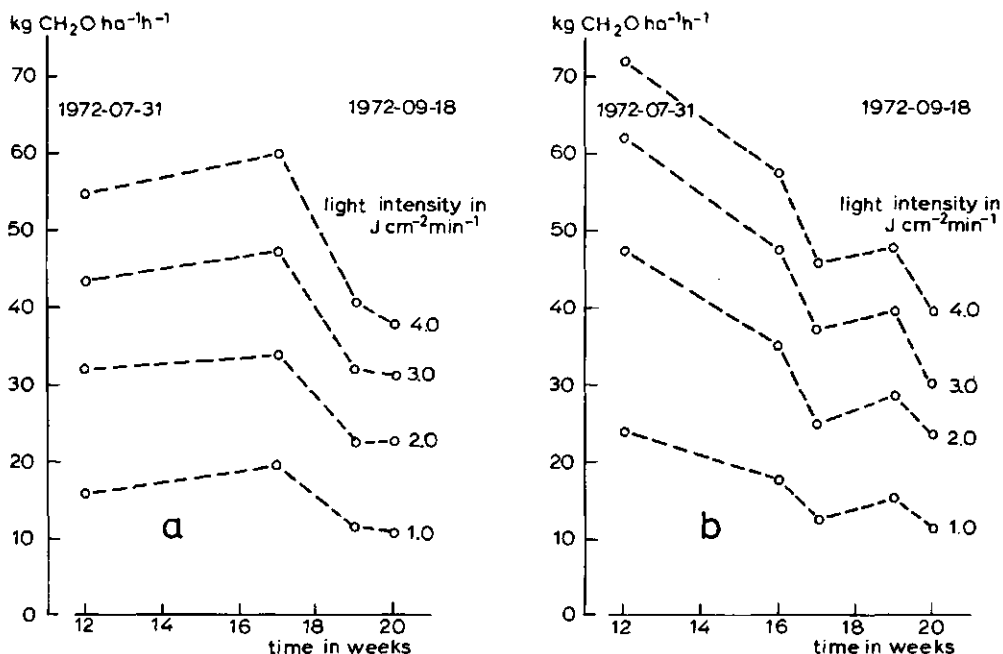

Fig. 10. CO_2 assimilation expressed in kg CH_2O ha^{-1} h^{-1} at the light intensities 1.0, 2.0, 3.0 and 4.0 J cm^{-2} min^{-1} as a function of time of a maize crop (2 replicates).
   Species: *Zea mays* cv. Caldera 535; density: 10 plants m^{-2}; sowing date: 1972-04-28; location: Droevendaal, Wageningen.

Measuring date	LAI (3a) (m^2 m^{-2})	LAI (3b) (m^2 m^{-2})	Dry wt. (3a) shoot (kg ha^{-1})	Dry wt. (3b) shoot (kg ha^{-1})	Stage (Hanway)
1972-07-31	3.01	3.83	4373	5650	2.5 (12 weeks)
1972-08-21	3.62	3.76	10009	10208	4.0 (16 weeks)
1972-08-30	4.08	3.60	11156	11220	4.5 (17 weeks)
1972-09-11	3.15	3.53	11766	13461	5.0 (19 weeks)
1972-09-18	3.06	3.13	11937	11461	5.5 (20 weeks)

decrease in photosynthetic capacity of the leaves, decrease in leaf area index (LAI), interception of light by non-photosynthesizing tissue, temperature, lack of sink capacity, and so on. In so far as the problem of linking laboratory and field data through simulation is concerned, the difficulty remains that fully grown maize plants can hardly be obtained and analysed under controlled conditions. Experiments on the influence of temperature on assimilation were done with young and old crop surfaces. Closed crop surfaces with young plants in stage 1 (after Hanway, 1966) were obtained by a 6 to 10 times higher planting density than normal.

The temperature was varied throughout the day in a range dictated by ambient temperatures, by the capacity of the cooling system and of the additional heating system. Daily courses of temperature and assimilation are given in Fig. 11a and 11c. The dark periods were included to evaluate the effect of the temperature changes on respiration. The light response curves, based on these data are given in Fig. 11b and 11d.

The scattering of the observations for the crop surface of old plants is much smaller than for the crop surface of young plants and further analyses of these and other data show indeed that the influence of temperature on assimilation is small for plants in their later stages of growth and higher for plants in younger stages. The largest measured effects of the temperature are given in Fig. 12a and 12b for young plants.

However, even with young plants the temperature influence on assimilation is considerably smaller than that simulated from laboratory data for the temperature response. The physiological causes for this difference between plants grown under field and laboratory conditions are further analysed. Practical experience in the Netherlands has already indicated that weight increases at the end of September are unexpectedly high for this 'heat loving' plant.

The influence of the CO_2 concentration in the enclosure is presented in Fig. 13. The assimilation is independent of CO_2 concentrations above 200 cm^3/m^3 and this confirms the observations in the laboratory that in this range the stomata close with increasing CO_2 concentration to such an extent that the internal CO_2 concentration is maintained at about 100 cm^3/m^3. This closure of the stomata is also reflected in a reduced transpiration rate. Since it is difficult to change the water content of the soil, experiments on the relation between water status, assimilation and transpiration are being done by cutting the plants in the enclosure at the base but keeping them otherwise in the same position. The transpiration rate is measured at low resolution
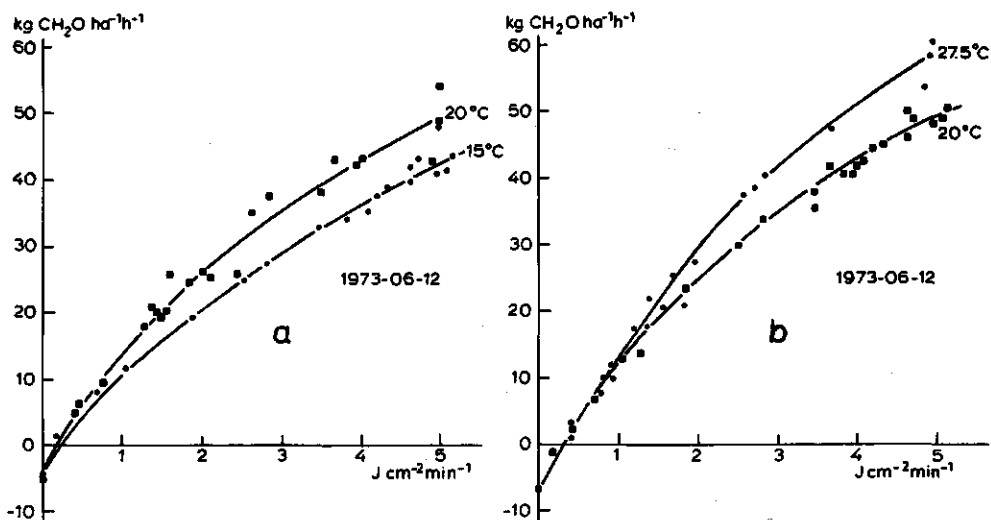
YOUNG CROP 1973-08-22

OLD CROP 1973-08-22

18
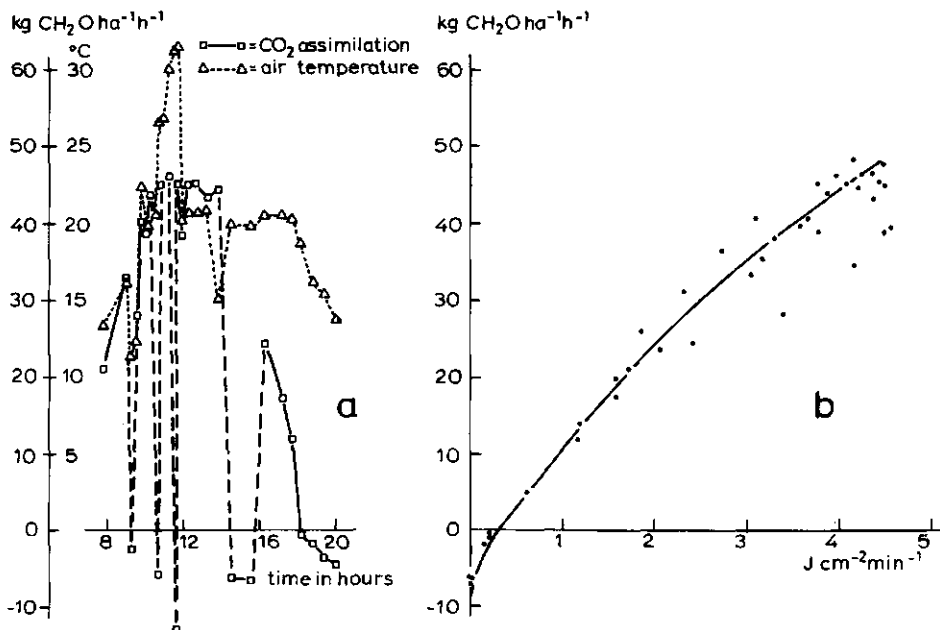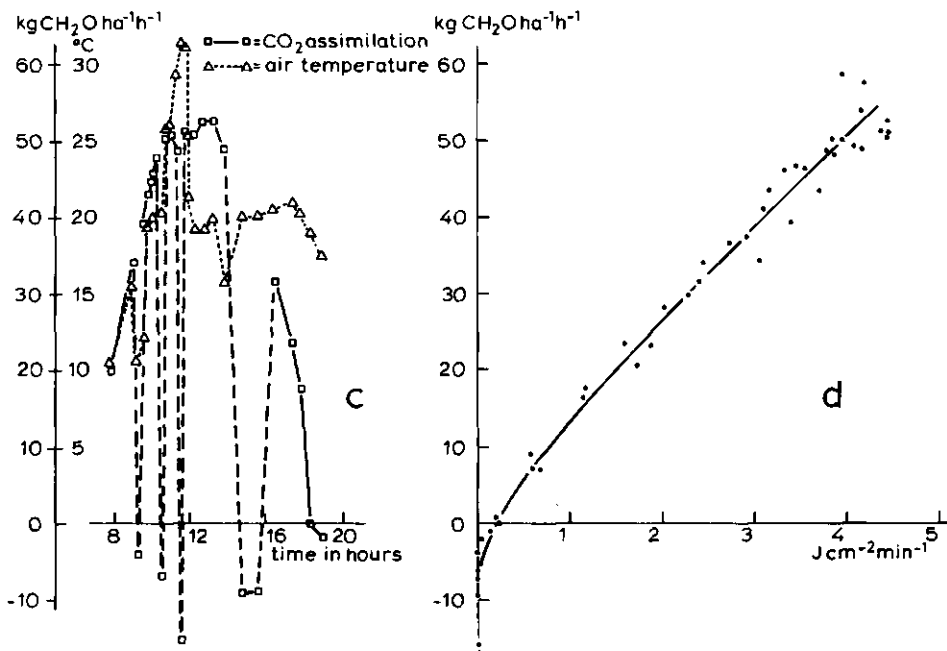
Fig. 12. CO_2 assimilation expressed in kg CH_2O ha^{-1} h^{-1} at 15, 20 and 27.5 °C as a function of light.

 Species: *Zea mays* cv. Caldera 535; density: 3 x 3 cm (a), 4 x 4 cm (b); measuring date: 1973-06-12; sowing date: 1973-05-01; location: Droevendaal, Wageningen; leaf area index: 17.5 m^2 m^{-2} (a), 14.7 m^2 m^{-2} (b); dry weight shoot: 3708 kg ha^{-1} (a), 3297 kg ha^{-1} (b); stage: about 1.0 (Hanway, 1966); height: about 30 cm.

Fig. 11. CO_2 assimilation expressed in kg CH_2O ha^{-1} h^{-1} as a function of time (a, c) and as a function of light (b, d) of a young and an old maize crop. Also air temperature as a function of time (a, c).

 Species: *Zea mays* cv. Caldera 535; density: 10 plants m^{-2}; measuring date: 1973-08-22; location: Droevendaal, Wageningen.

 Young crop: sowing date: 1973-07-11; leaf area index: 15.5 m^2 m^{-2}; dry weight shoot: 5010 kg ha^{-1}; stage: 0.5 - 1.0 (Hanway, 1966); height: 75 cm.

 Old crop: sowing date: 1973-05-01; leaf area index: 5.7 m^2 m^{-2}; dry weight shoot: 16 300 kg ha^{-1}; stage: 4.5 (Hanway, 1966); height: 280 cm.
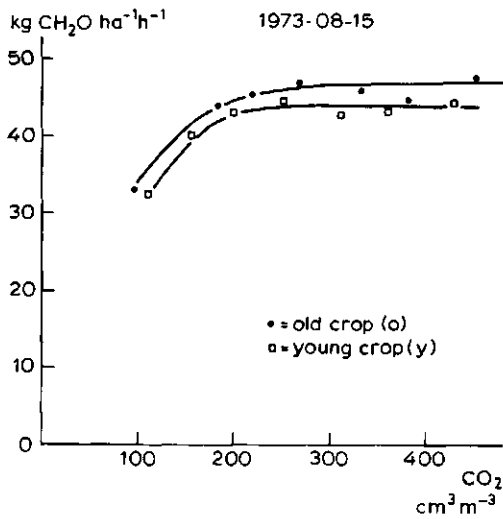
 Broken line: dark respiration during the day (a, c).

19

Fig. 13. CO_2 assimilation expressed in kg CH_2O ha^{-1} h^{-1} as a function of CO_2 concentration of a young (y) and an old (o) maize crop.
    Species: *Zea mays* cv. Caldera 535; density: 10 plants m^{-2}; measuring date: 1973-08-15; sowing date: 1973-05-01 (o), 1973-07-11 (y); location: Droevendaal, Wageningen; leaf area index: 10.7 (y), 5.3 (o) m^2 m^{-2}; dry weight shoot: 3403 (y), 12645 (o) kg ha^{-1}; stage: 0.5 - 1.0 (y), 4.5 (o) (Hanway, 1966); height: 50 (y), 280 (o) cm.

via the rate of condensation of water on the cooler, corrected for the humidity of the ingoing and outgoing air. The outcome of one experiment is given in Fig. 14a and 14b.

    Fig. 14a gives the assimilation rate and the transpiration rate dependent on time. The loss of water from the shoot and with this the drop in fresh weight may be found by integrating the transpiration rate, so that the results may also be presented with shoot fresh weight along the horizontal axis, as done in Fig. 14b.

    It is observed that assimilation drops more rapidly than transpiration and this observation is contradictory to what is expected from the laboratory measurements where the decrease in water supply is affected by gradually drying of the soil.

    From harvests it has been known for a long time that the potential crop growth rate of maize in the cool climate of the Netherlands is at least as high as that of other species, even late in the season, so that the adverse effect of temperature on the assimilation of maize, as found in the laboratory, does not manifest itself so strongly in the field. A comparison of the light response curves of maize with those of other species in this paper con-
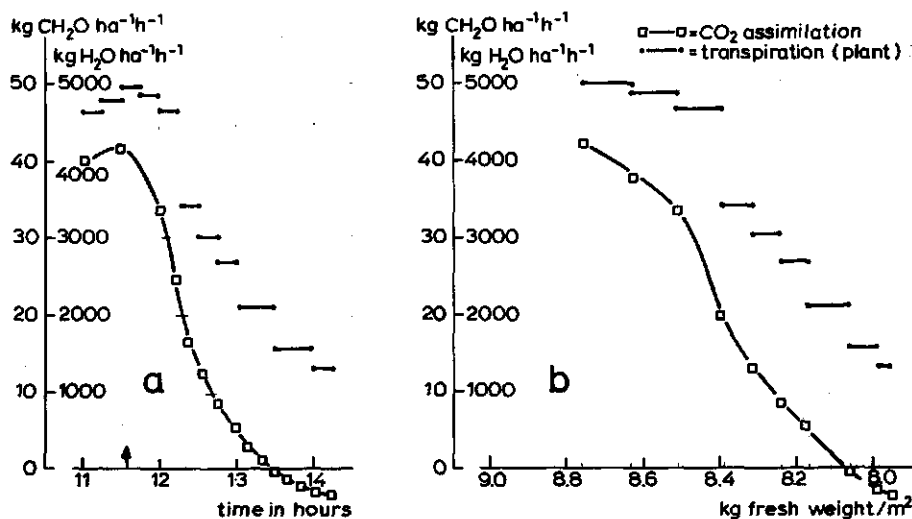
20

Fig. 14. CO_2 assimilation and transpiration expressed in kg CH_2O ha^{-1} h^{-1} and kg H_2O ha^{-1} h^{-1}, respectively as a function of time (a) and as a function of fresh weight (b).

Species: *Zea mays* cv. Caldera 535; density: 10 plants m^{-2}; measuring date: 1973-08-16; sowing date: 1973-05-01; location: Droevendaal, Wageningen; leaf area index: 5.3 m^2 m^{-2}; dry weight shoot: 12 645 kg ha^{-1}; stage: 4.5 (Hanway, 1966); height: 280 cm.

firms that maize also grows very well in cool climates. Further physiological research may be centered around a more thorough analysis of the influence of temperature on assimilation in association with its effect on germination and early growth.

Detailed comparisons between simulated and experimental results for maize and other crops also show that the effect of different environmental conditions on the simulated results is in general larger than on the experimental results. Hence adaption mechanisms to changing environmental conditions are not very well presented in the simulation program. Relatively little attention has been paid to these adaptation phenomena in laboratory studies up to now, both for adaptation with time constants of the order of a day that are reflected in the biochemical properties of the plants and for adaptations with longer time constants that are reflected in morphological properties.

5 Wheat

N.M. de Vos

5.1 GENERAL REMARKS

In cereals the period after flowering is decisive for grain yield, because most carbohydrates stored in the grain are derived from post-anthesis assimilation. Therefore, the photosynthetic activity of the green plant parts during the post-anthesis phase is an important crop parameter which also applies to the senescence rate during this phase.

Usually it is assumed that senescence sets in rather rapidly after flowering, but it is doubtful whether this occurs under favourable growing conditions. To attain a high yield level a prolonged active period seems to be a prerequisite. The duration of the active period is highly influenced by such factors as pathogen infection, nitrogen supply and also temperature. It is not known whether genetic differences, as shown to exist for flag leaf photosynthesis, can lead to appreciable differences in rate of photosynthesis under field conditions as well.

The first aim of the measurements, carried out in 1973 and 1974, was to provide data on the photosynthesis level of field-grown wheat and especially that after flowering and during senescence. We tried to obtain crops grown with as little stress as possible and to compare the effects of some limiting factors with this 'ideal' crop. Further different varieties were compared.

5.2 ENCLOSURES

For the measurement of net photosynthesis rates (P) a 3 mm perspex chamber with a ground surface of $80 \times 80 \ cm^2$ was placed over the wheat crop and on an iron frame, hammered 30 cm into the soil. The height of the enclosure was 120 cm, consisting of a 60 cm bottom part and a 60 cm top part. The air inlet and outlet were placed in such a way that the tubes could be situated between the rows to avoid any interference with the crop. The rows had the usual 25 cm distance. So the enclosure was placed over three rows of wheat, comprising 270 to 330 ear-bearing culms.

5.3 EXPERIMENTAL CONDITIONS

In 1973 some measurements were made on spring wheat, cv. Orca and Fundus, during the ear emerging phase. Due to heavy lodging of the crop after flowering, later measurements did not yield satisfactory results.

In 1974 measurements were taken during a 5½-week period in a winter wheat crop, var. Clement, during the post-anthesis phase. The whole crop was sprayed with chlormequat in stage F5, to avoid lodging. Part of the plots was treated frequently with fungicides to prevent any deleterious effect of such diseases as eyespot, *Septoria tritici*, *Septoria nodorum*, mildew, stripe rust and leaft rust, which were all present in the control crop, although at a relatively low level. Nitrogen was applied at two levels, 80 kg N and 120 kg N per ha (N1 and N2), by spraying a 39 % N solution in growth stages F3 and F7.

5.4 DAILY COURSE OF P

Fig. 15 presents an example of the daily course of P under nearly cloudless conditions during most of the day. The data pertain to an Orca spring wheat crop at the ear emergence stage. It is clear that the increase of P slows down rather markedly when the incident light increases above 3 J cm^{-2}
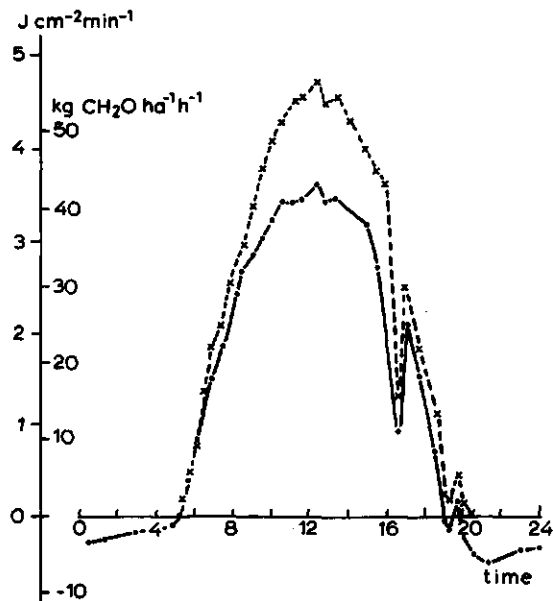

Fig. 15. Daily course of incident light (x---x) and net photosynthesis (●——●) of spring wheat cv. Orca at the ear emergence stage.

min^{-1}. This is demonstrated more distinctly by the light response curve as
given in Fig. 16. As in several other cases the afternoon data are below
those found for the morning hours, especially on days with high radiation and
during a prolonged dry period. The course of the line shows that light satu-
ration is not fully reached but approximated at about 5 J cm^{-2} min^{-1}.

Similar figures are given for Clement winter wheat (Fig. 17 and 18). In
this case P attained a somewhat higher level, with a maximum of 45 kg CH_2O
ha^{-1} h^{-1}. Again the data are lower for the second half of the day.
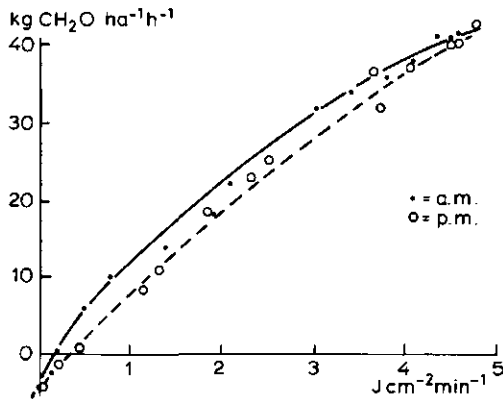
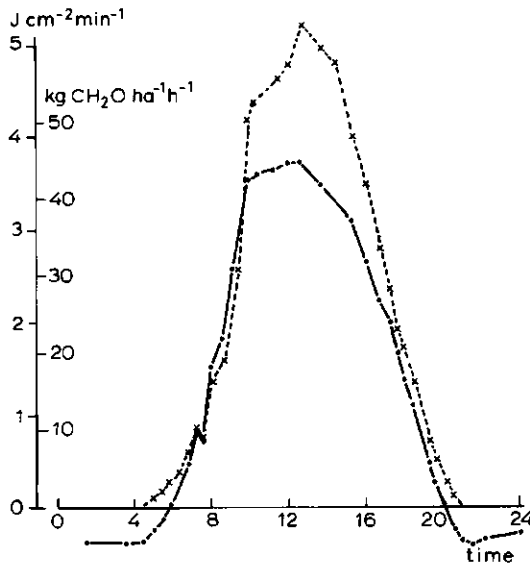Fig. 16. Light response curve for
spring wheat cv. Orca.

Fig. 17. Daily course of inci-
dent light (x---x) and net pho-
tosynthesis (●——●) of winter
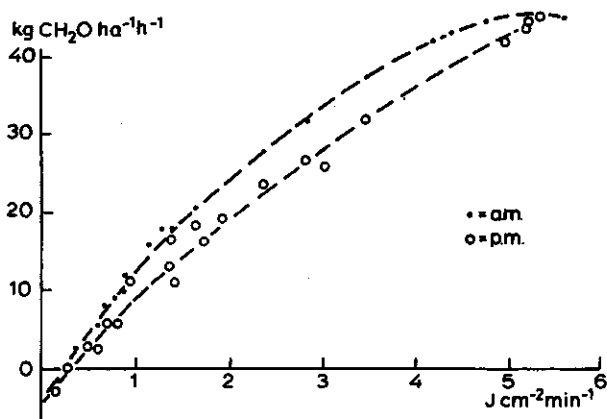wheat cv. Clement at the start
of the grain filling stage.

24

5.5 EFFECT OF AGE

In 1974 P was determined weekly in Clement winter wheat plots during the period 24 June to 31 July. At the first measuring date grain growth had just started, the average grain weight being 1.7 mg. Fig. 19 presents the light response curves for six successive weeks. They pertain to plots with the higher nitrogen level and frequent fungicide treatments, which could prevent losses by pathogens almost completely.

During the first week a level of 45 kg CH_2O ha^{-1} h^{-1} was achieved, just as in the preceding year with spring wheat. Unfortunately, no observations
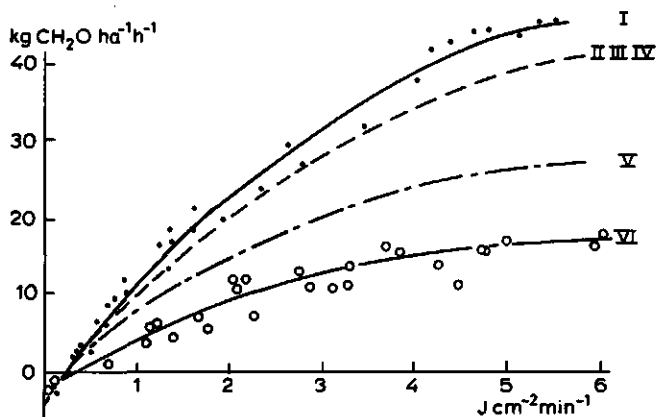

Fig. 19. Light response curve for six successive weeks, starting on 24 June; Clement winter wheat frequently treated with fungicides. Only points for curve I and curve VI are given.
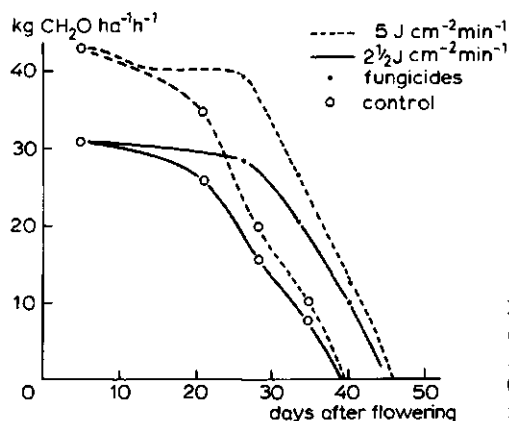
Fig. 20. Course of net photosynthesis during the grain filling period for fungicide-treated and control crops of Clement winter wheat at two levels of incident light.

are available from an earlier growth stage as was the case for the spring wheat crop. So it is not known whether senescence had already set in at the beginning of the grain filling stage or not. If so, it did not proceed any further during the next three weeks for which similar response curves were found, though on a somewhat lower level than found for the first week. There-after a decrease set in extending over a three-week period. The course of P at two levels of incident light is given in Fig. 20. Light saturation did not occur below $5 \ J \ cm^{-2} \ min^{-1}$ but the increase in P at a higher rate of radi-ation is only slight.

The final grain yield was 10.000 kg ha^{-1} (16 % moist) indicating fair growing conditions throughout the measuring period. Maximum air temperature did not surpass 26 ^{O}C in June and 23 ^{O}C in July. Under these conditions se-nescence was slow, especially that of the flag leaf blade and sheath and the peduncle. Crop observations from the two previous years indicate that such a prolonged grain filling phase is rather normal for Dutch conditions, provided pathogen infection could be excluded by frequent fungicide application.

5.6 EFFECT OF DISEASES AND VARIETY

A comparison of P on the control plots (C) and of the plots treated with fungicides (F) shows no difference for the first week of measuring (Fig. 20). A distinctly lower P of the control was found for the measurements in the third week. As C and F were not measured on the same day of the week, the effect of the treatment can best be shown in graphs for P versus time. These are given in Fig. 20 for two levels of incident light. The differences are
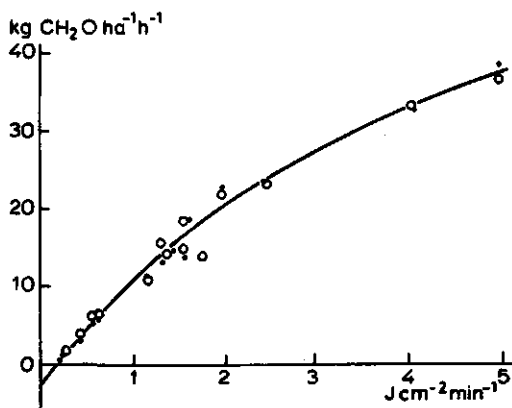
Fig. 21. Light response curve for Clement (●) and Manella (O) winter wheat, 15 days after flowering.

due in the first place to an accelerated loss of green area in the control plots, which led to a yield loss of about 2400 kg grain per ha in the N2 plots. According to Fig. 20 there is a difference of about 10 days in the course of 'senescence', which is large enough to explain the yield difference. The winter wheat Clement used in these experiments was the newest leading variety and the results mentioned point to the very pronounced effect of diseases on crop performance, even for such a new variety.

Comparison of the two varieties Clement and Manella, the latter being 15 % less productive than Clement according to several years of variety trials, showed that no differences in P were present about 15 days after flowering (Fig. 21). Neither was there any difference between the two spring wheat varieties (Fig. 22). Due to the growth stage difference, already indicated, no direct comparison can be made between the spring and the winter wheat.

5.7 EFFECT OF TEMPERATURE

Variation in temperature, especially in the 1973 experiments, enabled a first estimate to be made of the influence of this factor on P. As shown in Fig. 23, this effect is rather small in the range 12-20 $^{\circ}$C. At higher temperatures a decrease in P can be observed, which becomes rather pronounced at 30 $^{\circ}$C. Apparently there is no obvious interaction with the level of incident light. It must be stressed that these effects apply to short-term changes of temperature and might be quite different from long-term effects, which are known to influence the senescence rate.

Dark respiration is highly dependent on temperature as shown in Fig. 24a for Orca and Fundus spring wheat and in Fig. 24b for Clement winter wheat. In
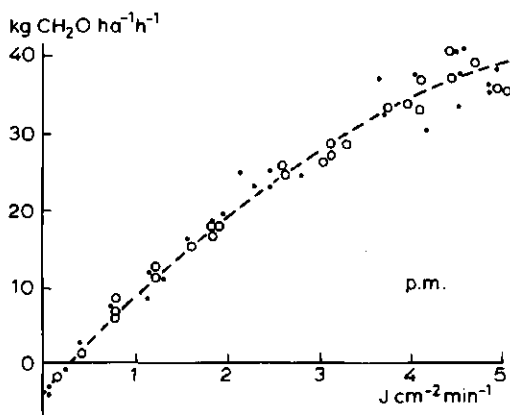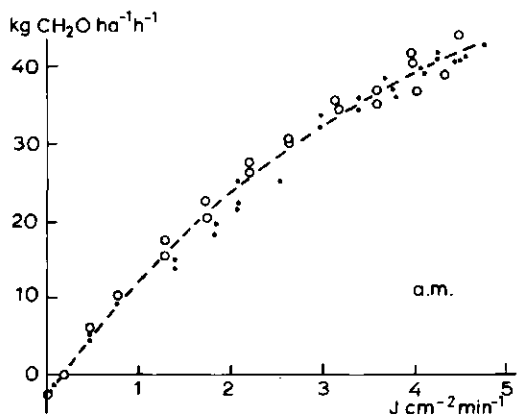
27

Fig. 22. Light response curves
for Orca (●) and Fundus (0) spring
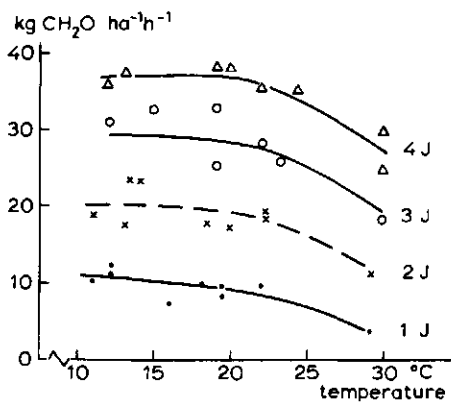wheat for a.m. and p.m., respect-
ively.

Fig. 23. Effect of temperature on pho-
tosynthesis of Orca spring wheat, at
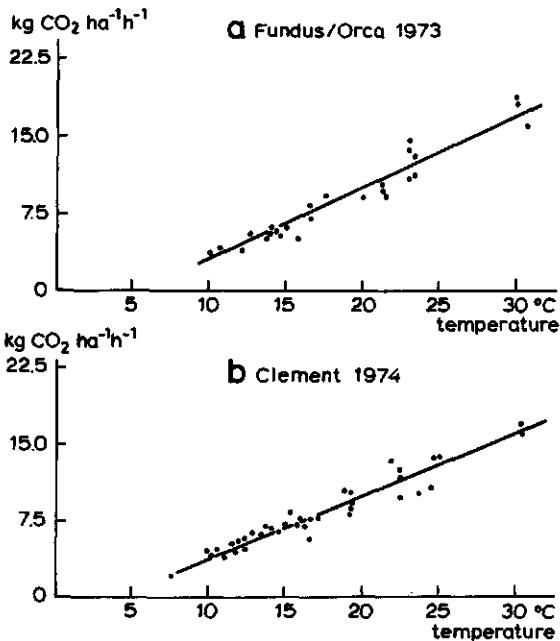various levels of incident light.

Fig. 24. Effect of temperature on dark respiration in Orca and Fundus spring wheat (a), and Clement winter wheat (b).

spite of the large difference in dry matter present at the measuring dates, the lines are almost identical.

5.8 EFFECT OF NITROGEN

No difference was found for P at the first measurement between the two nitrogen levels of Clement winterwheat. After that a more rapid decline occurred at the lower nitrogen level, induced by a more rapid decrease in green area. The course of P is shown in Fig. 25 for two levels of incident light.

5.9 CONCLUSIONS

The data presented in the foregoing sections are based on a rather limited series of observations. Obviously the level of P under field conditions will be influenced by many factors which were not considered in this study. Thus the relative low temperature during the measuring period may have caused a certain extension of the period with high P. The small number of varieties tested so far gives no information about the genetic variation to be expected in modern varieties nor about the effect of crop structure. On the other hand, the crops grown in 1973 and especially in 1974 can be looked
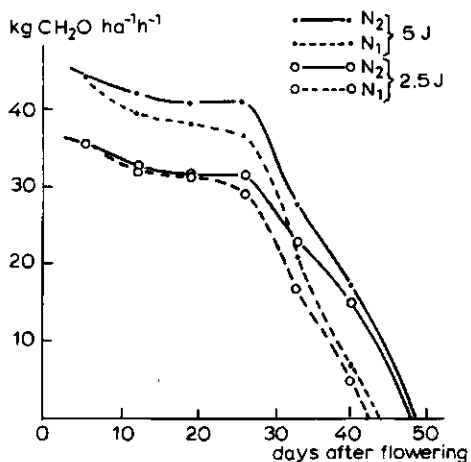
29

Fig. 25. Effect of nitrogen on photo-
synthesis during the grain filling
period at two levels of incident light.
Clement winter wheat.

upon as the best that could be achieved by agronomic measures. Thus the re-
sults can be seen as kind of reference level, especially with respect to
breeding purposes.

To obtain further insight in the way in which cereal productivity can be
increased, much more information is needed on the effect of temperature, crop
structure and genetic variation as well as on losses due to pathogens. Field
determinations of P can evidently contribute to a better understanding of
crop production, but on the other hand the number of observations will be
restricted due to the limited capacity of the field apparatus. Thus they have
to be used in combination with other methods in order to obtain a more gen-
eral picture.

6 Potatoes

K.B.A. Bodlaender

6.1 INTRODUCTION

In some field trials with periodical liftings the tuber yield decreased later in the season, even when the foliage was still quite green. In other trials, however, the tuber yield was still increasing in that part of the growing period. The changes in yield can be caused by regrowth of the foliage after treatment with a growth retardant such as B9 (see Bodlaender & Algra, 1966; Bodlaender, 1968), top-dressing with nitrogen, or a drought period. This regrowth can cause a redistribution of dry matter to the different parts of the plants (leaves, stems, tubers) or affect the rate of photosynthesis and respiration of the crop. Therefore photosynthesis and respiration of potato crops with different foliage growth were measured under field conditions on several dates in the years 1971-1973.

6.2 EXPERIMENTS

The measurements were carried out with the late variety Alpha; in 1971 and 1972 on a humous sandy soil near Varsseveld which permits vigorous foliage growth, in 1973 on a light sandy soil near Renkum (Sinderhoeve) which produced a less abundant growth and was irrigated every two weeks. Only the results of 1971 and 1973 will be presented here.

In 1971 the growth retardant B9 was sprayed on the foliage on 9 June. B9 reduces stem growth for some weeks, later stem elongation of the treated plants is accelerated, causing regrowth of the foliage. Measurements were made in the following periods: (a) 21-25 June; (b) 9-12 August (plants were lodging); (c) 1 and 2 September (plants were lodging, senescence had started).

In June and August two untreated and two treated plots were measured, in September just one untreated and one treated plot.

In 1973 half of the plots obtained late extra dressings of nitrogen, phosphate, potassium and magnesium, eight times between 12 June and 27 August. These minerals were dissolved in water and applied in the furrows between the

plants. The untreated plots obtained only irrigation water on the same dates. Measurements were made during four periods: 25-29 June, 9-12 July, 6-9 August and 17-19 September. In August and September the plants were lodging. In all periods two untreated plots and two plots with extra dressings were measured, in September only two plots with extra dressings.

6.3 ENCLOSURES

For the measurements transparent enclosures were used: in 1971 small enclosures (76 cm x 67 cm, containing 3 plants) and in 1972 and 1973 large ones (150 cm x 133 cm, containing 12 plants).

The air was blown into the furrows between the potato ridges through openings in the metal frames. The enclosures were 70 cm high at the beginning of the season and changed to 120 cm high for later measurements.

A great difficulty was the lodging of the potato plants. Due to this lodging the plants were often bent to one side of the plots; on the later dates the soil was not completely covered by the foliage. The results of August and September therefore have a restricted value.

6.4 RESULTS

Fig. 26 shows the rates of photosynthesis and respiration of treated and untreated plots on some dates in 1971, together with light intensity and temperature. The curves of the light intensity and the net photosynthesis resemble each other. The influence of the temperature on photosynthesis is less pronounced; the rate of respiration is of course increased by higher temperatures. The influence of the light intensity on net photosynthesis in three growth stages is presented in Fig. 27. The measurements indicate that photosynthesis later in the season is saturated at lower light intensities. The rate of photosynthesis decreases during the growing period especially at higher light intensities.

Fig. 26. Light intensity, temperature and net photosynthesis and respiration in kg CH_2O ha^{-1} h^{-1} of two potato crops (untreated and treated with B9) at several dates. Varsseveld, 1971. Between arrows: dark respiration during the day.
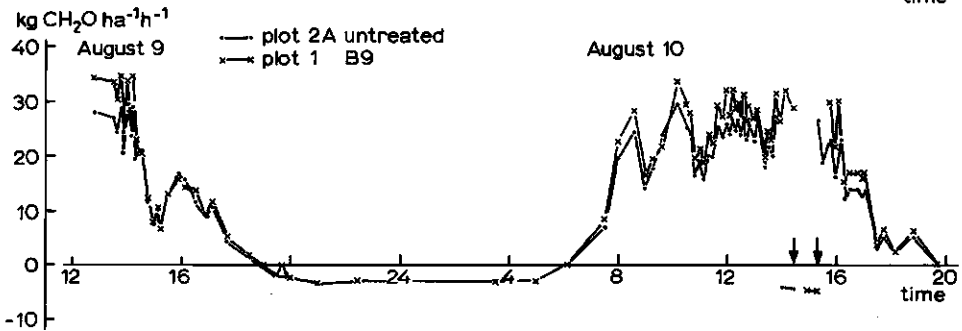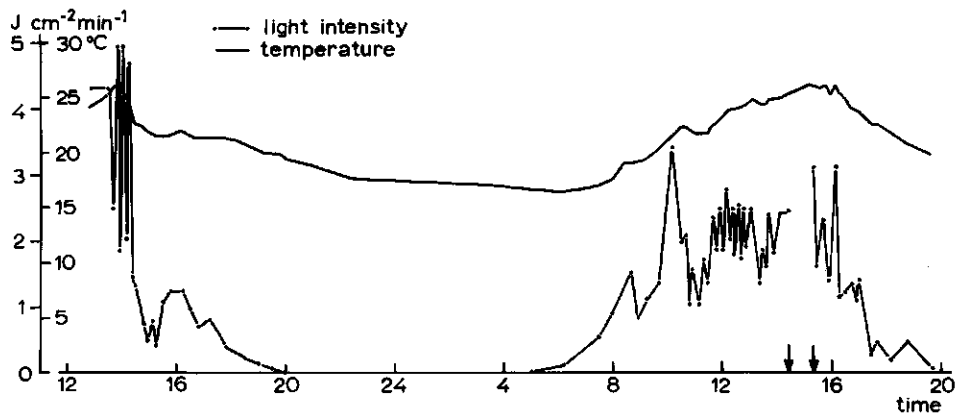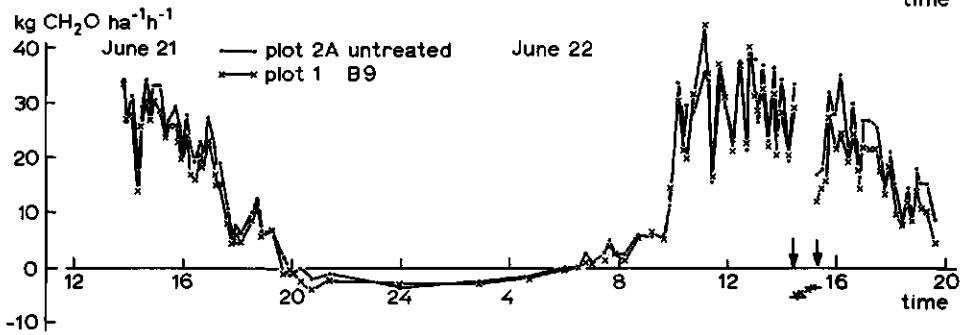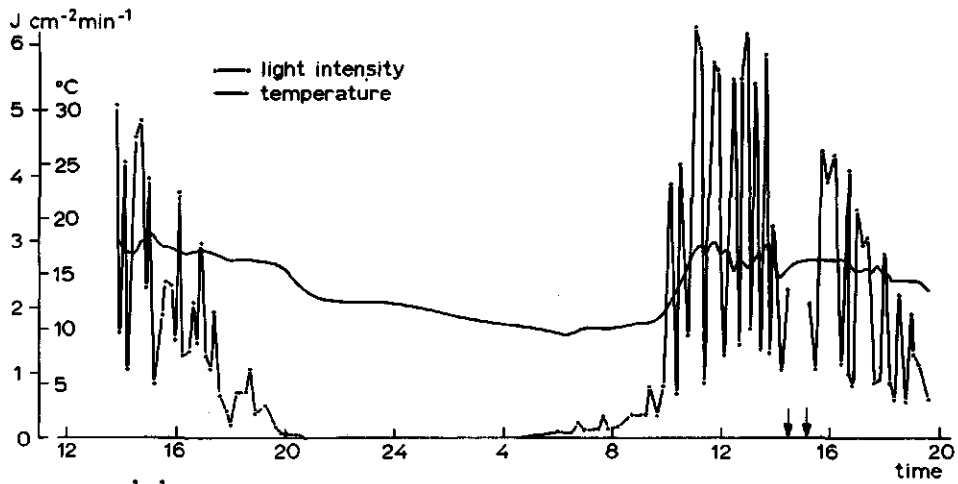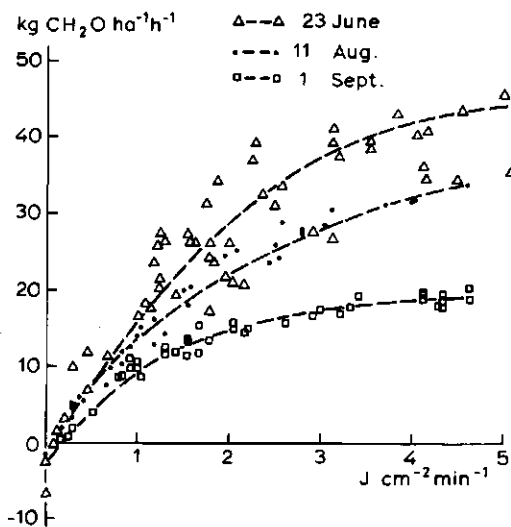
Fig. 27. Light response curves of an untreated potato crop on several dates. Varsseveld, 1971.
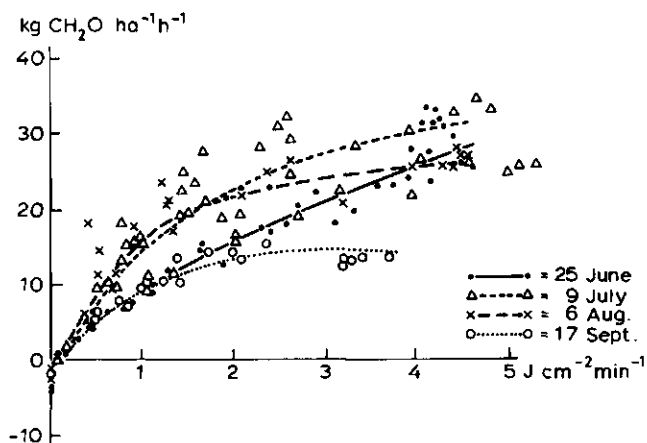
Fig. 28. Light response curves of a potato crop (with extra dressings of N, P, K and Mg) on several dates. Sinderhoeve, 1973.

Table 1. Net production (photosynthesis minus respiration) integrated from the CO_2 measurements over 24 hours. Varsseveld, 1971.

Dates	Total radiation J cm^{-2} day^{-1}	Plotnumbers	Net production (kg CH_2O ha^{-1})	
			untreated	B9
22 June	1487	2A, 1	218	199
23 June	1907	2A, 1	300	292
24 June	2205	6, 5B	383	350
9 August	1037	2A, 1	168	197
11 August	1067	6, 5	179	194
31 August	1302	6, 5	116	111

34

The net production per day (photosynthesis minus respiration) in 1971 is presented in Table 1. The treated plots had a slightly lower net production than the untreated plants in June, and a higher one on 9-11 August. The results do not permit any conclusion on the effect of the growth retardant B9 on photosynthesis of potatoes.

In the experiment of 1973 the maximum rate of net photosynthesis (Fig. 28) was much lower than in 1971 probably because of the dry and hot summer and the light soil. The rate of net photosynthesis decreased during the season independent of the light intensity. In Fig. 29 the photosynthesis
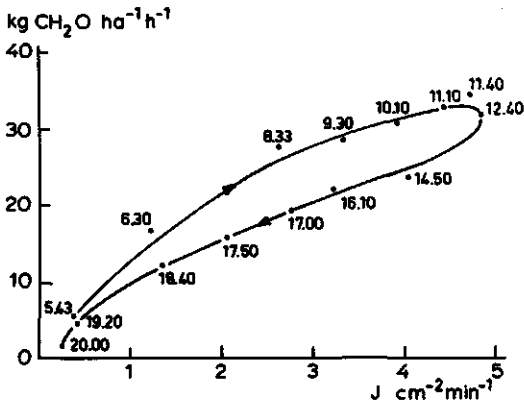
Fig. 29. Light response curve of a potato crop (with extra dressings of N, P, K and Mg) at different moments of the day. Sinderhoeve, 9 July 1973.

Table 2. Net production integrated over 24 hours. Sinderhoeve, 1973.

Dates	Total radiation ($J\ cm^{-2}\ day^{-1}$)	Plotnumbers	Net production (kg $CH_2O\ ha^{-1}$)	
			untreated	with extra dressings
26-27 June	2432	4, 3	249	271
27-28 June	1907	4, 3	208	221
28-29 June	1382	4, 3	202	210
9-10 July	2251	1, 2	272	282
10-11 July	1714	1, 2	200	200
11-12 July	777	1, 2	148	159
6- 7 August	2029	4, 3	200	243
7- 8 August	2041	4, 3	217	264
8- 9 August	2155	1, 2	213	292
17-18 September	878	2		94
17-18 September	878	3		99

at subsequent moments of the day is plotted against light intensity. The net photosynthesis - at the same light intensity - is lower in the afternoon than in the morning. The net production per day of the plots with extra dressings was in all cases except for one larger than that of the untreated plots, even shortly after the first extra-dressing in June (Table 2). In some other field experiments the effect of new growth of foliage on tuber yield was unfavourable. However, no adverse effect of such regrowth was found in the present measurement of photosynthesis and respiration.

7 Flax

K.B.A. Bodlaender

Heavy lodging can reduce the yield and quality of flax crops. The risk of lodging can be prevented or reduced by spraying the growth regulating substance Ethephon on the foliage. Stem elongation is temporarily reduced (Bodlaender & van der Waart, 1973). In 1974 the direct effect of Ethephon on the photosynthesis and respiration of flax was studied.

The flax crop, variety Reina, was grown on river clay near Lienden. Ethephon was sprayed on 31 May at a plant height of 30-45 cm. Due to the very dry spring emergence and plant growth were irregular and soil coverage by the foliage was suboptimal in the treated plots. The untreated plants were about 15 cm higher than the treated ones during the measurements of the photosynthesis.

The enclosures had a surface of 80 cm x 80 cm, and a height of 70 and 120 cm, respectively. The measurements were made from 10 June till 20 June.

In Fig. 30 the net photosynthesis and respiration, together with light intensity and temperature, are plotted against time. The untreated plots had a higher rate of net photosynthesis than the treated one, but also a higher rate of respiration. The difference in net production per ha is also shown in Table 3.

The lower rate of photosynthesis of the treated plots may be due to the lower soil coverage of these plots. In Fig. 31 the net photosynthesis of treated and untreated flax crops on two dates is plotted against light inten-

Table 3. Net production (photosynthesis minus respiration) integrated from the CO_2 measurements over 24 hours. Lienden, 1974.

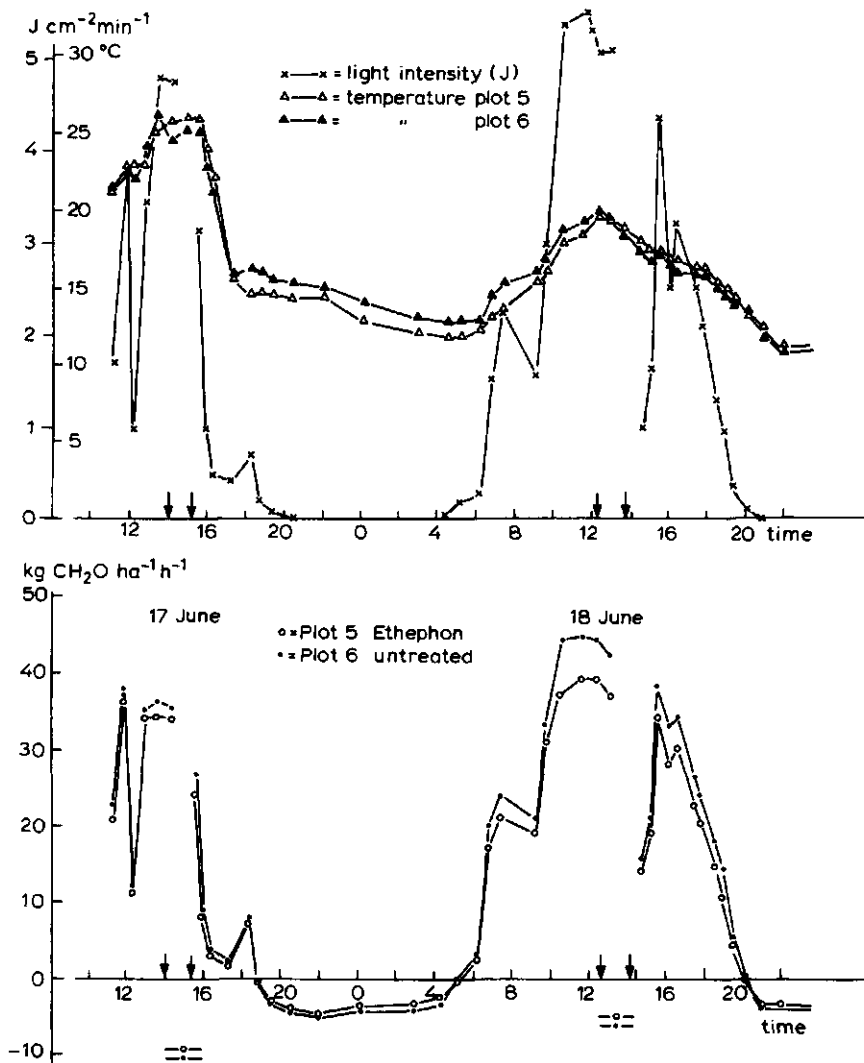| Dates	Total radiation (J cm^{-2} day^{-1})	Plotnumbers	Net production (kg CH$_2$O ha^{-1})	
			untreated	Ethephon
10-11 June	1289	1, 2	182	187
12-13 June	2369	3, 4	301	298
17-18 June	1982	6, 5	258	230
19-20 June	1739	8, 7	255	232

Fig. 30. Light intensity, temperatures (in two enclosures) and net photosynthesis and respiration (in kg CH_2O ha^{-1} h^{-1}) of two flax crops (untreated and treated with Ethephon on 31 May) during two days. Lienden, 1974. Between arrows: dark respiration during the day.

sity. In the first week no difference was found between treated and untreated plants; in the second week, however, the difference was distinct.

High light intensity was more effective at the later measurement than at the earlier one.
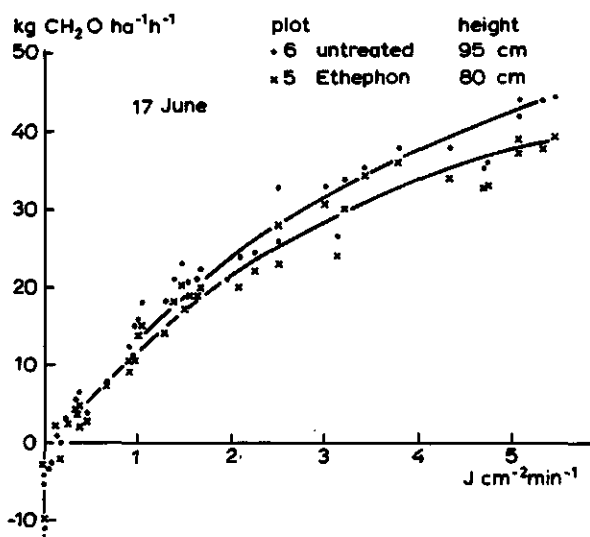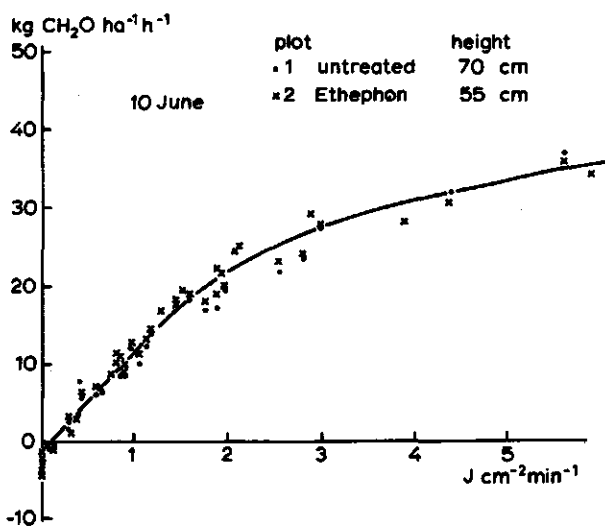
Fig. 31. Light response
curves of two flax crops
(untreated and treated
with Ethephon on 31 May)
on two dates. Lienden,
1974.

8 Sugar beets

K.B.A. Bodlaender

In sugar-beets regrowth of the foliage in the later part of the season can influence root and sugar production unfavourably under certain conditions. Several growth regulating substances were sprayed on the foliage to inhibit this foliage growth and to promote root growth and sugar production. Photosynthesis and respiration of treated and untreated plots were measured.

The growth regulating substances B9 and MH were sprayed on 18 July, 1974 on a sugar-beet crop, variety Monohil, on clay soil near Kraggenburg, Noordoostpolder. The foliage growth of the untreated plots was not very vigorous and ended rather early. Some regrowth of the foliage occurred.
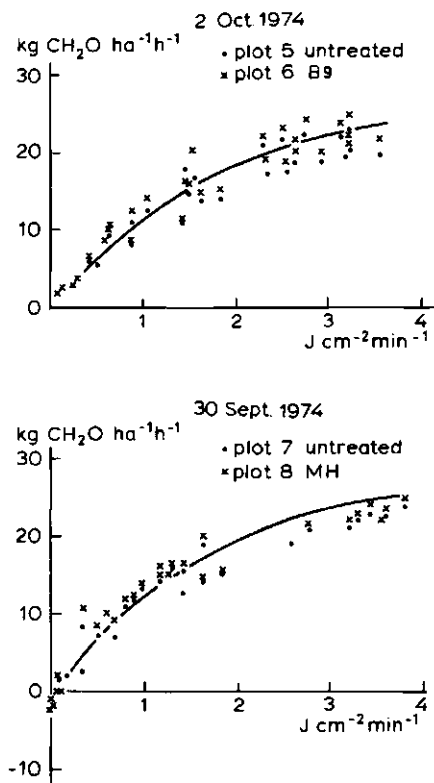

Fig. 32. Light response curves of sugar-beet crops (untreated and treated with B9 or MH on 18 July). Kraggenburg, Noordoostpolder, 1974.

40

Table 4. Net production (photosynthesis minus respiration) integrated from the CO_2 measurements over 24 hours. Kraggenburg, Noordoostpolder, 1974.

Dates	Total radiation ($J\ cm^{-2}\ day^{-1}$)	Plotnumbers	Net production (kg $CH_2O\ ha^{-1}$)		
			untreated	B9	MH
23 September	651	7,8	103		113
25 September	1407	5,6	174	183	
30 September	811	7,8	123		130
2 October	920	5,6	119	128	

The enclosures measured 150 cm x 133 cm, and were 70 cm high; they contained 15 plants (3 rows). The measurements were made late in the season from 23 September till 2 October. Weather conditions were bad, light intensity being often low. The older leaves were yellowing, the younger leaves (regrowth) were still quite dark green. In Fig. 32 the net photosynthesis was slightly higher in the treated than in the untreated plots. The net production per day is also slightly higher in the treated plots than in the untreated ones (Table 4). These few results do not allow more definite conclusions.

41

9 Stubble turnips

H. Toxopeus

Crop photosynthesis activity of canopies of stubble turnip plots were measured during October (1973) at which time of the year the crop is supposed to be still growing. The purpose of the measurement was to get information on the photosynthesis activity during late autumn.

This fresh fodder crop is one of the cultivated forms of the 20-chromosome group of *Brassica* species: *Brassica (campestris* ssp.) *rapa* L. In practice stubble turnips are sown after small grain crops, like rye or summer barley on around 10 August. Depending on autumn conditions the crop canopy closes in the second part of September. Canopy build up continues into early October when the leaf area index attains values of about 4. At about this time bulbing starts and is supposed to continue until the end of November and onwards depending on weather conditions.

Harvesting takes place from early November onwards. Average yields are in the order of 40-50 tonnes fresh fodder (with foliage and roots). Dry matter content of the roots is between 8 and 10 % and of the foliage 9-12%. The experimental plots were drilled on 2 August at a spacing of 37.5 cm between rows (the equivalent of $1\frac{1}{2}$ kg seed per ha), on a light sandy soil at Renkum (SVP experimental fields). During early September the rows were thinned to an approximate spacing of 2-4 cm between individual plants. Three varieties were sown: Siloga, an old variety highly valued on account of its 'strong'

Table 5. Yield of single plots of two varieties of stubble turnips.

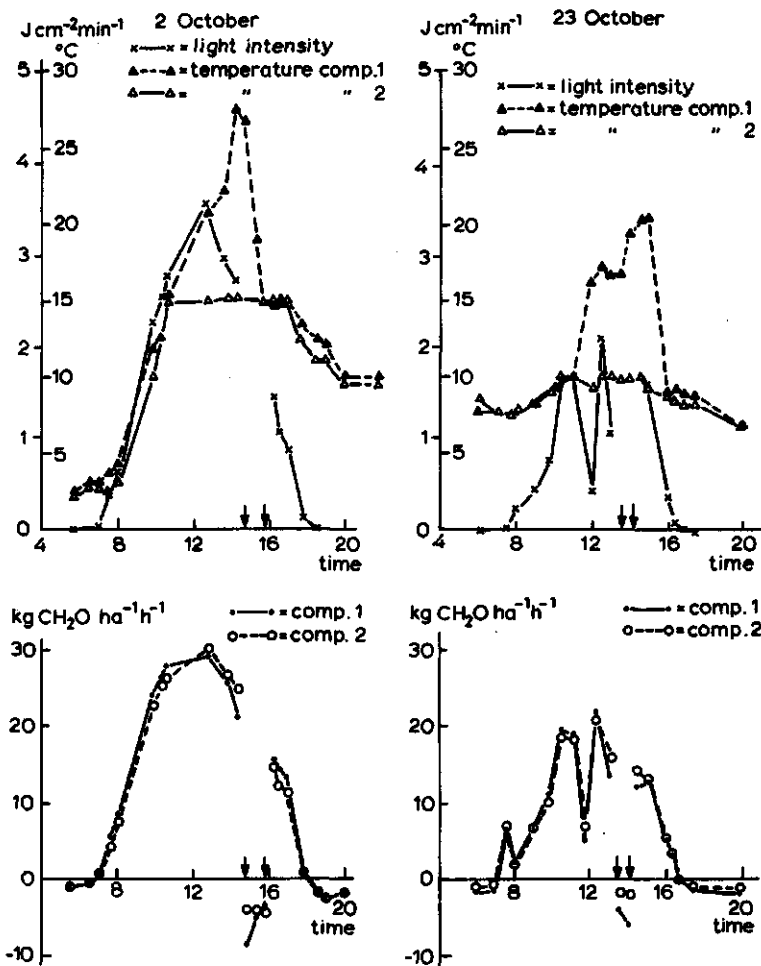|	Date of harvest	LAI	Weight in tonnes per ha					
			fresh weight			dry weight		
			total	foliage	roots	total	foliage	roots
Siloga	1 October	4.8	39.1	35.7	3.4	2.9	2.6	0.3
	22 October	4.3	51.6	43.5	8.1	4.5	3.7	0.8
Ponda	1 October	4.1	39.1	35.9	3.2	2.7	2.4	0.3
	22 October	4.8	65.8	57.5	8.3	4.9	4.2	0.7

Fig. 33. Light intensity, temperature and net photosynthesis and respiration in kg CH_2O ha^{-1} h^{-1} of two stubble turnip crops, varieties Siloga (comp. 1) and Ponda (comp. 2), on two dates.

foliage but with a relatively poor turnip quality (compartment 1); Ponda, one of the higher-yielding modern varieties with good foliage and bulbing characters (compartment 2); and Taronda, a new variety. Only the results of Siloga and Ponda are shown (Fig. 33 and 34). A single plot of 2.25 m^2 was harvested of each variety on 1 and 22 October. Leaf area index and fresh and dry matter yields computed to tonnes per ha are shown in Table 5.
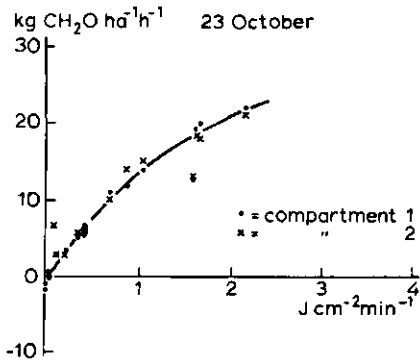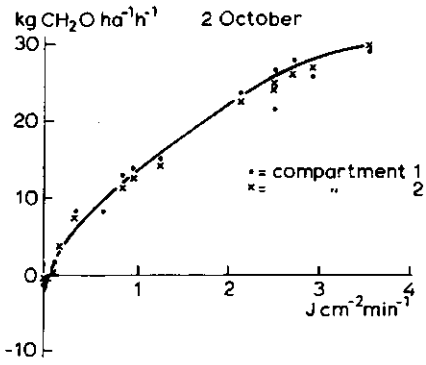
kg CH$_2$O ha^{-1}h^{-1} 2 October

30

20

10

0

-10

1   2   3   4
J cm^{-2}min^{-1}

• = compartment 1
x =   "   2

kg CH$_2$O ha^{-1}h^{-1} 23 October

30

20

10

0

-10

1   2   3   4
J cm^{-2}min^{-1}

• = compartment 1
x x   "   2

Fig. 34. Light response curves of two stubble turnip crops (varieties Siloga, comp. 1 and Ponda, comp. 2) on two dates.

9.1   RESULTS

At certain times during the experiments warm air was blown into one of the compartments and within these periods light was shaded during a short time in both compartments. Temperature as such does not seem to affect net photosynthesis. A high temperature during a dark period, however, results in a substantially higher loss of carbohydrates (dissimilation loss) as compared to the low temperature treatment.

Otherwise the net photosynthesis curves of both compartments follow the energy curve very closely as is visualized in the light response curves.

Literature

This list contains some papers referred to in the text. Most titles, however, are given to provide some information on other work by Dutch authors on this subject.

Alberda, Th., 1969. The effect of low temperature on dry matter production, chlorophyll concentration and photosynthesis of maize plants of different ages. Acta. bot. neerl. 18: 39-49.

Alberda, Th., 1970. The influence of carbohydrate reserves on respiration, photosynthesis and dry matter production. Proc. 11th int. Grassld Congr.: 517-522.

Alberda, Th. & L. Sibma, 1968. Dry matter production and light interception of crop surfaces. J. Br. Grassld Soc. 23: 206-215.

Bodlaender, K.B.A., 1968. The influence of the growth retardant B995 on potato growth and yield. Seed Potato 8: 194-196.

Bodlaender, K.B.A. & S. Algra, 1966. Influence of the growth retardant B995 on growth and yield of potatoes. Eur. Potato J. 9: 242-258.

Bodlaender, K.B.A. & M. van der Waart, 1973. The influence of growth regulating substances on growth and yield of flax. Fibra 18: 4-26.

Dantuma, G., 1973. Rates of photosynthesis in leaves of wheat and barley varieties. Neth. J. agric. Sci. 21: 188-198.

Hanway, J.J., 1966. How a cornplant develops. Spec. Rep. Iowa St. Univ. 48.

Keulen, H. van & W. Louwerse, 1973. Simulation models for plant production. Proc. Symp. Agromet. Wheat Crop. (Braunschweig, 1973).

Keulen, H. van, W. Louwerse, L. Sibma & Th. Alberda, 1975. Crop simulation and experimental evaluation. In: J.P. Cooper (Ed.), Photosynthesis and productivity in different environments, 623-643. Cambridge University Press, London.

Laar, H.H. van & F.W.T. Penning de Vries, 1972. CO_2-assimilation light response curves of leaves; some experimental data. Versl. Inst. Biol. Scheik. Onderz. Landb.gew. 62.

Louwerse, W. & J.W. Eikhoudt, 1975. A mobile laboratory for measuring photosynthesis, respiration and transpiration of field crops. Photosynthetica 9: 31-34.

Louwerse, W. & J.L.P. van Oorschot, 1969. An assembly for routine measurements of photosynthesis, respiration and transpiration of intact plants under controlled conditions. Photosynthetica 3: 305-315.

Makkink, G.F. & H.D.J. van Heemst, 1972. De weestand van bladeren als functie van hun watergehalte en het licht. Versl. Landbouwk. Onderz. 774.

Penning de Vries, F.W.T., 1972. Respiration and growth. In: A.R. Rees, K.E. Cockshull, D.W. Hand & R.G. Hurd (Ed.), Crop processes in controlled environments, pp. 327-347. Academic Press, London/New York.

Penning de Vries, F.W.T., 1975. Use of assimilates in higher plants. In: J.P. Cooper (Ed.), Photosynthesis and productivity in different environments, pp. 459-480. Cambridge University Press, London.

Penning de Vries, F.W.T., 1977. Simulation der Assimilation und Transpiration der Pflanzendecke nach grundlegenden Gesetze. Proc. Symp. Biophys. Pflanzl. Systeme. Fischer Verlag, Jena (in press).
Wit, C.T. de & F.W.T. Penning de Vries, 1977. Simulation of assimilation respiration and transpiration of crop surfaces. Series 'Simulation Monographs'. Pudoc, Wageningen.