

Predicting dry matter production of cauliflower
(*Brassica oleracea* L. *botrytis*) under
unstressed conditions
I. Photosynthetic parameters of cauliflower leaves
and their implications for calculations
of dry matter production

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Abstract

Measurements of CO₂ exchange of cauliflower leaves were carried out in a field experiment which included two nitrogen fertilisation rates. Irradiance and CO₂ concentration were varied at the leaf level within a leaf cuvette and additionally a temperature treatment was applied to field grown plants moved into climate chambers. These measurements were used to estimate parameter values of a rectangular hyperbola describing cauliflower leaf CO₂ exchange as a function of irradiance and CO₂ concentration. The obtained parameter estimates were used to derive empirical regression equations with temperature and nitrogen content of the leaves as independent variables. The resulting relationships were applied within a simple photosynthesis–respiration based dry matter production model in order to derive functional relationships between light use efficiency and irradiance, leaf area index and temperature.

The rectangular hyperbola was able to describe the gas exchange data as varied by irradiance and CO₂ concentration on the single leaf level with sufficient accuracy, but estimates of initial light use efficiency (about 25 µg J⁻¹) were too high because of the bias emanating from the limited flexibility of this model. Light saturated photosynthesis rate (P_{\max}) showed an optimum response to temperature and an increase with increasing nitrogen content of leaves. The initial slope α of the rectangular hyperbola showed no consistent responses to ambient temperature and nitrogen content of leaves. The respiration per unit leaf area β increased exponentially with increasing temperature,

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resulting in a Q_{10} value of 1.86. Because only a limited number of plants was evaluated in this study, additional work is needed to further substantiate the results of the gas exchange measurements.

The model analysis demonstrated that LUE is independent of the light integral over a range 5–10 MJ m⁻² per day photosynthetically active radiation if one assumes an adaptation of P_{\max} within the canopy and over time according to the incident irradiance. Acclimatisation within the canopy and higher leaf area indices, LAI, reduce the decrease of LUE with irradiance but a substantial decline remains even for LAI values of 4. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Cauliflower; Model; Temperature; Irradiance

1. Introduction

Two main approaches to calculate dry matter production are used in crop growth models: one describes photosynthesis and respiration either scaling-up from the single leaf level to the canopy level (Spitters et al., 1989) or using the big leaf approach (de Pury and Farquhar, 1997). The other more empirically founded approach calculates dry matter production simply as the product of intercepted radiation and empirically derived values of light use efficiency, LUE (Monteith, 1977; Gallagher and Biscoe, 1978; Jones and Kiniry, 1986; Williams et al., 1989). Whereas the first approach is regarded to be more physiologically founded, parameterisation from field experiments is difficult, since key parameters like the light saturated photosynthesis rate of single leaves, P_{\max} , underlie complex environmental influences (Berry and Björkman, 1980). The second approach is more easily parameterised, but environmental conditions may modify LUE values, limiting its usefulness (see Spitters, 1990; Boote et al., 1996; Marcelis et al., 1998, for further discussion). Variations of LUE may occur even for the same crop species grown at the same location if weather conditions vary substantially between the cropping periods. This is especially likely for crops with a relatively short growing period, like cauliflower, which may be cultivated within one year during quite contrasting radiation and temperature regimes. Estimates for LUE may therefore vary for cauliflower crops grown under different radiation regimes (Kage and Stützel, 1999).

Some of the variation of LUE values may arise from a non-linearity of the canopy dry matter production vs. radiation interception relationship. This hypothesis is supported by the results from Olesen and Grevsen (1997), who have shown a considerable decrease of LUE values for cauliflower with increasing irradiance in climate chamber experiments. The shape of the LUE–irradiance function and therefore the influence of irradiance on LUE may be deduced by up-scaling from the photosynthetic characteristics of single leaves to the crop level using dry matter production models (de Wit, 1965; Norman and Arkebauer, 1991; Sinclair et al., 1992; Medlyn, 1998). One difficulty of this

task is to consider possible effects of acclimatisation of photosynthetic characteristics of leaves to a changing light environment within the canopy and during time.

The aim of this study is to examine the influence of the factors irradiance, CO₂, temperature and nitrogen on the efficiency of light utilisation of cauliflower crops. This paper therefore presents parameter estimations describing cauliflower leaf CO₂ exchange as influenced by these environmental parameters. A simple photosynthesis–respiration based canopy dry matter production model is used to derive the functional dependencies of LUE on temperature, irradiance and LAI.

In a forthcoming study (Kage et al., 2000a) both model approaches will be tested against data from field experiments using a previously published model module (Kage and Stützel, 1999) describing development and dry matter partitioning in cauliflower.

2. Materials and methods

2.1. Field experiment

Cauliflower plants on which the photosynthesis measurements were taken originated from a field experiment carried out in 1995 on a humic loamy sand in Hannover, Germany. The experiment had two nitrogen treatments, i.e. 100 and 50% of recommended fertilisation level. Nitrogen was given as ammonium nitrate according to the N_{min}-fertilisation schedule (Scharpf and Wehrmann, 1975). For cauliflower this defines a target supply level of 270 kg N/ha (135 kg N/ha for the 50% treatment) 6 weeks after planting including soil nitrate from 0 to 60 cm depth. At planting N_{min} was adjusted to 130 kg NO₃-N/ha from 0 to 30 cm (65 kg N/ha for the 50% treatment). It was laid out as a randomised block design with four replications. The plot size was 8×6 m². Seeds of cauliflower cv. Fremont were germinated in planting plates filled with peat and transplanted by hand into peat cubes with 4 cm edge length after about 3–5 days. When the plants had about 2–4 visible leaves they were transplanted in the field. The planting density was 4 plants m⁻². Before planting in the field prophylactic applications of chlorfenvinphos (BirlaneTM) against cabbage fly, and of molybdenum sulphate were applied to the peat cubes. Within each plot of this experiment six perforated buckets of 10-l volume containing field soil were buried. In each of these buckets one cauliflower plant was planted. The buckets containing the plants were taken out of the soil into growth chambers for temperature treatments. On 2 June, 8 weeks after planting, the potted plants of the fully fertilised treatment received an additional amount of 4 g N per plant because they showed slight symptoms of N deficiency, probably because of their limited root volume. The temperature and daily radiation integral during the experiment are shown in Fig. 1.

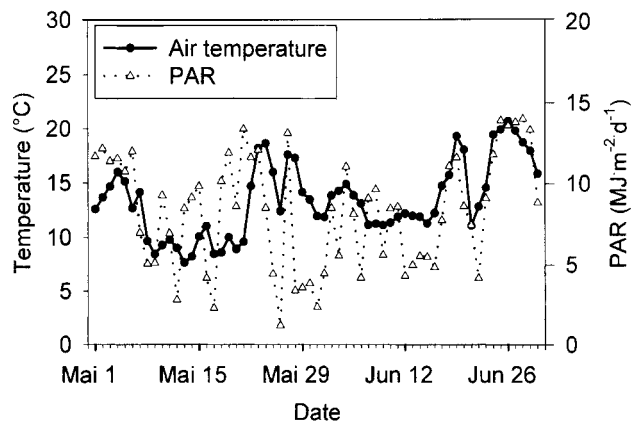


Fig. 1. Daily mean air temperature ($^{\circ}\text{C}$) and daily integral of photosynthetic active radiation (MJ m^{-2} per day) during the period from 1 May to 30 June, 1995 measured near the experimental field in Hannover, Germany.

2.2. CO_2 exchange measurements

The CO_2 exchange measurements were carried out using a CIRAS-1 combined infrared gas analysis system combined with a Parkinson leaf cuvette (PP-Systems, Hitchin Herts, UK) measuring the gas exchange of 2.5 cm^2 leaf area. The cuvette was supplied with an artificial illumination unit using halogen lamp as a light source, providing a maximum irradiance of about 420 W PAR m^{-2} . The irradiance levels were adjusted using light diffusers and wire meshes of different transmission in the steps 0.0, 39.6, 52.7, 68.1, 107.7, 164.8, 228.6 and $417.6 \text{ W PAR m}^{-2}$. CO_2 concentrations were varied from 145 to 706 mg m^{-3} . All photosynthetic measurements were carried out within the uppermost third on the youngest fully expanded leaf. The incubation time for one measurement was around 1–3 min. Irradiance and CO_2 concentration were varied from low to high values. Measurements in the field (18 May, 2 June) were performed between 11 a.m. and 2 p.m. The more time consuming measurements on 19 and 20 June started at 9 a.m. and were finished at 3 p.m. A summary of the measurement dates is presented in Table 1.

Table 1

Measurement dates, parameter variation and location of measurement of gas exchange measurements on cauliflower plants

Date	No. of plants	Parameter variation	Location of measurement
18 May	1	Light, CO_2	Field
2 June	1	Light, CO_2	Field
19 June	1	Light, CO_2 , temperature	Growth chamber
20 June	6	Nitrogen content of leaves, light, temperature	Growth chamber

On 19 June, four plants from the ‘low’ and another four from the ‘high’ fertilisation plots, were taken out of the field into the climate chamber. Before the measurements of CO₂ exchange the plants were treated with temperatures of 8, 12, 16, 20, 26 and 30°C. The time for acclimatisation to the new temperatures levels was at least 20 min. Afterwards two plants from the ‘high’ fertilisation plots showed obviously a reduced turgor. These plants were discarded from the measurements. The CO₂ concentration during all these evaluations was 350 (±10) mg m⁻³. The nitrogen content of the leaves from the low N treatment were 1.21, 1.52, 1.72 and 2.1% N, from the high N treatment 3.83 and 4.79% N in DM, respectively.

2.3. Model calculations

One widely used equation to describe the reaction of single leaf net photosynthesis P_n (μg CO₂ m⁻² s⁻¹) on irradiance I (W m⁻²) and CO₂ concentration (mg m⁻³) C is the rectangular hyperbola corrected for dark respiration (Thornley and Johnson, 1990)

$$P_n = \frac{\alpha I \tau C}{\alpha I + \tau C} - \beta \quad (1)$$

with the parameters initial LUE, α (μg J⁻¹), leaf conductance to CO₂ transfer, τ (m s⁻¹) and leaf dark respiration rate, β (μg CO₂ m⁻² s⁻¹). For a constant CO₂ concentration it is convenient to define the lumped parameter, P_{\max} (μg CO₂ m⁻² s⁻¹), which is the product of τ and C .

One of the nice characteristics of Eq. (1) is that is it possible to integrate it analytically over the whole canopy if one assumes an exponential decline of irradiance and a constant value of τ within the canopy. Aggregating the effects of radiation reflection and transmission within the canopy into the light extinction coefficient k and using P_{\max} for the product of τ and C the equation for the whole canopy net photosynthesis, P_c (μg m⁻² s⁻¹), becomes (Thornley and Johnson, 1990)

$$P_c = \frac{P_{\max}}{k} \ln \left(\frac{\alpha k I_0 + P_{\max}}{\alpha k e^{-k \text{LAI}} + P_{\max}} \right) - \beta \text{LAI} \quad (2)$$

where I_0 is the irradiance at the top of the canopy (W m⁻²) and LAI the leaf area index (m² m⁻²). The extinction coefficient k depends upon several factors such as the zenith angle of the sun, the fraction of direct and diffuse radiation, the leaf angle distribution and others. For simplicity here it was taken as a constant empirical parameter. From our own unpublished measurements we derived an average value of 0.65.

Since irradiance usually declines within the canopy and because the photosynthetic capacity adapts to the light environment the assumption of a

constant P_{\max} is probably not correct for higher values of LAI (Hirose and Werger, 1987). A computationally simple method to investigate possible effects of a declining P_{\max} on the productivity of the canopy is available if one assumes a decline of P_{\max} proportionally to the decline in I within the canopy

$$P_{\max} = P_{\max 0} e^{-k \text{LAI}} \quad (3)$$

The solution for whole canopy net photosynthesis then becomes (Charles-Edwards, 1982)

$$P_c = \frac{\alpha I_0 P_{\max 0} (1 - e^{-k \text{LAI}})}{\alpha k I_0 + P_{\max 0}} - \beta \text{LAI} \quad (4)$$

In order to calculate daily canopy assimilation from Eq. (2) or Eq. (4) they have to be integrated over the day accounting for the changing light environment. This can efficiently be done using the three point Gauss integration method (Goudriaan, 1986) thereby assuming a sinusoidal function of irradiance during the daytime.

Calculation of CO_2 losses through respiration is still one of the weak points of crop simulation model. The most widely used set of assumptions are implemented in the SUCROS model (Spitters et al., 1989) based on the work of McCree (1970) and Penning de Vries (1975). This concept distinguishes between maintenance and growth respiration, the former being proportional to the mass of the crop organs and the latter being a function of the growth rate of the organs. Because the term βLAI of Eqs. (3) and (4) does not take into account these facts, we did not use this approach for the respiration calculations in our model analysis. Instead, maintenance respiration, R_m , of an organ i was calculated as the daylength D_L corrected values of night and day respiration from the organ mass W_i and the maintenance coefficient MC_i

$$R_{m_i} = \text{MC}_i W_i \left(T_{\text{eff,day}} \left(\frac{D_L}{24} \right) + T_{\text{eff,night}} \left(1 - \frac{D_L}{24} \right) \right) \quad (5)$$

Typical values for MC are 0.03, 0.015 and 0.015 for leaves, stem and roots, respectively (Goudriaan and van Laar, 1994) which were also used here. The temperature effects, T_{eff} , are derived from the Q_{10} value approach

$$T_{\text{eff}} = Q_{10}^{(T - T_{\text{ref}})/10} \quad (6)$$

The weight of the leaves may be calculated for a given leaf area index, LAI from the specific leaf area, SLA ($\text{cm}^2 \text{g}^{-1}$). For cauliflower a constant value for SLA of $120 \text{ cm}^2 \text{g}^{-1} \text{DM}$ was used as an approximation.

Stem weight was derived from the leaf mass using the allometric relationship between stem and leaf masses (Kage and Stützel, 1999). Root mass was assumed to be 10% of the sum of leaf and stem masses (Kage et al., 2000b). For growth

respiration the crude assumption of a conversion efficiency of 0.7 from assimilates to dry matter was used (Goudriaan and van Laar, 1994). The dry matter produced per day of the crop is calculated from the numerical integral of gross photosynthesis as calculated from Eq. (2) or Eq. (4) without the dark respiration term minus the sum of the maintenance respiration of the different plant organs. From this amount of available net assimilates dry matter production is calculated using the conversion efficiency. Canopy LUE (g DM MJ PAR⁻¹) may then be calculated as the ratio of net dry matter produced per day dW_t/dt (g DM m⁻² per day) and the amount of intercepted PAR (MJ PAR m⁻² per day)

$$\text{LUE} = \frac{dW_t}{dt} \frac{1}{I(1 - e^{-kLAI})} \quad (7)$$

2.4. Statistical analysis

Statistical analysis of the data was performed using the procedures REG and NLIN of the SAS software package (SAS Institute, 1988). For a multiple regression analysis of the influence of temperature, T , and nitrogen content, NC on P_{\max} and α the following equation was suggested: $P_{\max}, \alpha = a + b \text{ NC} + cT + dT^2 + e \text{ NC}^2 + f \text{ NC } T$. Non-significant regressors were eliminated using the backward option of 'PROC REG' with a critical significance level of 0.10.

3. Results

The rectangular hyperbola accurately describes the CO₂ exchange of single cauliflower leaves if fitted separately to the data from the first two different sampling dates (Table 2 and Fig. 2). The parameter estimates for α , τ and β , however, differ between both dates, being generally higher for 2 June (Table 2). The parameter values estimated on the third measurement date are comparable to the first measurement date regarding the parameter α but are higher for τ and β .

Table 2

Parameters of the rectangular hyperbola describing CO₂ exchange rates of cauliflower leaves (Eq. (1)). The values were determined at two dates on a single leaf from cauliflower grown in the field. The parameter P_{\max} shown is calculated from the fitted τ values assuming a CO₂ concentration of 350 mg m⁻³

Date	Ambient temperature	α ($\mu\text{g J}^{-1}$)	$\tau \times 10^3$ (m s ⁻¹)	β ($\mu\text{g m}^{-2} \text{s}^{-1}$)	P_{\max} ($\mu\text{g m}^{-2} \text{s}^{-1}$)	r^2	n
18 May	10.3	24.8 (± 2.4)	2.26 (± 0.083)	101 (± 12.5)	792	0.989	40
2 June	13.7	34.90 (± 1.01)	4.69 (± 0.067)	135 (± 12.12)	1642	0.997	79

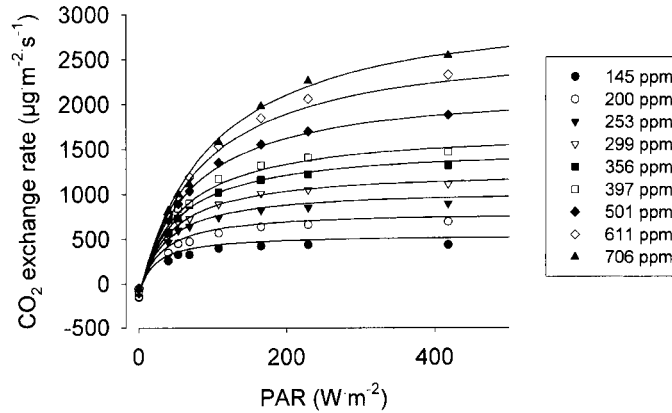


Fig. 2. Measured CO_2 exchange rate of a cauliflower leaf as a function of irradiance and external CO_2 concentration and values calculated from a fitted rectangular hyperbola. Measured on single cauliflower leaf on 2 June in the field.

The level of α and τ on this third measurement date was lower than the second, even if compared at the 17.2°C temperature level. A regression analysis using the parameter estimates from the third measurement date showed only significant effects of temperature on parameter values using an exponential equation ($\beta = 109.95 \exp(0.043T)$, $p = 0.0006$) fitted on the values of parameter β . Fits of quadratic equations (α , $\tau = a + bT + cT^2$) to α and τ were not significant ($p = 0.1324$ and 0.0759). There is an indication ($p = 0.06$) for a positive relationship between the estimates of α and τ for all measurement dates (Tables 2 and 3).

Using the parameter estimates obtained for α , β and P_{\max} for the plants transferred into the climate chambers on 20 June resulted in significant regressors for a multiple linear regression on temperature, square of temperature and nitrogen content (Table 4) in the case of the parameter P_{\max} . For the parameter α ,

Table 3

Effect of ambient air temperature on parameters of the rectangular hyperbola describing CO_2 exchange rates of cauliflower leaves. The values were determined on 19 June on a single leaf from a cauliflower plant grown in a buried pot within a field plot which was moved for the measurements into a climate chamber. The parameter P_{\max} was calculated from τ assuming a CO_2 concentration of 350 mg m^{-3}

Ambient temperature ($^\circ\text{C}$)	α ($\mu\text{g J}^{-1}$)	$\tau \times 10^3$ (m s^{-1})	β ($\mu\text{g m}^{-2} \text{s}^{-1}$)	P_{\max} ($\mu\text{g m}^{-2} \text{s}^{-1}$)	r^2	n
6.41	15.6 (± 1.5)	2.71 (± 0.13)	168.5 (± 16.5)	949	0.988	27
12.5	24.0 (± 1.2)	3.42 (± 0.07)	244.5 (± 10.8)	1198	0.997	27
17.2	27.0 (± 1.6)	3.83 (± 0.10)	276.3 (± 14.4)	1342	0.996	27
22.8	22.1 (± 1.2)	3.76 (± 0.10)	375.5 (± 12.5)	1317	0.996	27
27.9	20.8 (± 1.2)	2.60 (± 0.06)	443.1 (± 9.3)	909	0.995	27

Table 4

Results from a multiple linear regression of the parameter P_{\max} ($\mu\text{g m}^{-2} \text{s}^{-1}$) and α ($\mu\text{g J}^{-1}$) from the rectangular hyperbola describing the CO_2 exchange rate of cauliflower leaves as a function of the ambient air temperature, T ($^{\circ}\text{C}$) and the leaf nitrogen content, NC (% DM) and results from a non-linear regression relating leaf respiration rates, β , of cauliflower with temperature and nitrogen content, NC. Regression equations: $P_{\max}=a+b \text{ NC}+cT+dT^2$, $\beta=a \exp(bT_{\text{dif}})+c \text{ NC}$, $T_{\text{dif}}=(T-T_{\text{ref}})/10$, $T_{\text{ref}}=20^{\circ}\text{C}$

Parameter	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	r^2	<i>n</i>
P_{\max}	-935.7 (± 249.9)	152.8 (± 25.1)	140.3 (± 27.9)	-3.6 (± 0.7)	0.769*	22
β	202.7 (± 18.2)	0.62 (± 0.07)	4.02 (± 5.69)		0.883*	22

however, no significant relationship could be found (data not shown). The parameter β was fitted to an equation assuming exponential impact of temperature and a linear impact of nitrogen content on leaf respiration rates (Table 4). The value of 0.62 for the exponential temperature coefficient represents a Q_{10} value of 1.86.

Effects of daily radiation integral on LUE in g MJ^{-1} (Eq. (7)) were evaluated using the multiple regression model for P_{\max} (Table 1) and taking a value of 25 ($\mu\text{g J}^{-1}$) for the parameter α (see Tables 2 and 3). Both approaches for calculating canopy photosynthesis (Eqs. (2) and (4)), were used. The assumed nitrogen content of 4.5% and day temperature of 22°C resulted in a P_{\max} value of 1096 ($\mu\text{g m}^{-2} \text{s}^{-1}$). We used for our calculations day 240 of the year which has a daylength of 14.8 h at 52°N latitude.

The response function of LUE to daily radiation sum has for both canopy production models the shape of an asymmetric optimum function, becoming positive at around 1 MJ m^{-2} per day (Fig. 3a). Values of LUE are generally higher for the model assuming a constant P_{\max} than for the light adapting P_{\max} . After reaching the maximum of LUE at around $2\text{--}3 \text{ MJ m}^{-2}$ per day, the decrease of LUE with increasing daily radiation sum is in absolute figures more severe for the model assuming a constant P_{\max} within the canopy but relative changes of LUE are higher for the light adapting P_{\max} model. Higher LAI values (Fig. 3b) retarded the decline of LUE with increasing daily radiation sum for the model assuming a constant P_{\max} (Fig. 3b).

The assumption of a constant P_{\max} over such a wide range of daily radiation sums is at least over longer time periods is not realistic (Björkman, 1981; Pons and Pearcy, 1994). If we assume that the P_{\max} and $P_{\max 0}$ values increase linearly with the daily radiation sum, the resulting LUE vs. daily radiation sum functions now nearly became saturating functions with only minor response of LUE to daily radiation sum above 2 MJ m^{-2} per day for both photosynthesis models (Fig. 3c). However, the overall level of LUE was lower assuming a P_{\max} varying with the daily radiation sum.

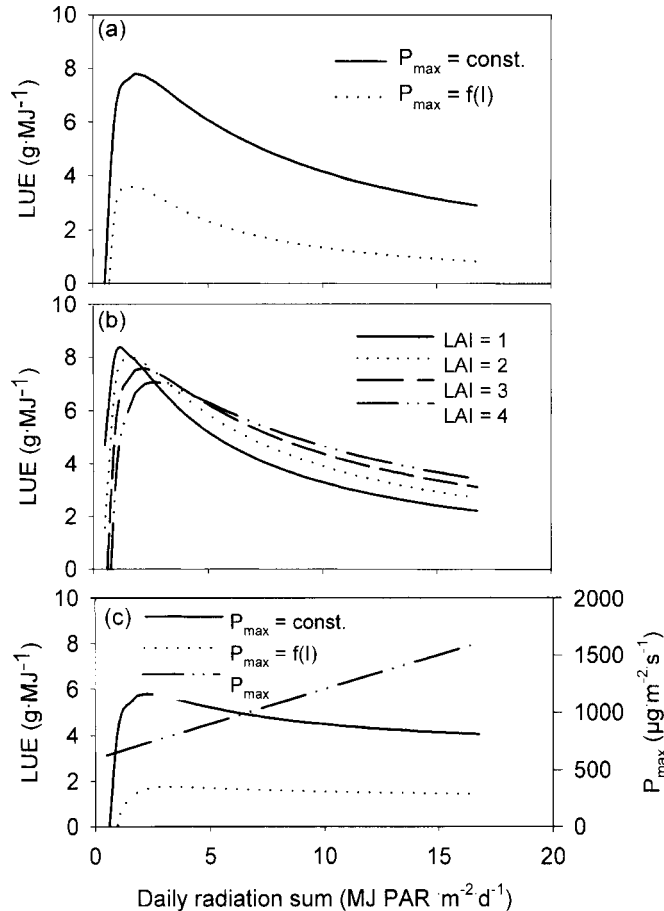


Fig. 3. LUE as a function of daily radiation sum calculated from a simple photosynthesis/respiration model. Assumed conditions: latitude 52°N, day 240 of the year, 4.5 (% DM) nitrogen content, day temperature 22°C, night temperature 14°C ($P_{\max}=1096 \mu\text{g m}^{-2} \text{s}^{-1}$), LAI=2.5, initial slope, $\alpha=25 \mu\text{g J PAR}^{-1}$. (a) Effect of constant P_{\max} over the entire canopy (Eq. (2)) or a P_{\max} varying within the canopy proportional to irradiance (Eq. (4)). (b) Effect of the LAI, assuming $P_{\max}=\text{const.}$ (c) P_{\max} and $P_{\max0}$ are assumed to be functions of irradiance ($P_{\max0}=400+50 \text{ PAR}$).

The LAI influences the calculated LUE of both models in different ways. If P_{\max} is assumed to be constant within the canopy, the LUE increases with increasing LAI. This is due to higher portions of the canopy operating at lower irradiance where the slope of the photosynthesis/light curve is higher (Fig. 4). Assuming a P_{\max} declining proportionally with irradiance within the canopy, however, the LUE of the canopy decreases with increasing LAI. This is because the average P_{\max} value of the canopy also decreases with increasing LAI. At low values of LAI both models predict the same LUE. Using the estimated temperature response of P_{\max} and β it can be deduced that LUE has an optimum response to temperature (Fig. 5), being between 15 and 25°C always higher than 95% of its maximum value, which is reached around at 18°C.

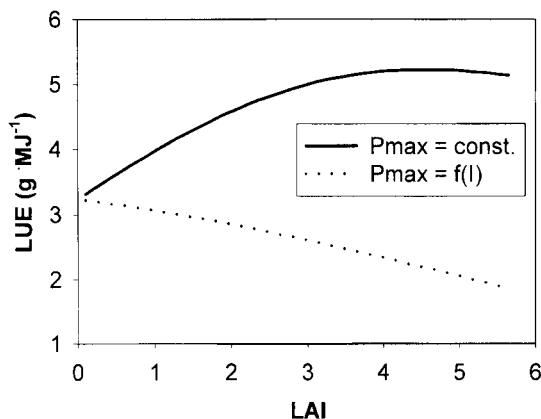


Fig. 4. LUE as a function of LAI calculated with two different photosynthesis models assuming either a P_{\max} constant within the canopy or decreasing proportionally with irradiance within the canopy. Assumed conditions: latitude 52°N, day 240 of the year, day temperature 22°C, night temperature 14°C ($P_{\max}=1096 \mu\text{g m}^{-2} \text{s}$), initial slope, $\alpha=25 \mu\text{g J PAR}^{-1}$, daily radiation 8.45 MJ PAR m^{-2} .

4. Discussion

The aim of this study was to examine the influence of the factors daily radiation sum, CO_2 , temperature and nitrogen on the efficiency of light utilisation by cauliflower crops. Since the temperature during the growing period does not usually deviate substantially from the optimum for net photosynthesis, field grown cauliflower plants were transferred into climate chambers with controlled temperature in order to get higher variation for the photosynthesis parameters.

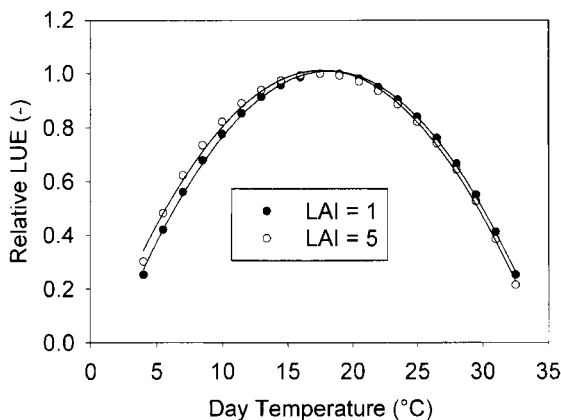


Fig. 5. Relative LUE, as a function of daily mean temperature (°C) for two values of the LAI calculated using a model assuming a constant P_{\max} within the canopy. Regression equations are $y=-0.1630+0.1303x-0.0036x^2$ for LAI=1 and $y=-0.0512+0.1237x-0.0036x^2$ for LAI=5.

One of the shortcomings of this method was the disturbance of the root system which resulted in the exclusion of two out of eight transferred plants.

The differences found for the parameters of the rectangular hyperbola between the first and the second measurement date (Table 2) may be due to the higher temperature and irradiance on the second date (Fig. 1). This assumption is supported by the parameter values obtained through temperature treatments on cauliflower plants in the climate chamber (Table 3) on 19 June which indicate influence of temperature on all parameters of the rectangular hyperbola.

The parameters of the photosynthesis functions of cauliflower leaves were generally similar to those of other C3 species (Berry and Björkman, 1980; Kirschbaum and Farquhar, 1984; Jensen et al., 1996). Values for τ or P_{\max} found here are in the upper range of the values reported in the literature for C3 species (Acock et al., 1978; Evans, 1989; Pachepsy and Acock, 1996). Also, the values for the initial LUE, α , we obtained are quite high. It has, however, to be considered that the parameter values of α obtained by fitting the rectangular hyperbola are generally higher than estimates for the non-rectangular hyperbola (Pachepsy and Acock, 1996). A comparison of both models, for example data set of single leaf assimilation (data not shown) gave values for α of 31.27 (± 8.65) using the rectangular hyperbola ($r^2=0.98$) but 14.21 (± 2.38), $r^2=0.99$ using the non-rectangular hyperbola. For the latter model the curvature factor θ (Thornley and Johnson, 1990) was estimated to be 0.92 (± 0.07). The high values and the scatter we found for the parameter α are therefore probably caused by the limited flexibility of the rectangular hyperbola rather than from a true variation of initial slope of the light response curve, which is generally assumed to be a quite conservative characteristic within the C3 group of plants (Ehleringer and Björkman, 1977; Long et al., 1993). Because of this shortcoming the non-rectangular hyperbola is now often used to describe single leaf CO₂ exchange (Boote and Loomis, 1991; Cannell and Thornley, 1998). However, despite the biased estimates of the parameter α the descriptive power of the rectangular hyperbola was still sufficient for fitting the data from CO₂ exchange measurements (Fig. 2). This is in accordance with the results of Pachepsy et al. (1996), who also concluded in a systematic comparison of photosynthesis models that this quite simple equation is adequate for predictive calculations of dry matter production.

It has, however, to be stated that the number of plants included in our analysis was limited and therefore our parameter estimates should be regarded as preliminary.

The assumption of randomly distributed canopy elements which is underlying our approach for light interception (Eq. (2)) is clearly an oversimplification during the early growth stage of cauliflower crops with planting densities of about 4 plants m⁻² (Röhrig and Stützel, 2000). We also did not include in our model the effect upon assimilation of variable fractions of direct and diffuse radiation,

which can influence LUE values (Sinclair et al., 1992; Sinclair and Shiraiwa, 1993; Hammer and Wright, 1994; Bange et al., 1997; Healey et al., 1998). Also, the assumptions about the distributions of P_{\max} within the canopy we used are extreme, but they may mark the maximum possible impacts of adaptation of P_{\max} within the canopy. Furthermore, different P_{\max} distributions within the canopy may influence the maintenance respiration rate of the canopy also if the total amount of photosynthetic nitrogen is altered. The decline of nitrogen content within the canopy is usually less than that of irradiance (Hirose and Werger, 1987), which is in contrast to the assumption of Eq. (4). Sometimes a linear instead of an exponential decline of nitrogen content within the canopy is found (Shiraiwa and Sinclair, 1993).

Despite all these simplifications the presented work should give a valid general overview on possible relationships between LUE, temperature and daily radiation sum emanating from different model assumptions.

The adaptation of P_{\max} within the canopy alone is not likely to result in a constant value of LUE over a wider range of daily radiation sum (Fig. 3a). But in combination with an adaptation of P_{\max} to changing average irradiance over time a conservative behaviour of LUE seems to be possible. The function we used to mimic this adaptation is somewhat speculative, but it seems to be in good accordance with the outcome of model based studies which optimised P_{\max} values (Johnson et al., 1995). The conclusions we derived from this calculation are in accordance with the model based studies of Dewar (1996), Dewar et al. (1998) and Haxeltine and Prentice (1996) which derived constant LUE vs. daily radiation sum relationships from an optimisation of nitrogen content of leaf layers within the canopy and within time.

The absolute LUE estimates obtained within the range 5–10 MJ PAR m⁻² per day are somewhat higher than the values reported in the literature (Wheeler et al., 1995; Olesen and Grevsen, 1997; Kage and Stützel, 1999) for the model assuming a constant P_{\max} but lower for the model assuming an exponential decline of P_{\max} within the canopy. This may also be regarded as an indication that the truth may lie in between our extreme assumptions about the behaviour of P_{\max} within the canopy.

The different influence of LAI on LUE predicted by both models (Fig. 5) should have significant influence on the calculated net dry matter production rate over time. This may be used to evaluate the validity of both assumptions by analysing predicted vs. measured time series of dry matter production.

5. Conclusions

The model analysis of this study is simplifying and also the number of plants investigated is limited, but despite these shortcomings the presented result gives

some insight into the consequences of parameter values on the level of single leaf photosynthesis and respiration, measured or assumed, on the aggregated level of crop dry matter production rate.

Regarding the key question of this paper, the relationship between dry matter production and the amount of intercepted radiation, one has to notice that the conclusions from this study remain ambiguous. Depending on the assumptions one makes about the acclimatisation of the photosynthetic parameters (P_{\max}) a severe decline of LUE with increasing daily radiation sum or a quite stable value of LUE within the range of PAR values usually observed under growing period conditions of mid-latitudes is found. A linear relationship between dry matter production rate and intercepted PAR, as assumed in many crop growth models, however, seems to be possible only for canopies with an adaptation of the maximum photosynthetic capacity P_{\max} to a changing radiation environment over time. If this adaptation is missing or incomplete, a substantial decline of LUE with increasing daily radiation sum should be expected.

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