

Crop photosynthesis, respiration and dry matter production of maize

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Abstract

Above-ground net photosynthesis and respiration of a maize crop (*Zea mays* L.) was determined in the field during the growing season (mid June – end of October) at regular intervals (1 à 2 weeks) at two temperatures (12.5 and 22.5 °C) by measuring the CO₂ uptake or release in mobile crop enclosures. The actual growth rate of the crop was determined from fortnightly harvests. Temperature dependence of photosynthesis was highest in the early (till mid July) and very late (begin October) stages of crop growth, showing a reduction of about 50 % at the higher irradiances (> 400 W m⁻²). In the period of major dry matter production (mid July-September) the reduction was only 12-15 %. Assuming maintenance respiration to become constant for cobs and grain exceeding a yield of 1000 kg ha⁻¹ and for stems exceeding 2500 kg ha⁻¹, the measured and calculated dark respiration at 22.5 °C matched fairly well. At 12.5 °C the calculation, using the same assumptions, overestimated significantly dark respiration during the first part of the growing period. The carbon balance sheet showed that from the total amount of CO₂ absorbed by the crop (equivalent to 30.7 t DM ha⁻¹), 30 % was lost by above-ground respiration and 50 % was invested in above-ground harvestable material. The remaining 20 % is assumed to be transported to plant parts under the ground. Substantial losses of dry matter at the end of the growing season did not occur.

Keywords: *Zea mays* L., dry matter distribution, gross photosynthesis, net photosynthesis, respiration, growth respiration, maintenance respiration

Introduction

Development, growth and yield of a crop is the result of an interactive response of plants to environmental conditions: temperature, irradiance, water and nutrient supply. For a maize crop, temperature strongly influences early leaf development, growth and duration of the growth cycle. The effects of temperature on development, dry matter production and allocation, and quality of forage maize have been studied extensively (Struik, 1983).

Low soil and air temperatures in N.W. Europe affect germination, seedling growth and leaf appearance to such an extent that full soil cover by the canopy is

delayed until early July (Sibma, 1977). As a consequence, relatively high levels of irradiance in early summer coincide with an incomplete soil cover.

Photosynthesis and respiration of maize plants increase with temperature (Duncan & Hesketh, 1968). Net photosynthesis, however, increases less than the rate of development and the shortening of the growth duration. The ultimate effect on crop yield will also depend on the seasonal pattern of photosynthetically active radiation (PAR). In N.W. Europe, daily radiation drops progressively during the grain-filling phase, due to shortening days and a lower angle of incident sunlight. Struik et al. (1985) found in a greenhouse experiment that under these light conditions a rise in temperature after the 8-leaf stage reduced final dry matter yield because development rate was enhanced more than growth rate.

To improve insight into limitations for growth and yield of a maize forage crop under temperate climatic conditions, whole crop photosynthesis and respiration was studied in a field situation. In particular the conditions which cause a net gain or loss of dry matter in the period close to maturation of the crop are of importance for assessing the optimum harvest date of forage crops. The seasonal pattern of crop photosynthesis and respiration was determined, as well as the effects of temperature and light level in the different growth phases. The theoretical values of the coefficients for growth and maintenance respiration (Penning de Vries et al., 1989) were used to estimate the fraction of the biomass taking part in the maintenance processes. In addition, from the measured photosynthesis and respiration and the dry matter determination at various intermediate harvests, a carbon balance of the plant/soil-system was derived.

Materials and methods

Crop data and equipment

A maize crop (*Zea mays* L., cv. LG 11) was grown at a plant density of 10-11 m⁻² on a sandy soil near Wageningen. The crop was sown on 1 May 1985 and well supplied with nutrients by adequate fertilization. Water shortage did not occur. Net photosynthesis, respiration and transpiration of the maize crop were determined from 17 June until the end of October 1985.

The actual growth rate of the crop was determined from fortnightly harvests of 4 plots with an area of 10.5 m². At each harvest, leaf area, fresh and dry weight of leaves, stems and cobs (husk + spindle + kernels) were determined. C content in the total biomass was determined by micro-elemental analysis.

The exchange of CO₂ and water vapour of 2 enclosed plots with an area of 80 cm x 80 cm was measured at two different temperatures (12.5 and 22.5 °C). The measurements were done with a mobile equipment as described before (Louwerse & Eikhoudt, 1975; Louwerse, 1980). The enclosure consisted of a transparent 'per-spex' chamber, sealed onto a metal frame in the soil. The temperature in the chambers was controlled by an airconditioning unit. A pressure head of 300-400 Pa in the plant chamber and a layer of 3-5 cm of fine gravel on the soil prevented the interference of soil respiration and evaporation. Gas exchange was determined continu-

ously using an open system, by measuring both the CO₂ and H₂O concentration in the ingoing and outgoing air by infra-red gas analysis and the air flux through the chambers. The CO₂ concentration in the enclosures was maintained between 320 and 350 $\mu\text{l l}^{-1}$ during daytime by adding CO₂ from a gas cylinder as required. During night time an occasional overshoot occurred. Temperature was monitored by copper/constantan thermocouples and the humidity with capacitive hygrometers (Vaisala probes).

The total global radiation was measured outside the chamber with a solarimeter (Kipp, spectral range: 305-2800 nm) and corrected for reflection and absorption of the walls of the chambers (about 12 %).

All the parameters were recorded every 5 minutes. During the first three weeks the measurements were carried out 4 to 5 days weekly, but from 8 July onwards only every second week. In the measuring period, temperatures in the chambers were changed at 24-hour or 48-hour intervals.

The microclimate in the crop enclosures differed in some respect from the ambient. In the enclosures, CO₂ and water vapour were uniformly distributed and temperature gradients were small. Moreover, the humidity in the chamber was lower than outside because of condensation at the cooling body of the air-conditioner. This occurred especially during the night at lower transpiration rates.

Calculations

The CO₂ exchange measurements (Louwse & Eikhoudt, 1975) were used to calculate the daily growth rate. To eliminate the effects of the response time of the equipment to rapid changes in light conditions, hourly means were used to construct light-response curves at both temperatures in each measuring period. The same procedure was used for the CO₂ release from respiration during the night. The rate of gross photosynthesis was obtained by summing up net photosynthesis rate and mean above-ground rate of respiration during the night, assuming an equal respiration during day and night at the same temperature. From these data, light-response curves for gross photosynthesis at 12.5 and 22.5 °C were derived.

For field conditions the actual gross photosynthesis and respiration were determined from these curves by linear interpolation using the actual hourly means of radiation and temperature. Daily gross photosynthesis, respiration, and consequently net photosynthesis were obtained by integration of these values. Finally, CO₂ exchange was converted to dry matter production using a conversion factor of 0.606, based on the measured carbon concentration in the tissue (45 % \pm 1 % by analysis) and transfer of CO₂ to C.

Interpolation of the photosynthesis-light-response curves and respiration data of the preceding and following period was used for calculating crop photosynthesis and respiration during the days and weeks when no measurements were made. Meteorological data from a nearby station (at 2.5 km) of the Wageningen Agricultural University were used as a basis.

Results

A typical time course of the irradiance and the corresponding net photosynthesis and respiration in a particular week (26/8-30/8) at 22.5 and 12.5 °C is given in Figure 1a and 1b, respectively. From such curves throughout the growing season the response of the crop gross photosynthesis at different light intensities for both temperatures (Fig. 2a-2i) and the time course of the mean dark respiration (Fig. 3a and 3b) were made. The development of the gross photosynthesis at a selected irradiance (600 W m⁻²) and the leaf area index is shown in Figure 4. These figures demonstrate that there is a strong increase of canopy gross photosynthesis during the first 4 weeks (17/6-15/7) followed by a stable period (15/7-5/8), a gradual decrease till about 23/9 and a strong decrease from 23/9-21/10. This coincides with the increase and decrease of the LAI (Fig. 4). The relative effect of temperature on photosynthesis at high irradiances was highest in the beginning and at the end of the growing season (Fig. 2 and 4). There was hardly any difference in the initial slope of the photosynthesis-light-response curves between the high- and low-temperature treatments, but the low-temperature treatment levelled off sooner at the higher light intensities. There was a strong increase in dark respiration on a ground area basis at both temperatures till about 15/7, followed by a smaller increase till the end of September and a rapid decrease afterwards (Fig. 3a). In the period between mid July and the end of September the dry matter of the standing crop increased from about 4000 kg ha⁻¹ to 14 000 kg ha⁻¹ (Table 1). So when respiration was expressed on a total dry matter basis (Fig. 3b) it strongly decreased in this period, indicating that respiration was more correlated with the growth of the crop or a specific part of the crop than with the overall size of the standing crop.

Using the hourly ambient temperature and irradiance, the daily gross photosynthesis and respiration were calculated (see 'calculations'). The outcomes are presented in Figure 5c together with the daily mean temperature (Fig. 5a) and the daily sum of global radiation (Fig. 5b). As could be expected from Figure 2 and Figure 4 the daily gross photosynthesis during the initial period (15/6-15/7) was rapidly increasing mainly due to an increasing leaf area. After the leaf area index stabilized at about 3.5 - 4.0 m² m⁻², daily gross photosynthesis is closely related with the daily irradiation and hardly dependent on temperature. A maximum of 950 kg CO₂ ha⁻¹ day⁻¹ (= 576 kg DM ha⁻¹ day⁻¹) is obtained on July 24. From the beginning of September, daily gross photosynthesis decreased due to a decreasing LAI and lower levels of incoming radiation.

Figure 5c shows a rapid increase of the recalculated daily dark respiration in the initial period (15/6-15/7). From 15/7-5/10 it varied from 150 - 200 kg CO₂ ha⁻¹ day⁻¹ and it closely related to the daily mean temperature, giving a maximum of 210 kg CO₂ ha⁻¹ day⁻¹ (= 127 kg DM ha⁻¹ day⁻¹) on 14/7. From 5/10 onwards, respiration decreased rapidly to about 25 kg CO₂ ha⁻¹ day⁻¹. On only six days with a low radiation and a relatively high temperature (17/9, 10/10, 15/10-18/10) dark respiration exceeded the gross photosynthesis, resulting in a negative net photosynthesis. The difference between the cumulated dry matter yields, calculated from the CO₂ fixation minus respiration, and the harvested crop is assumed to be

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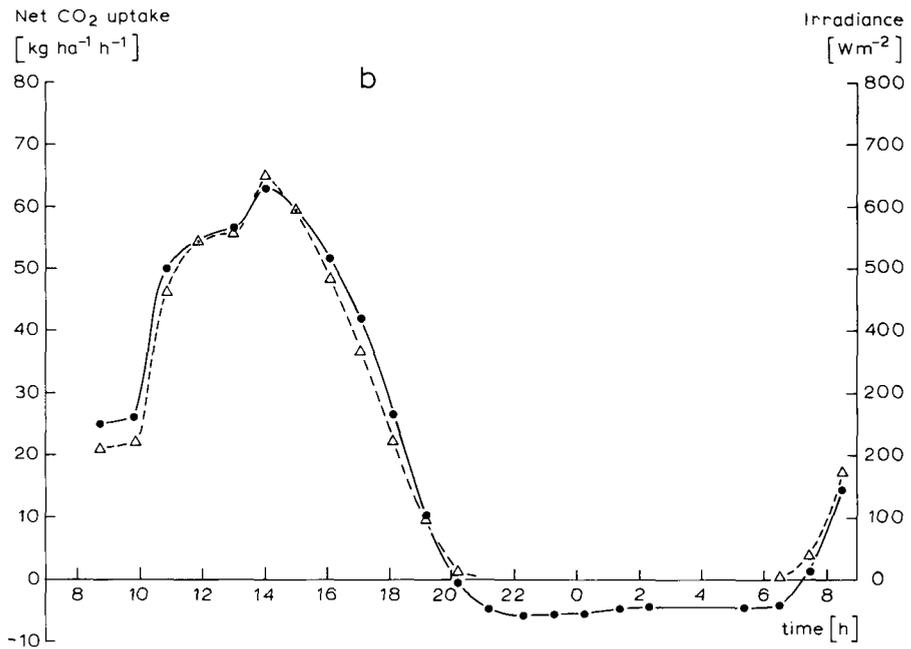
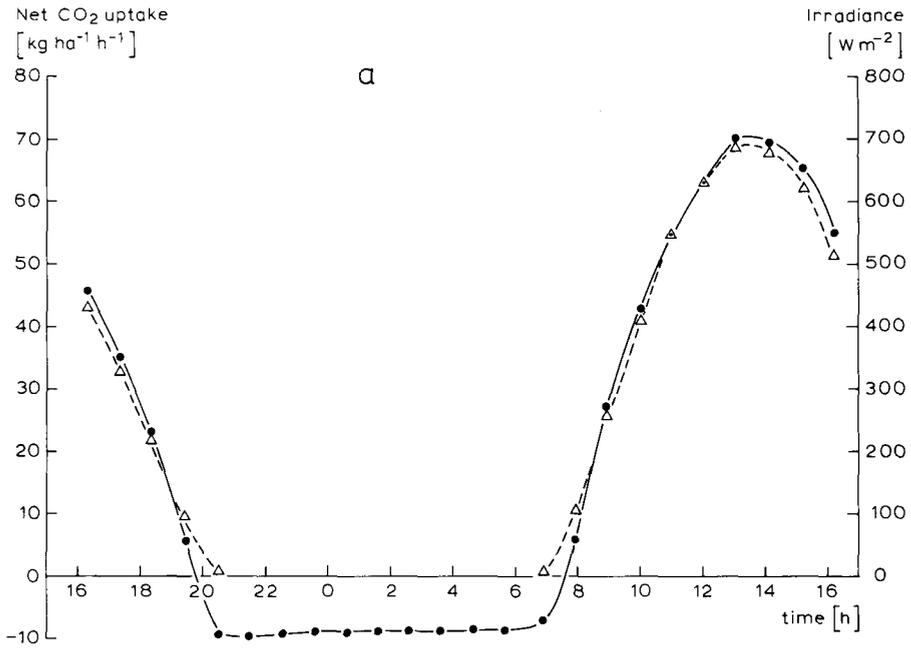


Fig. 1. Daily course of net CO₂ uptake (●—●) and irradiance (Δ--Δ). (a) Temperature: 22.5 °C, date: 27-28 August 1985. (b) Temperature: 12.5 °C; date: 29-30 August 1985.

an estimate of the amount of assimilates translocated under the ground, where it may be used for formation of roots, respiration and exudation into the rhizosphere (Table 1). Only in the first period (19/6-2/7) processes under the ground seemed to require on the average a high fraction of the assimilates (37 % of net photosynthesis). After this period this percentage dropped to about 30 % and remained constant.

GPHOT [$\text{kg}(\text{CO}_2) \text{ha}^{-1} \text{h}^{-1}$]

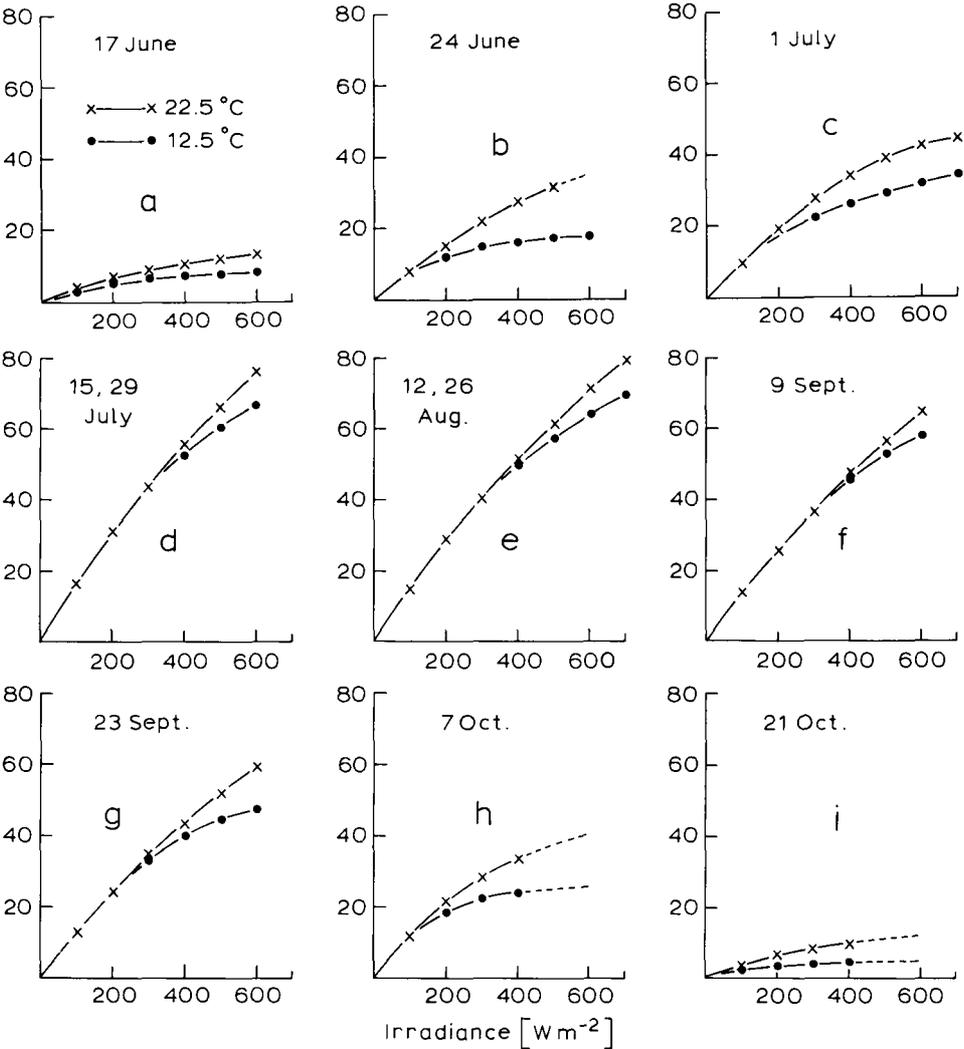


Fig. 2. Calculated rate of gross photosynthesis (GPHOT) as a function of irradiance at two temperatures at different times during the growing season (a-i) as described in 'Calculations'. The response curves at each temperature are fitted by eye from determinations with two enclosures on two days. The date indicates the first day of the measurement week.

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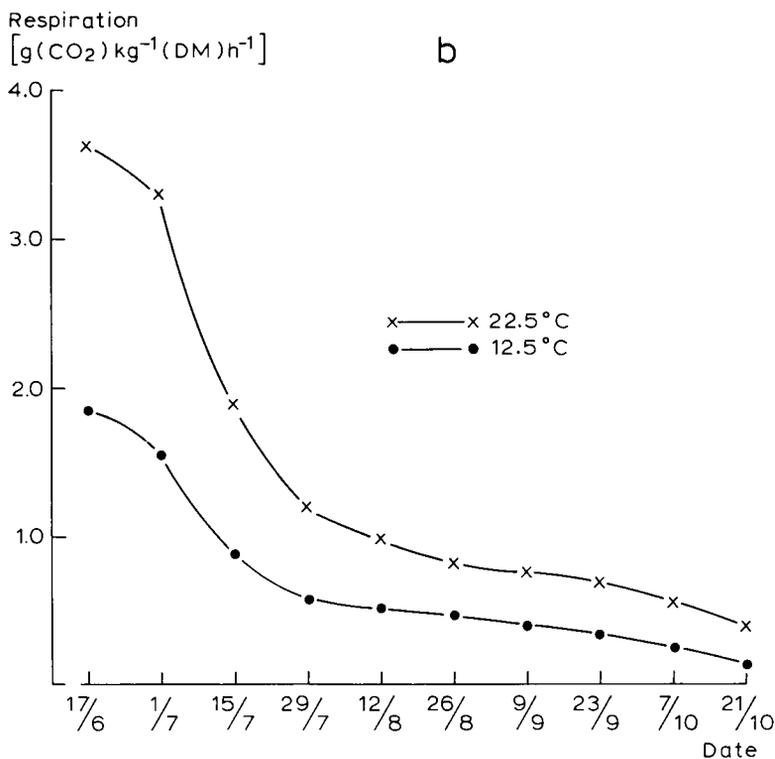
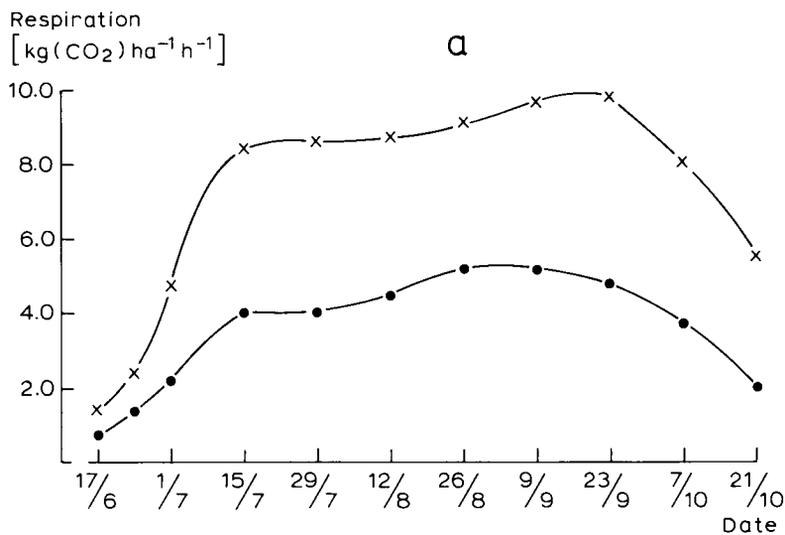


Fig. 3. Mean dark respiration rate of the above-ground parts at two temperatures (12.5 and 22.5 °C) as a function of time. The date indicates the first day of the measurement week. Every symbol is the mean of determinations with two enclosures on two days. (a) Expressed on a ground-area basis. (b) Expressed on a total dry matter basis.

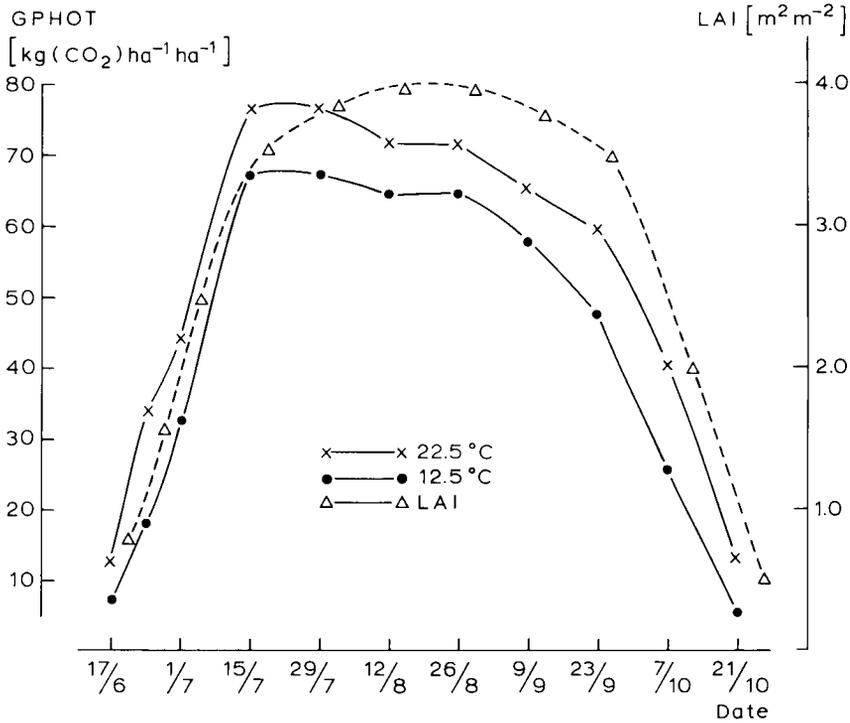


Fig. 4. Gross photosynthesis rate (GPHOT) at two temperatures at an irradiance of 600 W m^{-2} and the leaf area index (LAI) as a function of time.

Discussion

It is well documented that the rate of photosynthesis of C_4 plants at ambient CO_2 levels (at present about $350 \mu\text{l l}^{-1}$) is highly sensitive to temperature. Taylor & Rowley (1971) found a reduction in rate of photosynthesis of 90 % (after one day; later even more) when the temperature was lowered from 25°C to 10°C . Comparable results were reported by Charles-Edwards & Charles-Edwards, 1970; Hofstra & Hesketh, 1969; van Laar & Penning de Vries, 1972; and Raschke, 1970. Plants subjected to such temperature changes also showed a large after-effect when temperature was restored to initial values (Taylor & Rowley, 1971). This is in contrast with our findings, where only in the early stages (till July, Fig. 2a-2c) and very late stages (after the end of September, Fig. 2h-2i) a reduction of about 50 % at the higher light intensities was measured. In the period of major dry matter production (mid July until the beginning of September) this temperature effect was only 12 - 15 % at the higher light intensities (occurring only at midday). It may be suggested that light saturation is required to yield a maximum difference in response to changes in temperature. Lower leaf-layers in the canopy would therefore give only a limited

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Table 1. Calculated cumulative values of gross photosynthesis (GPHOT) (a), above-ground respiration (resp.) (b), net photosynthesis (NPHOT) (a-b), harvested standing biomass (c) and assimilate transport into the soil (a-b-c); all expressed in kg DM ha⁻¹. Standing biomass has been corrected for initial biomass on 19/6 (393 kg ha⁻¹). Above-ground respiration, standing biomass and assimilate transport into the soil are expressed as % of gross photosynthesis and net photosynthesis (standing biomass and assimilate transport only).

Date	Dry matter (kg ha ⁻¹)					% of GPHOT			% of NPHOT	
	GPHOT (a)	RESP (b)	NPHOT (a-b)	biomass (c)	soil (a-b-c)	RESP	biomass	soil	biomass	soil
19/6-2/7	1762	349	1413	882	531	19.8	50.1	30.1	62.4	37.6
16/7	6593	1374	5219	3717	1502	20.8	56.4	22.8	71.2	28.8
30/7	11769	2616	9153	6382	2771	22.2	54.2	23.5	69.7	30.3
13/8	16761	3728	13033	8647	4386	22.2	51.6	26.2	66.3	33.7
27/8	21095	4927	16168	11142	5026	23.4	52.8	23.8	68.9	31.1
10/9	24992	6111	18881	12432	6449	24.5	49.7	25.8	65.8	34.2
24.9	27558	7395	20163	14325	5838	26.8	52.0	21.2	71.0	29.0
8/10	29934	8515	21419	14777	6642	28.4	49.4	22.2	69.0	31.0
15/10	30456	8829	21627	14995	6631	29.0	49.2	21.8	69.3	30.7
22/10	30695	9023	21672	15567	6105	29.4	50.7	19.9	71.8	28.2

response to temperature. However, since a major part of the assimilate production is realized in the top layers, such an effect would not fully explain our results. Apparently the growth stages in which the plants are most sensitive to temperature regarding their photosynthesis, are leaf formation and senescence.

This observation may be the explanation for the detected high sensitivity to temperature, often found in laboratory experiments. In general these experiments have been carried out with young plants (20 -40 days), where leaves were not fully mature. Extrapolation of these data in simulation models to the whole growing period and to field situations may therefore be misleading. Net photosynthesis in the period from mid July until mid September, as the major increase in dry matter takes place, will hardly be affected by lower temperatures, as photosynthesis is only slightly lower and dark respiration will also decrease (Figs. 2 and 3a).

During the first growing period (17/6-15/7), dry matter of the above-ground biomass increased from 882 to 3717 kg DM ha⁻¹ (Table 1) and respiration rate from 1 to 8 kg ha⁻¹ h⁻¹ (Fig. 3a). From mid July until the end of August, however, the dry matter of the standing crop increased from 4000 kg ha⁻¹ to 14600 kg ha⁻¹, while respiration increased only from 8.4 to 9.7 kg CO₂ kg ha⁻¹ h⁻¹. This demonstrates that not only the amount but also the quality of living tissue determines the respiration rate.

The data from periodical harvests were used to quantify carbon utilization (growth and maintenance respiration) of the growing crop. Growth respiration was calculated using coefficients from Penning de Vries et al. (1989). The conversion costs for leaves, stems and cobs + grain were 0.46, 0.41 and 0.38 g CO₂ per g synthesized dry matter respectively. Maintenance respiration was calculated at 12.5 and

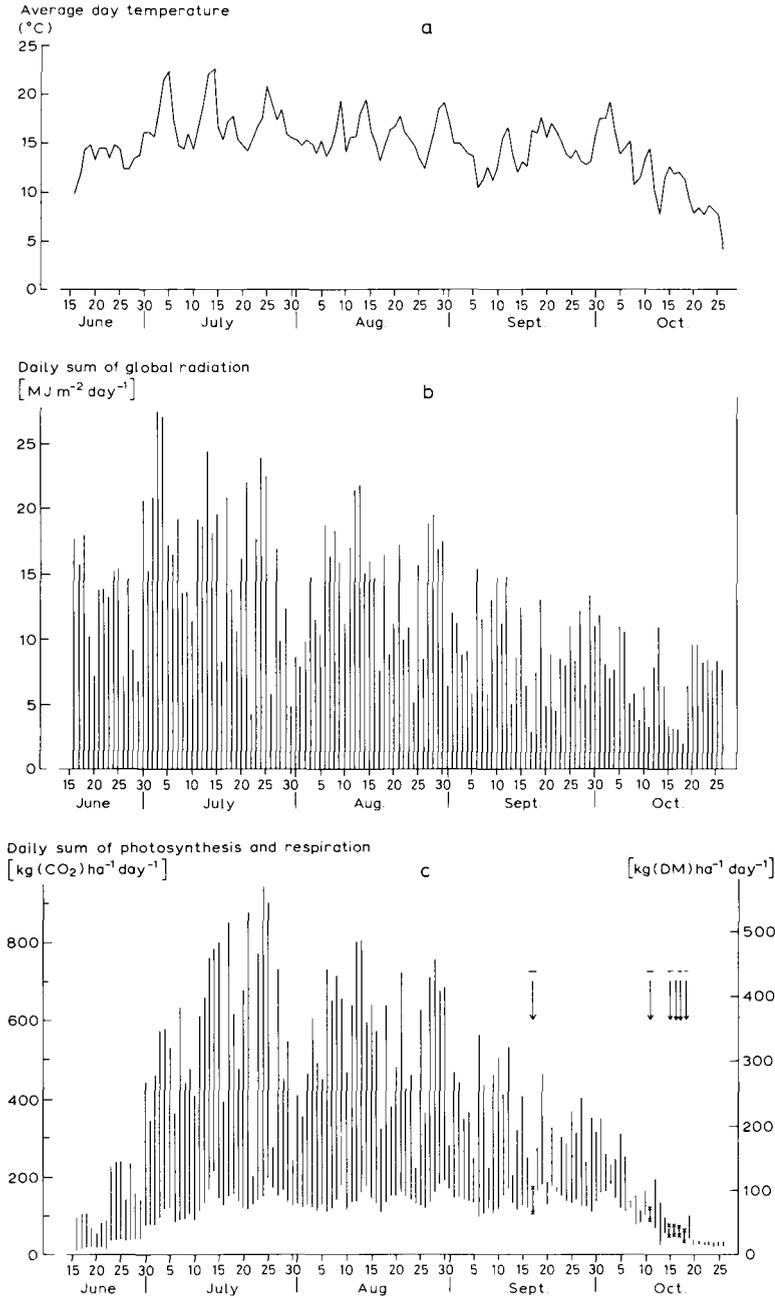


Fig. 5. Seasonal pattern of (a) daily mean temperature (hourly basis) (b) daily global radiation and (c) daily sum of photosynthesis and respiration. The calculated daily gross photosynthesis (top of bar), net photosynthesis (bar length) and respiration (lower end of bar) are expressed as CO₂ (left) and dry matter (right). The arrows in (c) indicate days with a negative daily net photosynthesis.

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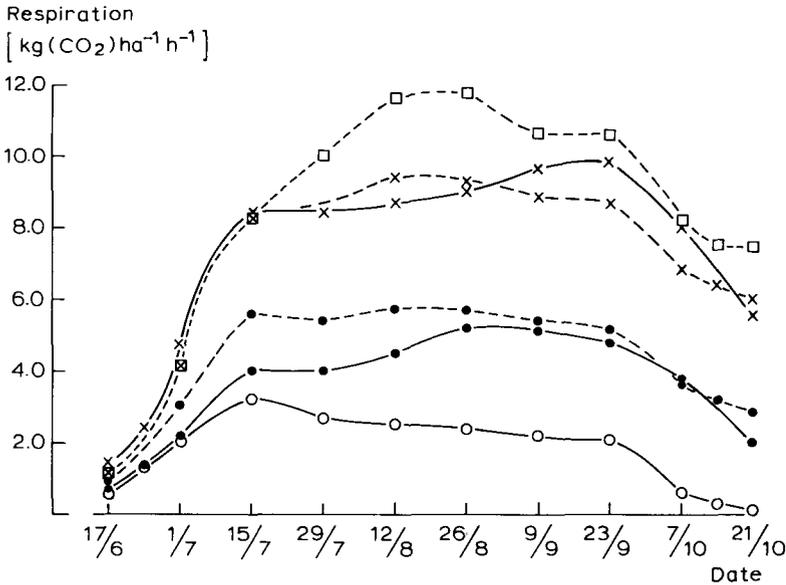


Fig. 6. Measured dark respiration at 12.5 °C (●—●) and 22.5 °C (x—x) and calculated growth + maintenance respiration at 12.5 °C (●--●) and 22.5 °C (x--x) as a function of time, assuming a maximum maintenance respiration for stems (at a yield of 2500 kg DM ha⁻¹) and for cobs and grains (at a yield of 1000 kg DM ha⁻¹) or a maximum maintenance respiration for cobs + grains only (□--□) at 22.5 °C. Growth respiration (○—○) was calculated from the increase in crop dry weight during the experimental period.

22.5 °C, also using maintenance coefficients from Penning de Vries et al. (1989) (leaves 0.04, stems 0.015 and cobs and grain 0.015 g CO₂ g⁻¹ DM day⁻¹ at 20 °C; Q₁₀ = 2.0). There is much evidence (Sibma, 1987) that beyond a dry matter amount in cobs exceeding 1000 kg ha⁻¹ the amount of proteins and minerals in the cob biomass no longer increases, and mainly starch is stored. Starch will require hardly any energy for maintenance. In our calculations the maintenance respiration for cobs was therefore kept constant for the period that the dry matter in cobs exceeded that amount (from 30/7 onwards).

Doing so, the sum of growth and maintenance respiration calculated in the initial growth period (until mid July) matches fairly well the measured dark respiration at 22.5 °C (Fig. 6). After this period however, the calculated value is much higher than the actual respiration. According to Sibma (1987) also the total amounts of nitrogen and minerals in stems hardly increase after mid July (dry matter of stems is about 2500 kg ha⁻¹). This would imply that maintenance respiration would also become constant. Using this, correspondence between calculated and measured values is improved (Fig. 6).

Total dark respiration at 12.5 °C, calculated from growth and maintenance respiration with the same assumptions as at 22.5 °C, was overestimated during the first growing period compared with the measured values. This deviation may be related

to changed properties of the plants grown at lower temperatures during this period. It may also be hypothesized that part of the assimilates, produced at the lower temperature, was not converted into structural dry matter, thereby reducing conversion costs. Within the relatively short measuring period at these temperatures (24-48 h), an eventual feed-back reaction of the rate of assimilation could however not be observed.

From the total amount of CO_2 absorbed by the crop, corresponding with $30.7 \text{ t DM ha}^{-1}$, 30 % is lost by above-ground respiration, and 50 % is invested in above-ground biomass (Table 1). The remaining 20 % is assumed to be transported under the ground. Only at the start of growth, investment in the roots may amount to some 30 % of gross photosynthesis (Table 1). In general, literature reports claim a much higher proportion of the gross photosynthesis to be translocated to plant parts under the ground. Merckx et al. (1989) found in laboratory experiments with wheat and maize that about 50 % of net photosynthesis (about 35 % of gross photosynthesis) is transported to the roots. Similar results were obtained by Barber & Martin (1976) with wheat plants, where 43 - 50 % of the net photosynthesis was transported to the roots. This difference might be due to the fact that these laboratory experiments were done with relatively young plants (3 - 6 weeks) with sometimes very high root/shoot-ratios (up to 0.8). This ratio is much lower in older plants (Brouwer, 1966), with a consequent smaller demand for assimilates. This is confirmed in the experiments of Keith et al. (1986), who found a decreasing proportion of the $^{14}\text{CO}_2$ fixed by wheat plants to be transported to the roots as plants mature and age.

Sauerbeck et al. (1975) found in wheat plants that about 25 % of the total amount of assimilated CO_2 (= $6000 \text{ kg DM ha}^{-1}$) transported to the soil, is still present as living roots at harvest. The remaining part (75 %) has been lost by respiration, exudation and decay of root hairs and roots. These results agree with those of Schäfer et al. (1984). Using this ratio with our data implies that from the $6000 \text{ kg DM ha}^{-1}$ (Table 1) transported to the soil, about 25 % ($1500 \text{ kg DM ha}^{-1}$) should be present as living roots at harvest. In our experiments root mass was not determined, but values between 1200 and $1500 \text{ kg DM ha}^{-1}$ have been reported for maize (Sibma, 1987).

From 10/9 onwards there is hardly any export of photosynthates to the roots (Table 1). So from that time all net CO_2 uptake will be invested in above-ground material and root respiration will take place at the expense of the roots itself.

From the results of the measurements and calculations it may be concluded that the sensitivity of maize crop photosynthesis to changes in ambient temperature may be dependent upon the growth stage of the maize plant. Even though the present experiments were not aiming at a precise determination of the respiration of different plant parts, it is very clear that there is no proportionality between standing biomass and respiration.

Such a proportionality is mostly taken as a basis for calculations in simulation models, which consequently will overestimate losses by maintenance respiration.

The present experiments lead to the conclusion that the risk of substantial losses of dry matter at the end of the growing season is not large. Only late in the season

on some dull days, dark respiration will exceed photosynthesis leading to a net loss of dry matter.

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