

Predicting dry matter production of cauliflower (*Brassica oleracea* L. *botrytis*) under unstressed conditions

Part II. Comparison of light use efficiency and photosynthesis–respiration based modules

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Abstract

Six different modules for dry matter production of cauliflower were parameterised and evaluated using a database of 22 cauliflower crops originating from 15 independent field experiments. The evaluation included a light use efficiency, LUE, based module assuming LUE to be constant, an LUE based module assuming a linear decrease of LUE with increasing daily photosynthetically active radiation sum, I , two photosynthesis–respiration based modules using an analytical integration of the rectangular hyperbola over the canopy, assuming either the light saturated photosynthesis rate of single leaves, P_{\max} , to be constant or to decrease proportionally to irradiance within the canopy. Furthermore two slightly modified versions of the light interception and photosynthesis algorithms of the SUCROS model were evaluated, where the negative exponential equation for single leaf photosynthesis was replaced by the rectangular hyperbola. In order to make these modules comparable with the analytical integration approach, P_{\max} was also assumed to be either constant or to decrease proportionally to irradiance within the canopy.

The results indicate that an estimated constant LUE ($3.15 (\pm 0.04) \text{ g MJ}^{-1}$) is only poorly able to predict total dry matter production for cauliflower (modelling efficiency $EF=0.69$) of an independent data set. Using a linear decline of LUE with I ($LUE=6.66 (\pm 0.80)-0.36 (\pm 0.08)I$) drastically increased the predictive value ($EF=0.88$) of the LUE approach. The descriptive and predictive value of the photosynthesis based modules was higher when assuming that P_{\max} declines within the canopy. Then the predictive value of the photosynthesis/respiration based approach was

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better than the simple LUE approach but not generally better than the LUE approach assuming a linear decrease of LUE with increasing daily radiation sum. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Cauliflower; Model; Dry matter production; Daily radiation sum

1. Introduction

The level of abstraction in modules for calculating crop dry matter production rate varies considerably, models relying on the concept of light use efficiency, LUE (Jones and Kiniry, 1986; Williams et al., 1989; Chapman et al., 1993) representing an approach at a higher abstraction level on the one hand and photosynthesis–respiration based modules (Spitters et al., 1989) representing a more detailed, bottom up approach on the other hand. The LUE concept has become a popular approach for calculating total dry matter production rates in crop growth models mainly due to its simplicity and to the experimental evidence that the ratio between the time integral of intercepted radiation and dry matter production seems to be quite constant (Monteith, 1977; Gallagher and Biscoe, 1978; Garcia et al., 1988). However, the validity of this concept has also been subject to exhaustive debate (Demetriades-Shah et al., 1992, 1994; Arkebauer et al., 1994; Monteith, 1994). Theoretical analyses (Hammer and Wright, 1994; Dewar, 1996; Haxeltine and Prentice, 1996; Dewar et al., 1998; Medlyn, 1998; Kage et al., 2001) have shown that a constant LUE over a wider range of daily photosynthetic active radiation sum is only likely as an effect of a combined adaptation of the photosynthetic apparatus to the radiation environment within the canopy and over time. It is, however, difficult to decide by up-scaling from single leaf to canopy photosynthesis and crop dry matter production rates alone whether LUE is strongly influenced by daily radiation sum as long as the functional relationships between parameters like the light saturated photosynthesis rate, P_{\max} , and environmental variables changing within the canopy and with time are not known.

If such detailed knowledge is not available, one can make assumptions about the behaviour of P_{\max} within the canopy, adjust the model to data measured at the crop level, i.e. total plant dry matter, and compare the consequences of the different hypotheses on the descriptive and predictive ability of the resulting models. Since the calculation of radiation interception is a prerequisite for calculations of total dry matter production, either photosynthesis/respiration or LUE based, the question of the needed level of detail for sufficient predictions of dry matter production is therefore closely coupled with the required level of detail of the light interception module within a crop growth model. The most simple but still often used approach for closed crop canopies is the one proposed by Monsi

and Saeki (1953). However, more detailed approaches have been developed since then (de Wit, 1965; Goudriaan, 1977; Spitters, 1986; Spitters et al., 1986), separating diffuse and direct radiation components and considering the effects of latitude and season on the radiation geometry. We therefore included also modules calculating radiation interception of crop canopies at a different level of detail within our analysis.

Our objective was to evaluate the usefulness of different approaches for calculating total dry matter production within the crop growth models differing in their level of detail in process description. We used for this study data from 22 crops from 15 field experiments with cauliflower grown for 4 years at one location in northern Germany.

2. Materials and methods

2.1. Field experiments

The field experiments used in this study are mainly the same as previously described by Kage and Stützel (1999b). Therefore, only a brief description will be given here. In addition to the data set described in Kage and Stützel (1999b) data from two nitrogen fertilisation trials from 1996 to 1997 on the same experimental fields are included. From this experiments only the optimum and super optimum nitrogen supply rates 300 and 450 kg N/ha were used.

The whole set of field experiments from four consecutive years were divided into two groups, one for derivation of the parameters of the model and a second, independent group for the evaluation of the model. Both groups of field experiments were conducted on the same experimental farm located 15 km south of Hannover, Germany, on a typical loess derived hapludalf soil. Whereas in the parameterisation group of experiments two cultivars were used, i.e. 'Fremont' and 'Linday' in the second group only the cultivar 'Fremont' was used. Crops were established in the field using transplants grown in peat cubes of 4 cm edge length, the average visible leaf number at planting ranged from 2.9 to 4.03 leaves per plant. Crop husbandry in all experiments was regarded to ensure a crop growth not limited by the supply of nitrogen or water. Pesticides were applied when needed to ensure a healthy growth.

Temperature and radiation data were taken from measurements of an automated weather station (Campbell Sci., UK) located on the experimental station. Measured values of global radiation were converted to photosynthetic active radiation, I , using a factor of 0.5 (Szeicz, 1974). Weekly average values of I and air temperature at 2 m height for the four experimental years are shown in Fig. 1.

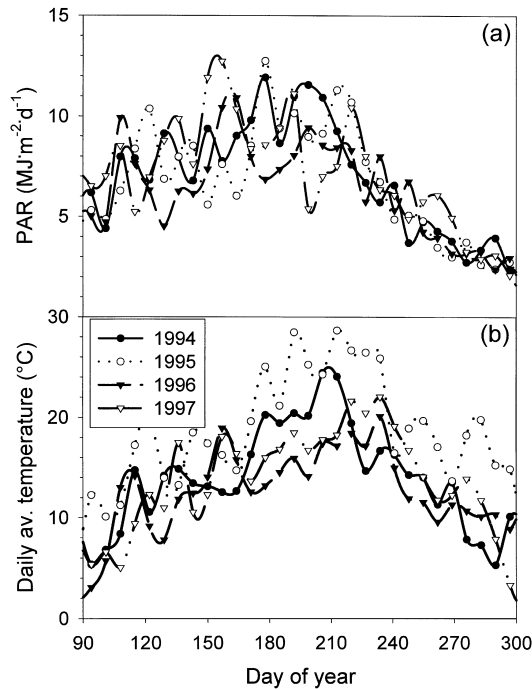


Fig. 1. Weekly averages of daily radiation sum and air temperature during the years 1994–1997 on experimental station ‘Ruthe’, near Hannover, Germany.

2.2. Modules

The modules used in this study for calculating development and partitioning are essentially the same as those described in Kage and Stützel (1999b). The development module distinguishes a juvenile, a vernalization and a generative phase in the development of cauliflower (Wiebe, 1972a,b,c). The dry matter partitioning part includes an allometric approach to dry matter partitioning between leaf and stem and an empirical logistic function describing the fraction of dry matter allocated to the curd depending on the temperature sum after the end of the vernalisation process. However, a slight re-parametrisation of the partitioning module was carried out in order to obtain the best possible description of development and partitioning. For this purpose the group of experiments was used from which also the parameters of the dry matter production modules were estimated.

For dry matter production six different modules were calibrated and evaluated against the data set. We used two modules based on the light use efficiency approach and four based on a photosynthesis–respiration approach (Table 1).

Table 1

Abbreviations and short description of the modules for total dry matter production used in this study

Module name	Short description
LUE I	Constant LUE, radiation absorption according to Monsi and Saeki
LUE II	As LUE I, but LUE assumed to be a linear function of average daily radiation sum
ACOCK I	Analytical integration of the rectangular hyperbola for single leaf photosynthesis over the canopy, numerical 3-point gauss integration over time, respiration according to SUCROS assumptions
ACOCK II	As ACOCK I, but assumption of a decline of P_{\max} within the canopy proportional to irradiance
SUCROS I	Original algorithms from SUCROS, separating direct and diffuse radiation, but negative exponential function for single leaf photosynthesis replaced by rectangular hyperbola
SUCROS II	As SUCROS I, but assumption of a decline of P_{\max} within the canopy proportional to diffuse radiation

The amount of absorbed photosynthetically active radiation (PAR), Q (MJ m^{-2} per day) is calculated from the daily sum of photosynthetically active radiation recorded above the canopy, I (MJ m^{-2} per day) and the leaf area index, LAI (Monsi and Saeki, 1953):

$$Q = I(1 - e^{-k\text{LAI}}) \quad (1)$$

where k is the extinction coefficient for I (–), taken as 0.65. The growth rate of shoot dry matter of the crop (g DM m^{-2} per day) may be calculated as the product of Q , LUE and a temperature correction factor f_{Temp} (–):

$$\frac{dW}{dt} = QLUEf_{\text{Temp}} \quad (2)$$

The value of f_{Temp} is 1 within a range from 10 to 25°C average daily air temperature and is linearly decreasing to 0 from 10 down to 0°C and from 25 to 35°C. The model module LUE I assumes LUE to be constant, therefore being a parameter within the model. In this study we examined, however, also the hypothesis that LUE is a function of I . This function may be approximated as being linear for a particular range of I :

$$\text{LUE} = \text{LUE}_0 - a_{\text{LUE}}I \quad (3)$$

LUE then is a variable dependent on the two parameters LUE_0 (g MJ^{-1}), a_{LUE} ($\text{g DM MJ}^{-2} \text{m}^2$ per day) and the level of I .

Differently from the model presented in Kage and Stützel (1999b), the specific leaf area, SLA ($\text{cm}^2 \text{g}^{-1}$) of newly formed leaf area is now calculated as a function of the average PAR during the last 10 days I_{av} using the function of Alt (1999):

$$\text{SLA} = 590I_{\text{av}}^{-0.851} \quad (4)$$

The LAI of the crop then is calculated from

$$\frac{dLAI}{dt} = \frac{dW_L}{dt} SLA \quad (5)$$

The SLA of the analysed cauliflower crops at transplanting was not always measured but with an average value of about $200 \text{ cm}^2 \text{ g}^{-1}$ was consistently higher than predicted from Eq. (4) which was derived from measurements at later growth stages. LAI was therefore initialised using measured leaf dry matter at transplanting and a value for SLA of 200.

It has to be noticed that we neglected root growth at this stage of the analysis; our estimates for LUE are, therefore, also only valid for calculations of aboveground dry matter production.

The two photosynthesis based modules, ACOCK I and ACOCK II, have been described in Kage et al. (2001). Also the respiration part of these modules, which is essentially based on the assumptions used in the SUCROS model (Goudriaan and van Laar, 1994) is described there.

In order to evaluate the effect of differentiation between shaded and unshaded leaf classes within the canopy and of a more detailed approach of radiation interception on the descriptive and predictive capability, we included also the algorithms from the procedures ASTRO, ASSIM and TOTASS of the SUCROS model (Goudriaan and van Laar, 1994) to calculate total daily assimilate production in our evaluation. In order to make this module comparable with our ACOCK based submodules we replaced the negative exponential function used in ASSIM to calculate photosynthesis rate per unit leaf area with the rectangular hyperbola. This module is further referred as SUCROS I (Table 1). The parameter initial light use efficiency, α , of the rectangular hyperbola was set to a value of $25 \mu\text{g J}^{-1}$ as indicated by the measurements of Kage et al. (2001).

In order to facilitate a comparison between the SUCROS module and the ACOCK II module, we also included the option to let the light saturated photosynthesis rate P_{max} decrease within the canopy according to the profile of diffuse radiation

$$P_{\text{max}} = P_{\text{max}0} e^{-k_{\text{dif}}LAI} \quad (6)$$

where $P_{\text{max}0}$ is the light saturated photosynthesis rate of unshaded leaves at the top of the canopy and k_{dif} is the extinction coefficient for diffuse radiation which is calculated according to Spitters et al. (1989). This version of the SUCROS based module is further called SUCROS II (Table 1).

Radiation absorption R_{abs} within the canopy is calculated according to the fraction of sunlit leaf area, FSSLA, from the weighted sums of absorbed radiation per unit shaded, VISSHD, and unshaded, VISSUN, leaf area. Integrated over the day and over the canopy according to the Gauss 5 point integration scheme,

where D_L is the day length, W_{DL} and w_{LAI} are weighting coefficients:

$$R_{\text{abs}} = \sum_{i=1}^5 D_L W_{DL_i} \sum_{j=1}^5 \text{FSSLA}_{i,j} \text{VISSUN}_{i,j} + (1 - \text{FSSLA}_{i,j}) \text{VISSHD}_{i,j} \text{LAI } w_{LAI_j} \quad (7)$$

We had serious difficulties to simulate the dry matter production of the experiments from the evaluation group with early planting dates (day 97 in 1994, 94 in 1995 and 100 in 1996), the measured total dry matter being substantially and consistently smaller than the simulated total dry matter. We interpreted this as reflecting problems in plant establishment which were probably caused by frost and low temperatures. Since we are not yet able to include these effects into the model, we started our simulations for these data sets not from planting but from the first measurement of plant dry matter, which was usually about 4 weeks after planting.

2.3. Parameter estimation and statistics

The whole model is implemented within the HUME modelling environment (Kage and Stützel, 1999a). This modelling environment supports parameter estimation based on the Marquardt algorithm (Marquardt, 1963) and allows easily sub-model exchange because of its modular object oriented structure. We used the unweighted square sum of differences between simulated and measured total dry matter as the objective function for estimating LUE, LUE₀, a_{LUE} , P_{max} and $P_{\text{max}0}$. For a re-parametrisation of some of the parameters of the development and dry matter partitioning modules unweighted square sums of the differences between simulated and measured model variables were used. For the parameters k_1 , k_2 leaf numbers for g , h stem dry matter and for r_f curd dry matter was used as the objective variable. The whole parameter estimation procedure including the estimation of the parameters of the dry matter production modules was repeated 3–4 times until no further significant change in any parameter value could be detected. The new parameter values are shown in Appendix A.

The descriptive and predictive power of a model can be evaluated by linear regression of the output and measured data and several other statistical measures. One of them is the modelling efficiency, EF (Smith et al., 1997):

$$\text{EF} = 1 - \frac{\sum (y_i - \hat{y}_i)^2}{\sum (y_i - \bar{y})^2} \quad (8)$$

Comparing models having different numbers of parameters solely by their EF value, however, is not appropriate since no correction for parameter number is included within this measure. An approach to overcome this problem is the

Akaike information criterion, AIC (Akaike, 1969).

$$\text{AIC} = n \ln \left(\frac{\sum (y_i - \hat{y}_i)^2}{n} \right) + 2p \quad (9)$$

where n is the number of observations and p is the number of parameters. The descriptive and predictive power of models is higher the lower the value of the AIC. Another statistical parameter used in this study is the root mean square error, RMSE:

$$\text{RMSE} = \sqrt{\frac{\sum (y_i - \hat{y}_i)^2}{n}} \quad (10)$$

giving the average model prediction error.

3. Results

The two sets of field experiments used in this study differed with respect to the variability of mean daily radiation sum during the growing period of each crop (Table 2). Whereas in the first set that was mainly used for calibration, only a small variation, ranging from 8.35 to 9.29 MJ m⁻² per day could be observed, in the second set of experiments, that was mainly used for evaluation, a considerable range of I values from 5.45 to 8.13 MJ m⁻² per day was measured. The reason for this higher variability is the late planting date of some crops of this group (Fig. 1). The variability in mean air temperature is generally smaller than the variability in daily radiation sum, since temperature declines not as much in autumn as daily radiation sum does (Fig. 1).

As a first step in our analysis we estimated the parameters LUE of module LUE I as well as the P_{\max} and $P_{\max 0}$ values of the modules ACOCK I and II and their asymptotic standard errors, respectively, for every experiment separately and plotted them against the mean daily radiation sum during the crop's growth period (Fig. 2). Fitting the two parameter module LUE II was avoided during this step because of the limited number of observations in every experiment.

Linear regression analysis showed no significant correlation between LUE and mean photosynthetically active daily radiation sum for the calibration data set, nor for the evaluation data set alone. However, using the parameter estimates from both sets of experiments a significant correlation could be found (Fig. 2a). No correlation exists for the parameters P_{\max} and $P_{\max 0}$ and mean daily radiation sum during the growing periods of the different crops (Fig. 2b).

In the second step of our analysis we used all crops of the calibration set as a whole database for estimating the parameters of our six different dry matter

Table 2

Year, data group, planting and harvest dates, average daily sum of photosynthetically active radiation and average temperature during the growth period of the cauliflower experiments used in this study

Year	Group	Cultivar	Planting date	Harvest date	Average I (MJ m ⁻² per day)	Average temperature (°C)
1994	Calibration	Fremont	124	194	8.72	15.12
1994		Fremont	152	236	9.24	18.31
1994		Linday	124	194	8.72	15.12
1994		Linday	152	247	8.80	18.03
1995		Fremont	122	200	8.35	14.76
1995		Fremont	137	207	8.48	16.00
1995		Fremont	164	234	9.29	18.79
1995		Linday	122	204	8.41	15.13
1995		Linday	137	209	8.49	16.12
1995		Linday	164	253	8.41	18.02
1994	Evaluation	Fremont	97	185	8.13	13.12
1994		Fremont	207	293	5.45	14.52
1995		Fremont	94	187	7.59	12.13
1995		Fremont	200	291	6.10	16.49
1995		Fremont	207	298	5.56	15.69
1996		Fremont	100	189	7.41	12.59
1996		Fremont	200	284	6.18	14.34
1996		Fremont	206	305	5.11	13.45
1996 ^a		Fremont	170	240	7.78	16.08
1997 ^a		Fremont	190	258	7.23	18.56

^a Two N treatments were included in analysis.

production modules. Calibrating the module LUE I with the data of the calibration set gave a mean value for LUE of 3.15 (g DM MJ⁻¹) (Table 3). The parameter estimation for module LUE II, however, indicates a significant influence of the mean daily radiation sum on LUE, since we found a parameter value for a_{LUE} significant different from zero (Table 3). The values for a_{LUE} and LUE₀ we obtained are higher than slope and intercept of the linear regression between mean daily radiation sum during the growing period and LUE values estimated for a particular crop (Fig. 2b).

Estimating the values of P_{max} and $P_{\text{max}0}$ for the calibration data set gave significantly different values for both parameters either using the ACOCK or the SUCROS approach (Table 3). This is not an unusual result since an assumed decline of P_{max} within the canopy as in Acock II and SUCROS II has to be compensated by a higher P_{max} at the top of the canopy in order to predict the same dry matter production rate.

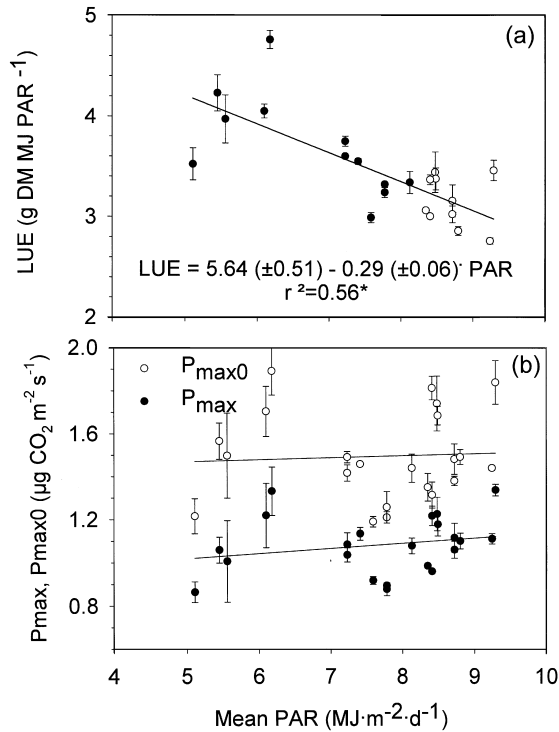


Fig. 2. Parameters average light use efficiency (a), P_{max} and $P_{\text{max}0}$ (b) estimated for different cauliflower crops as a function of the average daily radiation sum during the growing period of the crops. Open and closed circles in the upper graph correspond to different groups of experiments.

We also used the second data set which will later be used to evaluate the predictive value of our model for proving the constancy of parameter values. The values obtained from this database are slightly but not significantly different from the formerly estimated values for the module LUE II. For all photosynthesis based modules somewhat lower values for P_{max} were estimated for the evaluation data set. For the LUE I module a significant higher value of LUE was obtained (Table 3).

The descriptive and predictive value of the modules was evaluated by comparison of simulated with measured total dry matter production data from the parameterisation and evaluation data sets using, for both data sets, the parameter values obtained from the calibration data set. Both versions of the LUE based dry matter production module seem to have similar descriptive power for the calibration data set (Table 4 and Fig. 3a). The linear regressions between simulated and measured total dry matter values have in both cases a slope and an intercept not significantly different from 1 and 0, respectively, and comparable modelling efficiencies 0.92 for the LUE I and 0.94 for the LUE II module. The

Table 3

Parameter estimations for four dry matter production modules assuming either a constant LUE or an LUE being a linear function of daily average radiation sum, I (MJ m^{-2} per day) ($\text{LUE}=\text{LUE}_0-a_{\text{LUE}}I$) for two different photosynthesis/respiration based modules for two groups of experiments^a

Data set	Module	Parameter	Value	S.E.
Calibration	LUE I	LUE	3.15	0.04
	LUE II	LUE ₀	6.66	0.80
		a_{LUE}	0.36	0.08
		ACOCK I	P_{max}	1013
	ACOCK II	$P_{\text{max}0}$	1438	29
	SUCROS I	P_{max}	1349	29
	SUCROS II	$P_{\text{max}0}$	1928	64
	Evaluation	LUE I	LUE	3.49
LUE II		LUE ₀	6.74	0.51
		a_{LUE}	0.38	0.06
		ACOCK I	P_{max}	922
ACOCK II		$P_{\text{max}0}$	1306	32
SUCROS I		P_{max}	1269	43
SUCROS II		$P_{\text{max}0}$	1789	71

^a S.E.: asymptotic standard error, $n=60$ for calibration, $n=43$ for evaluation.

situation is, however, somewhat different for the application of the LUE based modules on the evaluation group of experiments. (Table 4 and Fig. 3). The LUE II module was able to give also for the evaluation data an acceptable prediction ($\text{EF}=0.88$), compared to the LUE I module ($\text{EF}=0.69$).

Looking at the descriptive and predictive value of the photosynthesis modules (Table 4 and Fig. 3), we see that the ACOCK II module has a descriptive value close to the LUE II module, whereas the ACOCK I module has a low, but still acceptable descriptive value for our calibration data set. It is, however, much less able to predict the dry matter production of our evaluation data set (Table 4 and Fig. 3). The descriptive value of the SUCROS modules is not superior to the ACOCK modules, but especially the SUCROS II module seems to have a relatively high predictive value (Table 4).

The data points of the photosynthesis/respiration modules tend to lie above the 1/1 line if one assumes a constant P_{max} and they lie mostly below the 1/1 line for the assumption of a decreasing P_{max} within the canopy (Fig. 3). This is due to the fact that the predicted time course of dry matter production differs in the way that, in general, the modules which assume a constant P_{max} within the canopy estimate a lower production during the early crop growth phase which is over-compensated during the later growing phase (Fig. 4). The LUE modules predict an almost constant dry matter increase under conditions of quite stable values of daily radiation sum. For a late planted crop, however, which is growing

Table 4

Number of fitted parameters p , coefficient of determination for the model prediction r^2 , AIC and parameters of the linear regression between simulated and measured total above ground dry matter of cauliflower crops from calibration and evaluation groups of experiments using four different dry matter production modules^a (for explanation of modules, see Table 1)

Data set	Module	p	EF	RMSE	AIC	Slope	Intercept	r^2	n
Calibration	LUE II	2	0.941	98.706	555.1	0.98 (± 0.03)	27.99 (± 17.20)	0.94	60
	ACOCK II	1	0.916	118.185	574.7	1.04 (± 0.04)	-35.78 (± 22.56)	0.92	60
	LUE I	1	0.916	114.381	574.7	0.95 (± 0.04)	23.22 (± 20.26)	0.92	60
	SUCROS I	1	0.901	127.918	584.2	0.98 (± 0.04)	1.83 (± 23.81)	0.90	60
	ACOCK I	1	0.886	137.684	593.0	0.89 (± 0.04)	47.80 (± 22.81)	0.90	60
	SUCROS II	1	0.882	139.944	594.9	1.10 (± 0.05)	-59.63 (± 27.26)	0.89	60
Evaluation	LUE II	2	0.879	113.914	411.2	0.88 (± 0.05)	39.39 (± 25.16)	0.90	43
	ACOCK II	1	0.833	134.040	423.2	0.86 (± 0.05)	11.56 (± 28.78)	0.88	43
	SUCROS II	1	0.820	139.003	426.4	0.93 (± 0.07)	5.19 (± 35.08)	0.83	43
	SUCROS I	1	0.780	153.566	434.9	0.82 (± 0.06)	70.87 (± 32.42)	0.82	43
	LUE I	1	0.690	182.547	449.8	1.07 (± 0.11)	108.79 (± 42.15)	0.78	43
	ACOCK I	1	0.682	184.784	450.9	0.70 (± 0.05)	93.54 (± 28.53)	0.85	43

^a Modules are grouped by data set and AIC.

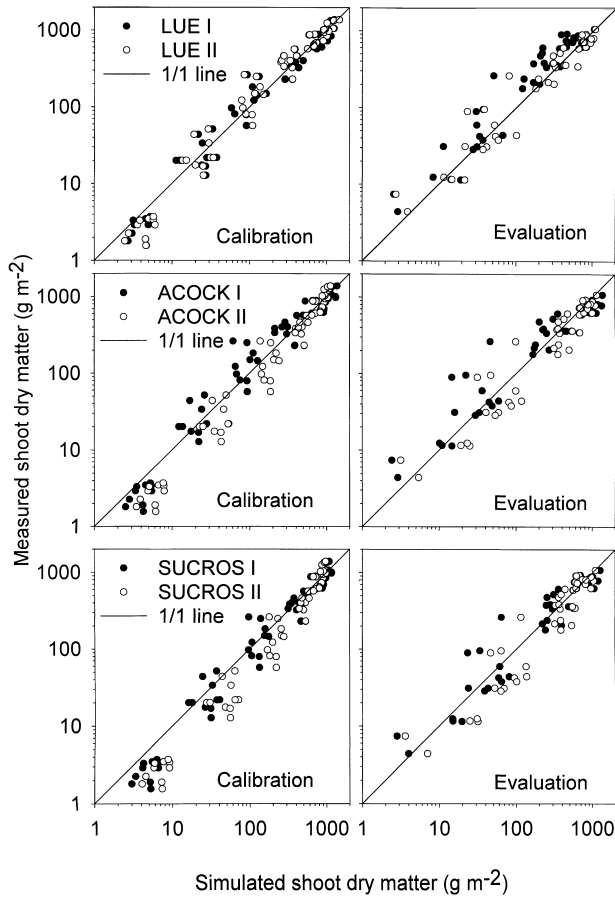


Fig. 3. Simulated and measured shoot dry matter of several cauliflower crops from calibration and independent evaluation experiments using six different modules for calculating dry matter production (for explanation of modules, see Table 1).

under a decreasing daily radiation sum, the LUE II module is clearly superior to all other modules, as it compensates lower daily radiation sum by an increasing LUE.

Plotting the calculated daily light use efficiencies of the ACOCK I and II modules for an early and a late planted cauliflower versus the daily radiation sum values, a considerable scatter of calculated LUE on a daily basis becomes obvious. This is because variations in temperature and crop dry weight at similar levels of daily radiation sum affect respiration losses and thereby net assimilation values. However, there is also a clear decrease of LUE with increasing daily radiation sum values (Fig. 5). This trend corresponds well with the functional relationship between LUE and I estimated for the LUE II module (Fig. 5).

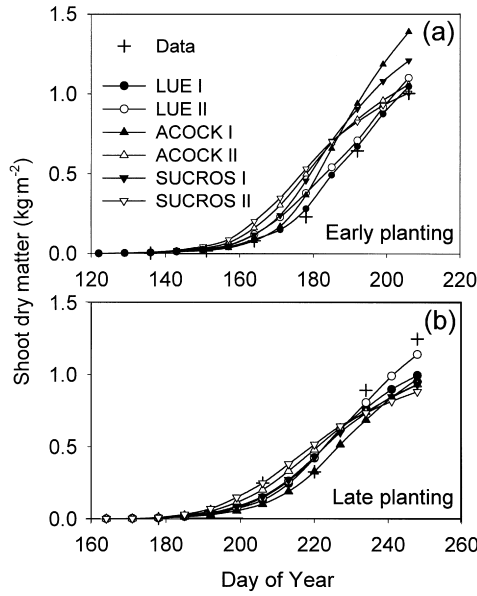


Fig. 4. Measured and simulated shoot dry matter of cauliflower crops cv. 'Freemont' planted early (a) (DOY 122) and late (b) (DOY 164) in 1995 vs. time using six different modules for calculating dry matter production (for explanation of modules, see Table 1).

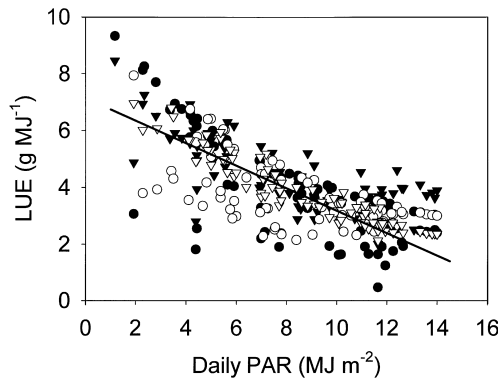


Fig. 5. Light use efficiency as a function of daily sum of photosynthetically active radiation simulated with two different optimised photosynthesis modules assuming either a constant P_{max} (ACOCK I, triangles) within the canopy or a P_{max} decreasing within the canopy proportionally to irradiance (ACOCK II, circles) for an early (closed symbols) and late (open symbols) planted cauliflower. Straight line represents the calibrated $LUE=f(I)$ model.

4. Discussion

The aim of this paper is to evaluate different modules for predicting dry matter production of cauliflower under unstressed conditions, i.e. in the absence of water and nutrient limitations and pest damages. The database we used for this purpose is quite large concerning the number of independent experiments included, but limited with respect to the kind of data we included in the analysis as we used only time series data of total dry matter and the environmental data of temperature and radiation.

Our analysis shows that LUE for unstressed cauliflower crops is not constant, but decreases with increasing daily radiation sum (Fig. 2, Table 3). The observed decrease of LUE with I agrees with measurements of Olesen and Grevsen (1997) and calculations of Medlyn (1998). From data of the first mentioned authors we estimated a linear decrease of LUE– I of $LUE=6.3-0.34I$, whereas for Medlyn's (1998) data we estimated a decrease of $0.33 \text{ g DM MJ}^{-2} \text{ m}^{-2}$ per day. From theoretical considerations (Kage et al., 2001), however, it seems to be likely that LUE is a non-linear function of I and that the slope of the LUE– I function is also less negative for higher LAI values. A linear approximation, like the one we present, may therefore be valid only for a limited range of daily radiation sum and may be further refined by including an influence of LAI.

The estimated values of P_{\max} and $P_{\max 0}$ for our photosynthesis based modules (Table 3) are within the range of the measured values presented in Kage et al. (2001), maybe despite the value for the SUCROS II module. But the assumption that P_{\max} values decline directly proportional to the irradiance level within the canopy probably overestimates the degree of light adaptation within the canopy (Kage et al., 2001). Too high estimates for $P_{\max 0}$ values are therefore needed to compensate this error.

Kage et al. (2001) showed that whether one assumes a decline of P_{\max} within the canopy or not, LUE seems to be a negative function of PAR. Therefore, the different predictive value of the ACOCK I and II and the SUCROS I and II modules for dry matter production (Table 4) cannot mainly be explained by a different change of LUE under varying daily radiation sum values. The difference in the predictive value of the modules seems to be mainly caused by the fact that for a constant P_{\max} within the canopy (ACOCK I, SUCROS I) LUE increases with increasing LAI whereas it decreases for a P_{\max} decreasing proportionally to irradiance level within the canopy (ACOCK II, SUCROS II). Consequently, different time courses of dry matter production are predicted (Fig. 5). This increase of LUE with increasing LAI, which is largest for the ACOCK I module, probably is the reason for its inferior descriptive and predictive power (Table 4). This may also hold as an argument that the assumption of the ACOCK II and SUCROS II modules, a decline of P_{\max} within the canopy, is somewhat more realistic than a constant P_{\max} . The failure of the constant LUE hypothesis on the

other hand may be regarded as an indication that the adaptation of P_{\max} to a changing radiation environment over time is limited, since the analysis presented in Kage et al. (2001) shows that this process seems to be a prerequisite for a constant LUE.

The more detailed light interception approach of the SUCROS modules did not improve the descriptive and predictive value compared to the simple Monsi–Saeki approach. Our data set indicates that different assumptions about the behaviour of P_{\max} within the canopy, seems to be more important than the consideration of direct and diffuse radiation in light interception calculations. But it has to be noticed that we did not include in our module comparison any approach which explicitly accounts for the inhomogeneous leaf area distribution of cauliflower during the first weeks after transplanting. Thereby, we may probably have overestimated light interception during the early growth phase. However, also the leaf angle distribution of cauliflower changes according to our observations to some extent from a quite planophile to a more spherical one. This may lead to a decreasing k value over time which may compensate for some of the effects of an uneven leaf distribution. Also the SLA of cauliflower at early growth stages is higher than calculated from Eq. (4) (data not shown), which leads to a more rapidly canopy closure and therefore also compensates for some of the structural errors of our light interception model. At least in the second half of their growth period, however, the crops we analysed had high values of LAI and a quite homogenous leaf area distribution (data not shown).

One reason for the popularity of the constant LUE concept seems to be the possibility to derive this parameter directly from measurements in field experiments by plotting total dry matter data of a crop vs. values of cumulative intercepted radiation and to interpret the slope of the linear regression as LUE. This method has the shortcoming that one usually has to assume a constant LUE throughout the growing season or at least over a longer time period in order to get a sufficient amount of data pairs. Variations of LUE due to rapidly changing environmental conditions like radiation and temperature can therefore not easily be detected. Even if one is able to identify such a relationship (Fig. 2) this is only valid at the timescale at which it was evaluated. This becomes clear from the distinct effects of daily radiation sum on LUE at the timescale of a cropping period and on a daily basis (cv. Fig. 2 and Table 3).

Parameters from photosynthesis based models on the other hand are more difficult to obtain. Furthermore, these parameters are not constant over time (Kage et al., 2001) and within the canopy and are always only interpretable on the crop scale after up-scaling using mathematical models. Some of this methodological drawbacks, however, may decrease because of the increasing computational power and the availability of commercial software like 'ModelmakerTM' (Cherwell Scientific, Oxford, UK, 1999) or by modelling environments (Kage and Stützel, 1999a) which allow parameter estimation within

dynamic models. But also LUE based approaches may be further refined by parameter estimation techniques and an appropriate database. The approach we used for calibration of our LUE II module, for instance, resulted in a simple structured module with good descriptive and predictive value. Adjusting parameters of dynamic crop growth models like LUE or P_{\max} by minimising the prediction error for an aggregated variable like total above ground dry matter on the other hand implies the risk, that structural errors of a model are masked and the estimated parameter values are biased. This cannot totally be ruled out for our analysis, but since the obtained parameter values are well within a physiological meaningful range, we do not expect that these effects are serious.

Recognising that P_{\max} seems to be a more conservative parameter than LUE (Fig. 2) one may conclude that even if based on several assumptions, the parameterisation of a photosynthesis–respiration based approach usually gives more generally applicable predictions than an LUE based approach. However, the usefulness of the constant LUE concept for calculating dry matter production in crop growth models cannot be judged ultimately from the presented analysis. At least for annual crops which have a limited time span for sowing or planting each year, it seems likely that year to year variation in average daily radiation sum during cropping time at one location is small (see analysis of Medlyn, 1998). For a particular crop grown under these conditions constant LUE values may allow sufficient exact predictions of crop productivity.

The failure of the constant LUE concept in predicting total dry matter production can be regarded as an indication that the requirements for a constant LUE which were deduced from theoretical analyses are not fulfilled for cauliflower. Possible reasons for this may be seen in the quite short growing season and the high growth rate of this crop, which limits the time available for adaptation processes. The fact that we were able to detect the limited constancy of LUE for cauliflower with experiments at one location only is probably due to the short growing period of this crop, which makes it possible to cultivate this crop under substantially different radiation regimes.

5. Conclusions

The constant LUE hypothesis is too crude a simplification for calculation of dry matter production by the short season crop cauliflower. Acceptable predictions seem to be possible by assuming a linear decrease of LUE with increasing levels of daily radiation sum, at least for the range 5–10 MJ m⁻² per day PAR we analysed. Parameter estimation techniques may help to calibrate photosynthesis-based dry matter production modules directly from field measurements, however, one should be aware of the possible influence of structural model errors. This type of model inherently implies a decline of LUE with increasing daily radiation sum

and is therefore of superior descriptive and predictive value compared to simple LUE models. Our results indicate that assumptions about the behaviour of P_{\max} within the canopy seem to be of higher importance for correct predictions than detailed calculations of light interception.

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Appendix A.

The following table shows the name and values of parameters from the development and partitioning model (Kage and Stützel, 1999b) as well as the equation number from the original publication. Parameters set with an * are changed in this study.

Name	Value	Equation No.
k_1^* (leaf per leaf °C ⁻¹ per day)	0.00392	(1)
k_2^* (leaf °C ⁻¹ per day)	0.0424	(3)
g^*	1.617	(18)
h^*	-4.958	(18)
f_0	0.000215	(21)
r_f^* (°C ⁻¹ per day)	0.0133	(21)
f_f	0.815	(21)

References

- Akaike, H., 1969. Fitting autoregressive models for prediction. *Ann. Inst. Statist. Math.* 21, 243–247.
- Alt, C., 1999. Modeling nitrogen demand of cauliflower (*Brassica oleracea* L. *botrytis*) by using productivity–nitrogen relationships. Ph.D. Thesis. University of Hannover, Germany.
- Arkebauer, T.J., Weis, A., Sinclair, T.R., Blum, A., 1994. In defense of radiation use efficiency: a response to Demetriades-Shah et al. (1992). *Agric. For. Meteorol.* 68, 221–227.
- Chapman, S.C., Hammer, G.L., Meinke, H., 1993. A sunflower simulation model. I. Model development. *Agron. J.* 85, 725–735.
- Demetriades-Shah, T.H., Fuchs, M., Kanemasu, E.T., Flitcroft, I., 1992. A note of caution concerning the relationship between cumulated intercepted solar radiation and crop growth. *Agric. For. Meteorol.* 58, 193–207.

- Demetriades-Shah, T.H., Fuchs, M., Kanemasu, E.T., Flitcroft, I.D., 1994. Further discussions on the relationship between cumulated intercepted solar radiation and crop growth. *Agric. For. Meteorol.* 68, 231–242.
- Dewar, R.C., 1996. The correlation between plant growth and intercepted radiation: an interpretation in terms of optimal plant nitrogen content. *Ann. Bot.* 78, 125–136.
- Dewar, R.C., Medlyn, B.E., McMurtrie, R.E., 1998. A mechanistic analysis of light and carbon use efficiencies. *Plant Cell Environ.* 21, 573–588.
- de Wit, C.T., 1965. *Photosynthesis of Leaf Canopies*. PUDOC, Wageningen.
- Gallagher, J.N., Biscoe, P.V., 1978. Radiation absorption, growth and yield of cereals. *J. Agric. Sci. (Cambridge)* 91, 47–60.
- Garcia, R., Kanemasu, E.T., Blad, B.L., Bauer, A., Hatfield, J.L., Major, D.J., Reginato, R.J., Hubbard, K.G., 1988. Interception and use efficiency of light in winter wheat under different nitrogen regimes. *Agric. For. Meteorol.* 44, 175–186.
- Goudriaan, J., 1977. *Crop micrometeorology: a simulation study*. Simulation Monographs. PUDOC, Wageningen, 249 pp.
- Goudriaan, J., van Laar, H.H., 1994. *Modelling Potential Crop Growth Processes*. Kluwer Academic Publishers, Dordrecht.
- Hammer, G.L., Wright, G.C., 1994. A theoretical analysis of nitrogen and radiation effects on radiation use efficiency in peanut. *Aust. J. Agric. Sci.* 45, 575–589.
- Haxeltine, A., Prentice, I.C., 1996. A general model for the light-use efficiency of primary production. *Funct. Ecol.* 10, 551–561.
- Jones, C.A., Kiniry, J.R. (Eds.), 1986. *CERES-Maize. A Simulation Model of Maize Growth and Development*. Texas A&M University Press, Texas, pp. 1–194.
- Kage, H., Stützel, H., 1999a. HUME: an object oriented component library for generic modular modelling of dynamic systems. In: *Proceedings of the ESA symposium “Modelling Cropping Systems”*, Lleida, Spain.
- Kage, H., Stützel, H., 1999b. A simple empirical model for predicting development and dry matter partitioning in cauliflower (*Brassica oleracea* L. *botrytis*). *Sci. Hort.* 80, 19–38.
- Kage, H., Alt, C., Stützel, H., 2001. 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. *Sci. Hort.* 87, 155–170.
- Marquardt, D.W., 1963. An algorithm for least-squares estimation of nonlinear parameters. *J. Soc. Ind. Appl. Math.* 11, 431–441.
- Medlyn, B.E., 1998. Physiological basis of the light use efficiency model. *Tree Physiol.* 18, 167–176.
- Monsi, M., Saeki, T., 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jpn. J. Bot.* 14, 22–52.
- Monteith, J.L., 1977. Climate and the efficiency of crop production in Britain. *Philos. Trans. R. Soc. London Ser. B* 281, 277–294.
- Monteith, J.L., 1994. Validity of the correlation between intercepted radiation and biomass. *Agric. For. Meteorol.* 68, 213–220.
- Olesen, J.E., Grevsen, K., 1997. Effects of temperature and irradiance on vegetative growth of cauliflower (*Brassica oleracea* L. *botrytis*) and broccoli (*Brassica oleracea* L. *italica*). *J. Exp. Bot.* 48, 1591–1598.
- Smith, P., Smith, J.U., Powlson, D.S., McGill, W.B., Arah, J.R.M., Chertov, O.G., Coleman, K., Franko, U., Frolking, S., Jenkinson, D.S., Jensen, L.S., Kelly, R.H., Klein-Gunnewiek, H., Komarov, A.S., Li, C., Molina, J.A.E., Mueller, T., Parton, W.J., Thornley, J.H.M., Whitmore, A.P., 1997. A comparison of the performance of nine soil organic matter model using datasets from seven long-term experiments. *Geoderma* 81, 153–225.

- Spitters, C.J.T., 1986. Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis. Part II. Calculation of canopy photosynthesis. *Agric. For. Meteorol.* 38, 231–242.
- Spitters, C.J.T., Toussaint, H.A.J.M., Goudriaan, J., 1986. Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis. Part I. Components of incoming radiation. *Agric. For. Meteorol.* 38, 217–229.
- Spitters, C.J.T., Keulen, H., van Kraalingen, D.W.G., 1989. A simple and universal crop growth simulator: SUCROS'87. In: Rabbinge, R., Ward, S.A., van Laar, H.H. (Eds.), *Simulation and Systems Management in Crop Protection*. PUDOC, Wageningen.
- Szeicz, G., 1974. Solar radiation in crop canopies. *J. Appl. Ecol.* 11, 1117–1156.
- Wiebe, H.J., 1972a. Wirkung von temperatur und licht auf wachstum und entwicklung von Blumenkohl. I. Dauer der jugendphase für die vernalisation. *Gartenbauwissenschaft* 37, 165–178.
- Wiebe, H.J., 1972b. Wirkung von Temperatur und Licht auf Wachstum und Entwicklung von Blumenkohl. II. Optimale vernalisationstemperatur und vernalisationsdauer. *Gartenbauwissenschaft* 37, 293–303.
- Wiebe, H.J., 1972c. Wirkung von Temperatur und Licht auf Wachstum und Entwicklung von Blumenkohl. III. Vegetative phase. *Gartenbauwissenschaft* 37, 455–469.
- Williams, J.R., Jones, C.A., Kiniry, J.R., Spanel, D.A., 1989. The EPIC crop growth model. *Trans. ASAE* 32, 497–511.