

Measurement and simulation of crop photosynthesis of cucumber (*Cucumis sativus* L.) in greenhouses

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Abstract

Short-term photosynthesis measurements were performed in a cucumber crop (*Cucumis sativus* L.) in three experimental greenhouse compartments. The greenhouse was used as a measuring cuvette for the whole canopy. The calculated carbon dioxide balance of the greenhouse was based on measurements of the carbon dioxide concentrations inside and outdoors, combined with on-line measurement of the ventilation rate.

The method is described and results of three characteristic days are presented. A positive correlation was found between photosynthesis rate and both radiation and CO₂ concentration. Measured environmental conditions were given as input data into a simulation model. The simulated and measured rates of photosynthesis generally showed a close similarity.

Introduction

In horticulture, as in other agricultural sectors, crop simulation models are being developed for several purposes, e.g. scientific analysis, production planning or crop management. In greenhouse horticulture, where crops are grown in an artificial environment, an additional purpose for models is to employ them for optimal, automatic climate control (Challa, 1985). A model for this application should meet special requirements, e.g. the time scale for calculations must be small (order of magnitude: some minutes). In the Netherlands a project group is working on a greenhouse climate control system consisting of a physiological, a physical and an economic model, combined with an optimization algorithm. As a first result an optimiza-

tion program for CO₂ control has been developed (Challa & Schapendonk, 1986; Nederhoff, 1988).

An essential part of the work is the validation of the physiological models for several crops. This should be done on different levels: light interception, photosynthesis, dry matter production and distribution, and crop growth and production. Ideally, validation should be performed on a fullgrown crop in a relatively large greenhouse. Photosynthesis measurements on such a scale are rare (Dayan et al., 1985). More often the photosynthesis is measured on one leaf (e.g. McPherson et al., 1983; Ho et al., 1984), on a single plant (e.g. Gaastra, 1959; Nilwik, 1980; Lakso et al., 1984) or on several plants (Schapendonk & Brouwer, 1985) in a measuring cuvette. In these small-scale measurements, the conditions differ from those in greenhouses, especially with respect to light interception (Nederhoff, 1983). Such measurements in cuvettes are therefore not suitable for validation of crop models meant for practical use.

Lake (1966) proposed photosynthesis measurements using the entire greenhouse as a measuring cuvette for a whole plant stand. This method is based on determining the carbon dioxide balance of the greenhouse air. At the same time the ventilation rate of the greenhouse should be measured (on-line) with a tracer gas, for which nitrous oxide (N₂O) can be used. This method with nitrous oxide as tracer gas was applied earlier for photosynthesis measurements (Hand & Bowman, 1969) and for ventilation measurements (Goedhart et al., 1984). Dayan et al. (1985) applied this method for photosynthesis measurements in relatively large-size greenhouses. Matthews et al. (1987) described a CO₂ control system, based on off-line ventilation measurements with N₂O.

In this paper, model validation on the level of crop photosynthesis is reported. The method of Lake (1966) is employed to measure photosynthesis of a cucumber crop in experimental greenhouses. The environmental data that were acquired in the experiment were given as input data into the simulation model. The photosynthesis rates simulated on the basis of these data were compared with the measured photosynthesis.

Materials and methods

Greenhouse

The measurements were done in three compartments (9.6 m × 6 m; average height 2.95 m), of a Venlo-type greenhouse complex. Ventilation windows, situated in the roof, were opened when necessary for cooling, also during the measurements. The walls between compartments were made as air-tight as possible with silicone paste, in order to avoid uncontrolled and unmeasurable inflow of CO₂ and N₂O from adjacent compartments.

The ventilation rate of the compartments was determined earlier with tracer gas measurements (Nederhoff et al., 1985) and appeared to be proportional with wind velocity and window aperture (up to 20 %):

$$S = 0.073 \times u \times (w + l) \quad (1)$$

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where: S = air exchange rate (volume per volume per hour) (h^{-1})

u = wind velocity (average in the time interval) (m s^{-1})

w = window aperture (relative: 100 % = 0.66 m gap) (%)

l = 1.33, a constant describing the leak of the greenhouse (%).

In principle it is possible to use Equation 1 for the estimation of ventilation and photosynthesis. This method is followed by Matthews et al. (1987). However, on-line measurement of the ventilation is preferred, because then any deviation or delay in air exchange rate is detected directly and the photosynthesis is calculated more accurately.

Crop

A cucumber crop (*Cucumis sativus* L. cv. Corona), was planted on rockwool on 13 August 1987. Plant density was 1.92 plants per m^2 . The photosynthesis measurements were started on 25 August, 12 days after planting, and ended on 20 October, when the LAI was 3.4, the dry weight of leaves was about 56 g and of stems about 58 g per plant. Every two or three weeks, five plants were taken from an adjacent, identical greenhouse compartment. From these plants the dry weights of leaves and stems, the number of leaves and the leaf area were determined.

Cucumber fruits were harvested twice a week, the first harvest was on 10 September and the last on 22 October. At each harvest the fruits were classified, counted and weighed. Sometimes, pruning of leaves was applied. A summary of the plant parameters is given in Table 1.

Table 1. Plant parameters of a cucumber crop on 5 dates in 1987 during the photosynthesis experiment. Data are given per plant, except leaf area index (m^2 leaf per m^2 cultivated greenhouse area) and dry matter content (%).

Parameter	20 Aug.	03 Sep.	19 Sep.	10 Oct.	22 Oct.
Leaf area (m^2)	0.2	1.5	1.8	1.6	1.8
Leaf area index	0.3	3.0	3.5	3.1	3.4
Fresh weight of leaves (g)	35.2	396.7	459.3	366.3	423.0
Fresh weight of stems (g)	54.5	511.4	703.6	784.1	1014.0
Dry weight of leaves (g)	4.6	41.6	47.5	42.3	55.6
Dry weight of stems (g)	2.7	25.5	32.9	41.7	57.6
Dry matter content of leaves (%)	13.1	10.5	10.3	11.5	13.3
Dry matter content of stems (%)	5.0	5.0	4.7	5.3	5.7
<i>Cumulative weights</i>					
Fresh weight of harvested fruits (g)	—	—	2109	5244	6625
Dry weight of harvested fruits ¹ (g)	—	—	57	142	179
Estimated dry weight of leaves removed by pruning (g)	—	—	5.5	7.6	7.6
Estimated dry matter production ² (g)	7.3	74.4	158	256	321

¹ Calculated from fresh weights, assuming a dry matter content of 2.7 %.

² Cumulative data, including fruits on plant, harvested fruits and removed leaves, excluding roots.

Environmental factors

The average weather conditions in the Netherlands at the beginning and the end of the experiment respectively, were:

- average minimum temperature: 14.1 and 8.5 °C;
- average maximum temperature: 19.6 and 15.0 °C;
- daily sum of global radiation: 16.0 and 7.2 MJ·m⁻²;
- daylength: 14.3 and 10.0 h.

The environmental conditions maintained in the greenhouse were comparable to those in commercial greenhouse culture. Setpoint for heating was 25 °C by day and 20 °C at night. From the beginning of October a minimum heating-pipe temperature of 50 °C and a small minimum ventilation were maintained in order to decrease relative humidity and consequently the risk of fungal diseases.

Relevant environmental factors were measured and recorded, to be used as input data for the photosynthesis model. The recorded factors were: CO₂ concentrations as measured by the CO₂ analyser, global radiation measured outside (diffuse and total), Photosynthetically Active Radiation (PAR) measured inside and outside the greenhouse, and temperature and humidity of the greenhouse air. The factors were measured on a one-minute basis, but were averaged over the calculation cycle (about 11 minutes, see below).

Determination of photosynthesis

In this work the photosynthesis rate of a greenhouse cucumber crop is determined by measuring the carbon dioxide mass balance of the greenhouse air. The greenhouse was an open system because the roof was not completely air-tight and the compartments were ventilated when necessary for temperature control. The general balance equation for CO₂ is:

$$dC_g(t)/dt = (G + I - P - L)/(h \times \rho) \quad (2)$$

where:

t = time (h)

$C_g(t)$ = CO₂ concentration in the greenhouse at time t (ppm = ml m⁻³)

G = release of CO₂ from the ground (g m⁻² h⁻¹)

I = suppletion (injection) of CO₂ (g m⁻² h⁻¹)

P = photosynthesis rate (g m⁻² h⁻¹)

L = loss of CO₂ by ventilation (including leak) (g m⁻² h⁻¹)

h = average height of the greenhouse (m)

ρ = gas density of CO₂ at 20 °C and 1013 mb, 1.83×10^{-3} (g ml⁻¹).

The supply of CO₂ (I) was off during the measurements and the release of CO₂ from the soil (G) was zero, since the soil was covered with concrete. Therefore Equation 2 can be rewritten as:

$$P = -dC_g(t)/dt \times \rho \times h - L \quad (3)$$

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The rate of decay of the CO₂ concentration in the greenhouse air, $dC_g(t)/dt$, was determined by frequent measurements of the CO₂ concentration in each compartment. The loss of CO₂ by leak and ventilation, L , was calculated from the ventilation rate S , as follows:

$$L = S \times h \times \rho \times \int C'(t)dt \quad (4a)$$

$$C'(t) = C_g(t) - C_a(t) \quad (4b)$$

where:

$C'(t)$ = CO₂ difference between inside and outside air (ppm)

$C_a(t)$ = CO₂ concentration of the ambient air (ppm).

For relatively short periods (some minutes) as were used in these experiments, the integral $\int C'(t)dt$ can be replaced by the average value $C'(t)$ over the period. Equation 4a can be written as:

$$L = S \times h \times \rho \times C'(t) \quad (4c)$$

S was determined accurately with the tracer gas nitrous oxide (N₂O). This gas was injected to a level of about 300 ppm. Then the N₂O supply was stopped and after a short waiting time to allow mixing of the gases in the air, the measurement was started. This method, known as the decay rate method, was described by Goedhart et al. (1984). In this experiment the time and frequency for the N₂O concentration measurements were the same as those for CO₂ (see below). The ventilation rate S was calculated according to:

$$S = d(\ln(N(t)))/dt \quad (5)$$

where:

$N(t)$ = N₂O concentration at time t (ppm).

The CO₂ concentration of the ambient air, necessary in Eq. 4, was measured in every measuring cycle. Because in one measuring period (some hours) the change in the ambient CO₂ concentration is rather small (some ppm), one average ambient CO₂ value over the measuring period was used.

Instruments and other equipment

The equipment consisted of two infra-red gas analysers (Hartmann & Braun, URAS 3G): one for CO₂ and one for N₂O, a microcomputer and, per greenhouse compartment, a gas sampling system and a gas supply and gas distribution system and fan. The system for injection and distribution of the gases consisted of a network of plastic tubes (diameter 0.04 m), located on the ground with intervals of 3.2 m. Carbon dioxide was obtained from a tank and nitrous oxide from pressure bottles.

Gas was subsequently sampled in four objects: three greenhouse compartments and the outside environment. There was one central air pump and one carbon filter for the four objects. In each compartment a sampling system of 6 mm tubes with four inlets was used. While one compartment was sampled, the air in the three other sampling objects was drawn continuously by another pump, in order to maintain air movement in the sampling system.

The gas concentration measurements were controlled and recorded on tape by an Epson HX-20 microcomputer. The data were transferred to a VAX-750 computer, on which the photosynthesis calculations were performed. Relevant environmental factors (radiation intensities, air temperature etc.) were recorded using a MICRO-VAX system and also transferred to the VAX-750.

Measuring and calculating cycles

Measurements were done by day and night. The first measurement was on 25 August and the last on 20 October. Mostly, a measurement lasted one to several hours, after which a new measurement was started, with a short delay of about 15 minutes. In this way, measurements were done on 36 days and 20 nights, together about 300 hours.

The measuring cycle depended on the relaxation time of the analysers, which was 30 s, the number of sampling objects, which was four and the time-dependent variation in gas concentration. By day the measuring cycle was set on 208 s (4×52). At night it was 688 s (4×172), because then the rate of changes of gas concentrations was comparatively low.

The calculation cycle was different. In order to smooth out the variances caused by measuring errors, the photosynthesis calculations with Equations 3, 4 and 5 were applied on four data of the CO_2 and N_2O concentration, using a regression calculation. So the time interval for the calculation of photosynthesis (at daytime) was 624 s (4×208 s). For the calculation of the respiration (at night) 2 data were used, making a calculation interval of 688 s.

Simulation model

The photosynthesis model is based on the model SUCROS (Simple and Universal CROp growth Simulator, Spitters et al., 1988). The model calculates the net crop photosynthesis from gross photosynthesis, maintenance and growth respiration, as described by Gijzen & ten Cate (1988). The model is an integration of physical models: one for the calculation of fluxes of direct and diffuse light into the greenhouse (Bot, 1983) and one for the calculation of the light distribution in the canopy, and a physiological model for leaf photosynthesis. For the light distribution the crop is assumed to be a horizontally homogeneous canopy.

The model for leaf photosynthesis was a summary model of the biochemical theory of leaf photosynthesis as described by Farquhar et al. (1980). The summary model is preferred because its two key parameters (the efficiency of light use at low light intensities and the rate of leaf photosynthesis at light saturation) can be compared

with many other values already published (e.g. Acock et al., 1978; Ehleringer & Pearcy, 1983). In the model, the values of both parameters are influenced by CO₂ concentration and temperature.

The values of the main parameters and variables in the model were:

- azimuth of greenhouse: North-South;
- transmissivity of greenhouse cover for diffuse¹ radiation: 0.63;
- leaf area index of crop: increasing with time, see Table 1;
- leaf angle distribution: horizontal;
- light use efficiency at low light intensity²: 0.011 mg CO₂ J⁻¹
- gross photosynthesis rate at light saturation²: 0.911 mg CO₂ m⁻² (leaf area) s⁻¹
- rate of maintenance respiration of total crop: 0.5 g CO₂ m⁻² (greenhouse area) h⁻¹. The maintenance respiration was derived from measurements at night. Then the plants released CO₂ by both growth respiration and maintenance respiration. At the end of the night, the growth respiration was supposed to have declined to zero.

Results

From the large amount of data (36 measuring days in three compartments), three characteristic examples were chosen: from one compartment one day at the beginning, one at the middle and one at the end of the experiment were selected to illustrate the comparison between simulated and measured photosynthesis rates.

Fig. 1 shows the results of 26 August, two weeks after planting. In Fig. 1a the environmental conditions are plotted: global radiation outside (measured), PAR inside the greenhouse (calculated) and CO₂ concentration of the greenhouse air. In Fig. 1b the measured and simulated photosynthesis rates are plotted. 26 August was a partly cloudy day. Peak radiation (of about 700 W m⁻²) occurred between 12.30 and 14.30 h. The temperature (not in the figures) was raised from 22 °C in the morning up to 28 °C around noon. There was no carbon dioxide enrichment on this day. Due to ventilation, which varied from 3.5 to 13.2 h⁻¹, the CO₂ concentration stayed on a level of about 330 ppm. The measured photosynthesis varied between zero (or even negative values) and almost 2 g m⁻² h⁻¹.

Fig. 2 shows the data of 2 October. This was a sunny, cloudless day with a maximum radiation intensity around 530 W m⁻². CO₂ was injected until about 500 or 700 ppm, every time the concentration fell below 330 ppm. The temperature varied between 20.5 °C in the morning and almost 28 °C between 12 and 14 h. The measured and simulated photosynthesis reached peaks of about 3 g CO₂ m⁻² h⁻¹.

Fig. 3 shows the same data for 20 October, the last day of the experiment. That day it was partly cloudy and the maximum radiation (about 300 W m⁻²) occurred around noon. The temperature fluctuated between 20.2 and 24 °C. CO₂ was injected three times on this day, up to 600-700 ppm. The peaks in (measured) photosynthesis exceeded 2 g CO₂ m⁻² h⁻¹.

¹ Light transmissivity for direct light was calculated.

² At 340 ppm CO₂ and 25 °C.

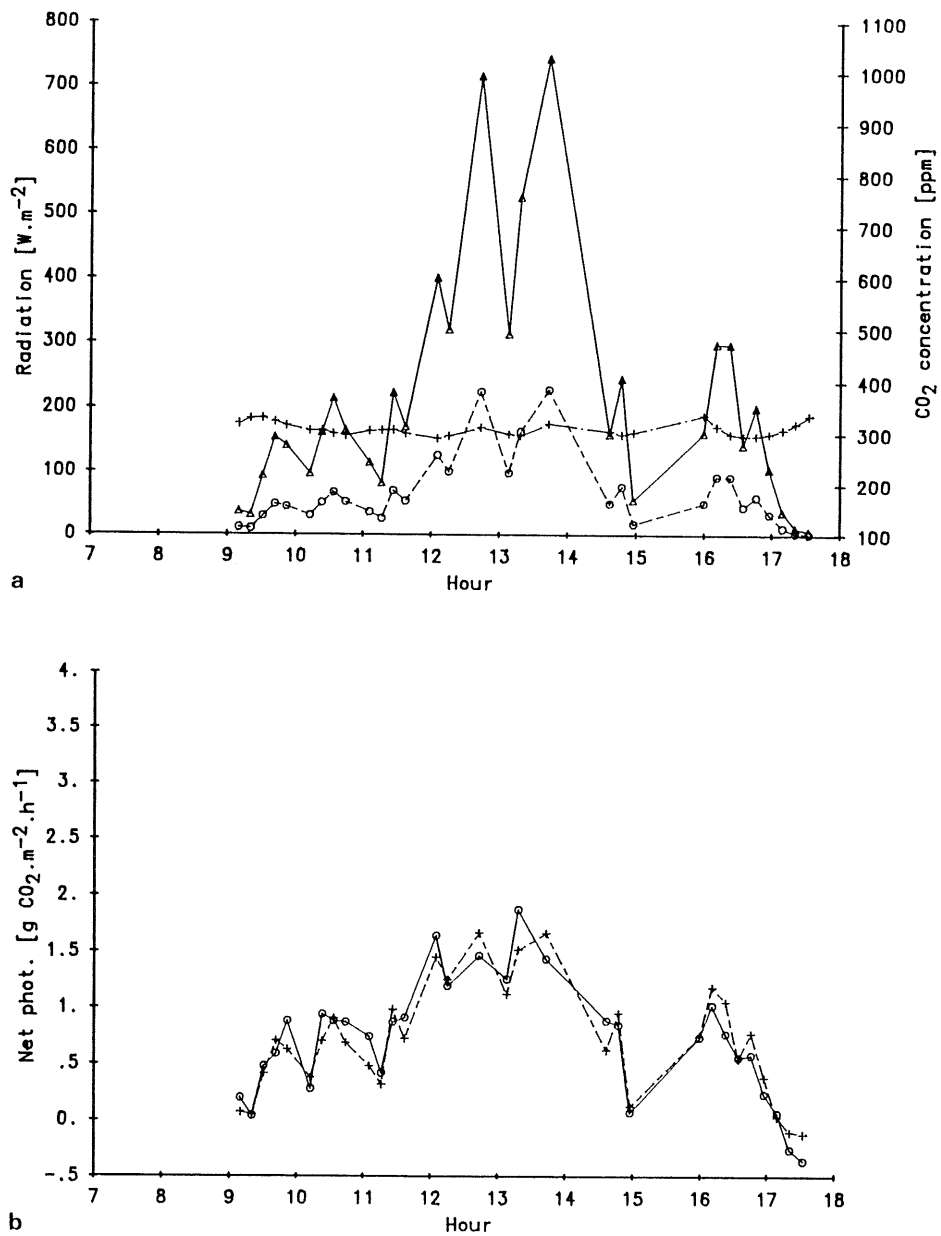
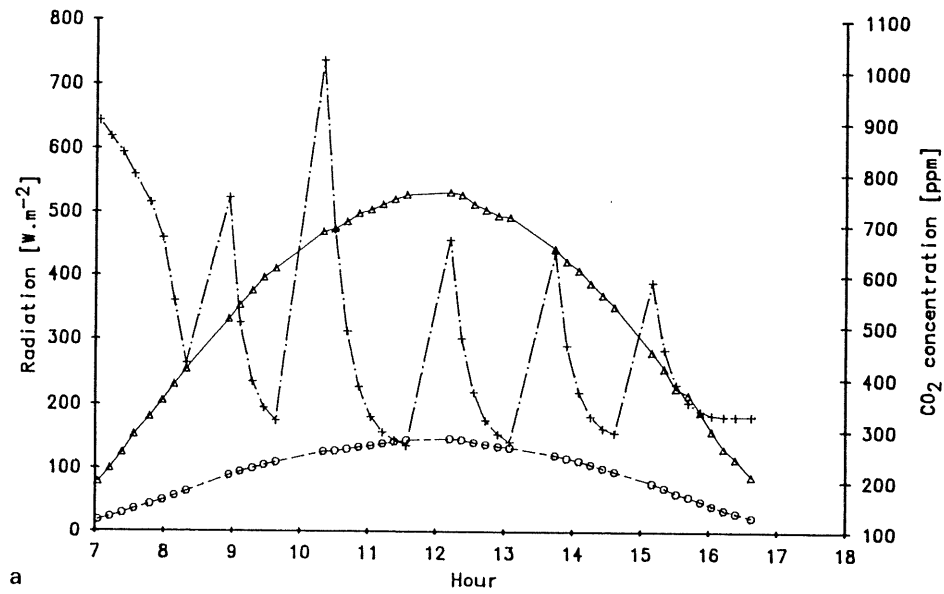
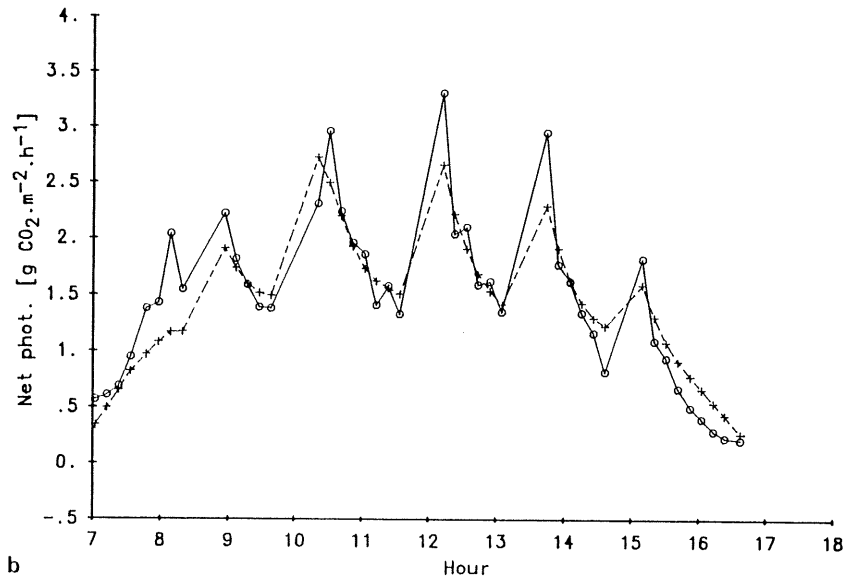


Fig. 1. (a) Main environmental data of 26 August 1987, acquired during photosynthesis measurements: Δ — Δ global radiation, measured outside ($W m^{-2}$); \circ - - \circ Photosynthetically Active Radiation, calculated values inside greenhouse ($W m^{-2}$); + — . — + CO_2 concentration of greenhouse air (ppm). (b) Photosynthesis rates ($g CO_2 m^{-2} h^{-1}$) of 26 August 1987, as measured in one greenhouse compartment and simulated with the acquired environmental data and plant parameters: \circ — \circ measured and + - - - + simulated photosynthesis.

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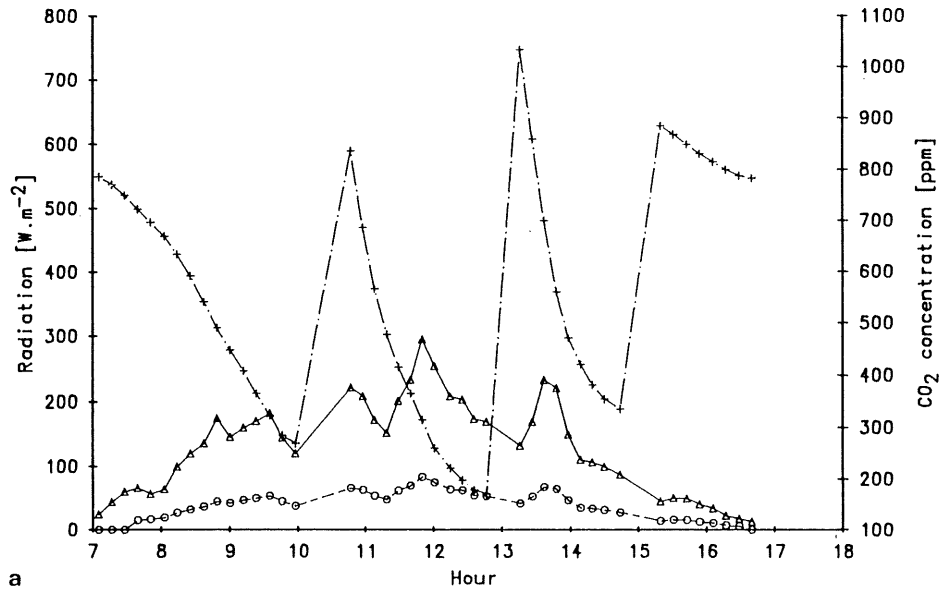


a

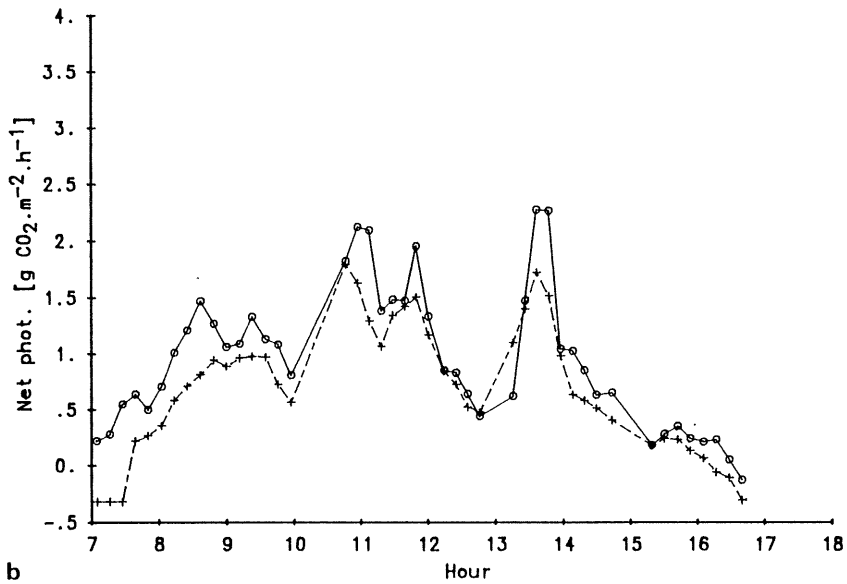


b

Fig. 2 (a,b). As Fig. 1, data of 2 October 1987.



a



b

Fig. 3 (a,b). As Fig. 1, data of 20 October 1987.

Discussion

In Fig. 1 the results of photosynthesis measurements and simulation are presented for a day with an almost constant CO₂ concentration and a varying radiation. The measured photosynthesis roughly follows the radiation curve. The simulated photosynthesis, which is calculated from the measured data of CO₂ concentration, radiation and temperature, follows exactly the radiation curve. The simulated values are lower than the measured data, especially around 11.00 h and at 13.00 h. These discrepancies cannot be explained. Generally, the discrepancies between simulation and measurement are rather small.

In Fig. 2 results are given for a day with an undisturbed radiation curve and varying CO₂ concentration. Then the photosynthesis measurements follow roughly the radiation line and exactly the CO₂ curve. The pattern in the CO₂ concentration with sharp peaks and dips, is found perfectly in the two photosynthesis curves. It is remarkable that at a peak, the discrepancies between measured and simulated photosynthesis are more pronounced. Apparently, after CO₂ injection the photosynthesis is underestimated by the model. It seems explicable that the crop reacts strongly on a CO₂ injection after a period of CO₂ shortage, as sometimes is suggested. This phenomenon is not taken into account in the simulation model, which is based on more or less continuous CO₂ concentrations. The measured photosynthesis shortly after a CO₂ peak (about 10 minutes later) again shows a good similarity. In general, except for the CO₂ peaks, the simulated data of this day are only slightly higher than the measured data.

The lines in Fig. 3, of 20 October, show a capricious pattern both in radiation and CO₂ concentration (Fig. 3a). Also the photosynthesis (Fig. 3b) is variable. After CO₂ injection peaks (at 10.55 h and 13.20 h) the measured photosynthesis exceeds the simulated photosynthesis, as in Fig. 2b. Again this could be a photosynthesis response to sudden CO₂ enrichment, which is not simulated by the model. In general the simulated photosynthesis is only slightly lower than the measured photosynthesis on this day.

The conclusion of these three measurement days is that the simulation corresponds quite well with the measurements. These results illustrate the utility of the simulation model. Only the performance of the model for dynamic conditions (strong elevation of the CO₂ concentration after a period of CO₂ depletion) causes discrepancies.

In a future publication, the results will be analysed further. Later the model will be improved if necessary and extended for dynamic conditions.

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