

## A simple empirical model for predicting development and dry matter partitioning in cauliflower (*Brassica oleracea* L. *botrytis*)

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Accepted 7 September 1998

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### Abstract

An empirical model derived from data of field experiments is presented that predicts development and dry matter partitioning in cauliflower under conditions of unrestricted nutrient and water supply. The model is a combination of an empirical relationship between temperature sum and leaf number, a vernalisation model, an allometric approach of 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. This model was incorporated in a simple dry matter production model which calculated dry matter production using the product of intercepted photosynthetic active radiation and light use efficiency. However, the parameter values light use efficiency and specific leaf area of the model had to be fitted to every experiment in order to get an acceptable description of cauliflower dry matter production. Applied to an independent data set the model was able to predict measurable parameters like leaf number ( $r^2 = 0.73$ ), the proportion of leaf, stem and curd on total dry matter ( $r^2 = 0.55, 0.08$  and  $0.77$ ) and the length of the growing season ( $r^2 = 0.69$ ). © 1999 Elsevier Science B.V. All rights reserved.

*Keywords:* Cauliflower; Partitioning; Development; Model; Leaf initiation; Vernalisation

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## 1. Introduction

Two problems have been identified to be of major importance in the production of cauliflower: The first is the high variability in the length of the growing season (Wiebe, 1980; Booij, 1990) which is a consequence of the vernalisation requirement of this crop. High summer temperatures, e.g. can delay vernalisation and thus lengthen the growing period.

The second problem is the high nitrogen leaching risk that is attributed to the usually high intensity of nitrogen fertilisation and low nitrogen use efficiency of cauliflower (Rahn et al., 1992; Everaarts, 1993a). Both problems are interrelated, the uncertainty of the length of the growing period also introduces a serious additional uncertainty in the estimation of the crop nitrogen demand. Of further importance in this context is the partitioning of the plant nitrogen between the harvested product and crop residues, as the amount of nitrogen in crop residues has to be known for an accurate fertilisation of the subsequent crop (Everaarts, 1993b).

The problems described above may be reduced if more precise predictions about the length of the growing season and nitrogen demand of the cauliflower crop as well as the partitioning of nitrogen between the harvested plant part and crop residues were possible. As a first step towards a quantitative model of cauliflower growth, nutrient uptake and partitioning this paper presents a simple empirical model of development and dry matter partitioning of cauliflower.

Several models for the development in cauliflower have been presented which distinguish three phases in the development of cauliflower, i.e. the juvenile, vernalisation and generative phase (Wiebe, 1972a, b, c; Wurr et al., 1990; Grevsen and Olesen, 1994b). Models of Pearson et al. (1994) and Wheeler et al. (1995), however, do not take a juvenile phase into account. All models cited above describe the vernalisation process as a function of temperature, with an optimum around 10–14°C. The length of the generative phase is mostly calculated as a function of a temperature sum beginning to accumulate when vernalisation is completed.

Whilst models for total dry matter production as well as data on light use efficiency of cauliflower have been published (Wheeler et al., 1995; Olesen and Grevsen, 1995, 1997), models for dry matter partitioning in cauliflower are missing.

## 2. Model

### 2.1. Development

During the juvenile phase the plant is not sensitive to the cold stimulus that is causing the vernalisation process. (Wiebe, 1972a; Fujime, 1983). The end of the

juvenile phase can be determined by a characteristic number of initiated leaves, which may vary with cultivars (Wiebe, 1972a; Hand and Atherton, 1987; Booij and Struik, 1990; Grevsen and Olesen, 1994a; Wurr et al., 1994). For the cultivars ‘Fremont’ and ‘Linday’, used in this study we assumed that 16 leaves have to be initiated before the juvenile phase is completed (Wiebe, 1972a, 1998, pers. commun.).

## 2.2. Development of leaves

Like other authors (Hand and Atherton, 1987; Booij and Struik, 1990; Grevsen and Olesen, 1994a) we found that during the early growth phase the rate of leaf initiation is increasing with increasing leaf number. This is described by the following differential equation:

$$\frac{dn_L}{dt} = k_1 \times T \times n_L \quad (1)$$

where  $n_L$  is the number of leaves larger than 1 cm diameter,  $T$  is the temperature (°C) and  $k_1$  is an empirical constant. Integration of Eq. (1) yields the well-known exponential growth equation:

$$n_L = n_{L0} \times e^{k_1 \times TS} \quad (2)$$

where  $n_{L0}$  is the leaf number measured at the day of transplanting and TS the sum of average daily temperatures above 0°C.

During the later growth phase, however, the leaf initiation rate for leaves >1 cm remains constant and is therefore described using a linear function of the temperature sum,

$$\frac{dn_L}{dt} = k_2 \times T \quad (3)$$

In order to obtain a continuously derivable function the exponential and linear part of the function have to predict the same leaf initiation rate at the switching point from one part to the other. Therefore, by combining the right hand sides of Eqs. (1) and (2) and solving for  $n_L$  the leaf number at this switching point,  $n_{Lc}$ , where maximum leaf initiation rate is reached can be calculated,

$$n_{Lc} = \frac{k_2}{k_1} \quad (4)$$

The temperature sum at which the leaf development rate switches from the exponential to the linear phase,  $TS_c$ , is obtained by substituting  $n_{Lc}$  from Eq. (4) for  $n_L$  in Eq. (2). Rearranging gives:

$$TS_c = \frac{\ln(n_{Lc}/n_{L0})}{k_1} \quad (5)$$

The leaf numbers >1 cm at any time after the plants received the critical temperature sum may now be calculated with the following equation:

$$n_L = n_{Lc} + k_2(TS - TS_c) \quad (6)$$

In order to calculate the number of leaves initiated,  $n_{iL}$ , from the number of visible leaves,  $n_L$ , the empirical regression equation of Booij and Struik (1990) was used:

$$n_{iL} = 1.86 \times n_L + 1.24 \quad (7)$$

### 2.3. Vernalisation

The vernalisation process is calculated according to Wiebe (1972b) using a daily vernalisation rate,  $dV/dt$ , which itself is an optimum function of mean daily temperatures,  $T$ .

This optimum function is defined by four cardinal temperatures,  $T1$ – $T4$ , and the maximum vernalisation rate,  $V_{max}$ .

$$\begin{aligned} \frac{dV}{dt} &= 0 & T &\leq T1 \\ \frac{dV}{dt} &= V_{max} - \frac{V_{max}}{T2 - T1}(T2 - T) & T1 &< T < T2 \\ \frac{dV}{dt} &= V_{max} & T2 &\leq T \leq T3 \\ \frac{dV}{dt} &= V_{max} - \frac{V_{max}}{T4 - T3}(T - T3) & T3 &< T < T4 \\ \frac{dV}{dt} &= 0 & T &\geq T4 \end{aligned}$$

The four cardinal temperatures  $T1$ – $T4$  are assumed to be 0°C, 10°C, 13°C and 28°C. The maximum vernalisation rate for the cultivars used was set to a value of 0.11 ( $\text{day}^{-1}$ ).

The vernalisation process is completed when the sum of the daily vernalisation rates has reached a value of 1. The parameters of the vernalisation temperature are cultivar dependent (Wiebe, 1998; pers. commun.). However, it is possible to summarise the actual cultivars of cauliflower in different groups and to use a unique parameter set for this group (Wiebe, 1998, pers. commun.).

### 2.4. Dry matter production

Approaches to calculate the dry matter production rate of a plant stand range from quite detailed models upscaling from the leaf level (Spitters, 1990) to more

comprehensive models on the crop scale (Jones and Kiniry, 1986; Amir and Sinclair, 1991) mostly based on the concept of light use efficiency, LUE (Monteith, 1977). One of the main advantages of the comprehensive models is their more simple parameterisation. Since the focus of this study is on development and dry matter partitioning aspects in cauliflower, we used at this step of analysis the simple LUE based approach for calculating net dry matter production rate of a cauliflower crop.

The growth rate of dry matter of a crop is calculated as a linear function of the absorbed photosynthetically active radiation  $Q$  and the LUE:

$$\frac{dW}{dt} = Q \times \text{LUE} \quad (9)$$

The amount of absorbed photosynthetically active radiation is calculated from the intensity of radiation incident on the plant canopy,  $I$  and the leaf area index, LAI (Monsi and Saeki, 1953):

$$Q = I(1 - e^{-k \times \text{LAI}}) \quad (10)$$

The light extinction coefficient,  $k$  was determined in other field experiments with the cauliflower cultivar ‘Fremont’ and with the same planting pattern of 0.55 (unpublished results).

### 2.5. Leaf–stem partitioning

The leaf–stem partitioning model used in this study is a simplification of the model of Stützel et al. (1988) and Stützel and Aufhammer (1991a). It is mainly based on the assumption of allometric growth of leaves and stem.

The growth rate of total dry matter for the whole plant,  $dW_t/dt$ , is the sum of the growth rate of the vegetative organs,  $dW_v/dt$ , and the growth rate of the curd,  $dW_c/dt$ :

$$\frac{dW_t}{dt} = \frac{dW_c}{dt} + \frac{dW_v}{dt} \quad (11)$$

Neglecting the root dry matter, the vegetative plant dry matter,  $W_v$  is simply the sum of the leaf dry matter,  $W_L$  and the stem dry matter,  $W_S$ :

$$W_v = W_L + W_S \quad (12)$$

Therefore, also the growth rate of vegetative dry matter is the sum of leaf and stem growth rate:

$$\frac{dW_v}{dt} = \frac{dW_L}{dt} + \frac{dW_S}{dt} \quad (13)$$

If allometric growth of stem and leaf dry matter is assumed, which implies that the ratio of the relative growth rates of leaves and stem are constant (Thornley

and Johnson, 1990), the relationship between the natural logarithms of leaf and stem dry matter is linear:

$$\ln W_S = h + g \times \ln W_L \quad (14)$$

The parameters  $h$  and  $g$  are constants, with  $g$  representing the ratio of the relative growth rates of leaf and stem. This relationship may be also expressed in the transformed form:

$$W_S = e^h W_L^g \quad (15)$$

Differentiation of Eq. (15) with respect to  $W_L$  yields:

$$\frac{dW_S}{dW_L} = e^h g W_L^{g-1} \quad (16)$$

Applying the chain rule to the left hand side of Eq. (16) and rearranging one gets:

$$\frac{dW_S}{dt} = \frac{dW_S}{dW_L} \frac{dW_L}{dt} \quad (17)$$

Combining Eqs. (16) and (17) and introducing the resulting relationship into Eq. (13) yields:

$$\frac{dW_L}{dt} = \frac{dW_V}{dt} \frac{1}{1 + e^h g W_L^{g-1}} \quad (18)$$

which expresses the leaf growth rate as a function of the vegetative growth rate and the leaf dry matter.

The leaf area index, LAI is calculated from the leaf dry matter using specific leaf area, SLA:

$$\text{LAI} = W_L \times \text{SLA} \quad (19)$$

The key parameters SLA and LUE are assumed to be constant over one growing period. However, we were not able to describe all experiments with the same values of SLA or LUE. We therefore fitted the values of SLA and LUE to the total dry matter data of every single experiment. This implies that the dry matter production part of the model is at this stage of development of purely descriptive nature.

## 2.6. Curd growth

The curd dry matter growth rate,  $dW_c/dt$  may be expressed as a fraction  $f$  of the total dry matter growth rate,  $dW_t/dt$ :

$$\frac{dW_c}{dt} = \frac{dW_t}{dt} \times f \quad (20)$$

The curd growth of cauliflower starts when the apical meristematic tissue initiates inflorescences instead of leaf primordia. During the generative phase the fraction of curd growth rate to total growth rate is usually increasing in a sigmoid manner. This reflects sink capacity limited growth for some time after curd initiation. Due to the increasing size of the curd, the sink capacity increases exponentially during this early curd growth phase. When the assimilates become limiting, the curd growth rate approaches a more or less stable maximum fraction of the total growth rate.

This is described in the model with a logistic growth function (Thornley and Johnson, 1990):

$$f = \frac{f_0 \times f_f}{f_0 + (f_f - f_0) \times e^{-r_f \text{TS}^3}} \quad (21)$$

where TS3 is the temperature sum the plants accumulated after the end of the vernalisation, i.e. in stage 3 of their growth period,  $f_0$  is the fraction of curd dry matter increase to total dry matter increase when  $\text{TS}^3 = 0$ ,  $f_f$  is the maximum fraction of dry matter growth allocated to the curd and  $r_f$  is a growth rate parameter of  $f$ .

The crop is assumed to be marketable when the curd has reached a diameter of 200 mm. An empirical regression equation derived from unpublished data was used to calculate the curd diameter CD (mm) from the curd weight  $W_F$  (g/pl.).

$$\text{CD} = 3.382 \times W_F^{0.422} \quad (22)$$

The differential equations of the model were programmed in Pascal and integrated numerically using the Euler–Algorithm (Thornley and Johnson, 1990) with a time step of 1 day.

### 3. Material and methods

#### 3.1. Field experiments

In this study two different sets of field experiments were used, one for derivation of the parameters of the model and a second, independent group for the validation of the model.

The parameterisation experiment set was a series of field experiments without replications using two different cauliflower cultivars, ‘Fremont’ and ‘Linday’. In 1994 and 1995 three and five experiments were conducted, respectively. The last experiment in 1994 and the first and the last experiment in 1995 were discarded from further analysis, because of too big transplants which caused problems in plant establishment or severe plant damages due to bird attacks. The dates of planting for both groups of experiments used in the analysis are summarised in Table 1.

Table 1  
Planting dates of the experiments which were used for model parameterisation and validation

Year	Experiment	Planting Date	Usage
1994	1	5 May	P
1994	2	1 June	P
1995	2	2 May	P
1995	3	17 May	P
1995	4	13 June	P
1994	1	7 April	V
1994	2	26 July	V
1995	1	4 April	V
1995	2	19 July	V
1995	3	26 July	V
1996	1	9 April	V
1996	2	18 July	V
1996	3	24 July	V

Abbreviation 'P' in the column 'usage' stands for used for parameterisation, 'V' used for validation.

The second group of experiments is a part of a long-term field trial where effects of crop rotation, nitrogen fertilisation rate and soil tillage on nitrogen use efficiency on the cropping system level are studied. In this experiment only the cultivar 'Fremont' was used. This field trial has a three factorial split-plot design with three replications. For the analysis presented here, only data from plots with optimal nitrogen fertilisation and conventional, mould board plough tillage system were used. 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.

Seeds of cauliflower were germinated in planting plates filled with peat and transplanted by hand in peat cubes with 4 cm edge length after about 3–5 days. When the plants had about two–four visible leaves they were transplanted in the field. The average planting density was four plants  $m^{-2}$ . Before planting in the field prophylactic applications of chlorfenvinphos (Birlane) against cabbage fly, and of molybdenum sulphate were applied to the peat cubes. 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 300 kg N  $ha^{-1}$  including soil nitrate from 0 to 60 cm depth that has to be adjusted by fertilisation. Insecticides and irrigation were given whenever needed.

In the parameterisation experiments a number of 10 plants in 1994 and 14 plants in 1995 were harvested every 2 weeks and divided into leaves including petioles, stem and curd. In the validation experiment six plants per plot were analysed in 3–4 week sampling intervals. Leaf number was counted from a diameter >1 cm considering bases of already aborted leaves. For determination of dry weight sub-samples of the plant organs were oven dried starting with a



temperature of 60°C and followed by a drying temperature of 105°C until a constant weight was reached.

Crops were harvested when about 50% of the plants had reached a curd diameter of 200 mm.

Temperature and radiation data were taken from measurements of an automated weather station (Campbell) located on the experimental station. Measured values of global radiation were converted to photosynthetic active radiation using a factor of 0.5 (Szeicz, 1974).

### 3.2. *Parameter estimation*

The parameters of the equations describing the leaf development rate were estimated by a least squares fit minimising the sum of square differences between predicted,  $n_{lpi}$  and observed leaf number,  $n_{loi}$ . The parameter optimisation was carried out using the procedure NLIN of the statistical software package SAS (SAS Institute, 1988).

Neither SLA nor light interception of cauliflower were continuously measured in the parameterisation experiments. Therefore, also the LUE could not be directly calculated. Both parameters, SLA (Biemond et al., 1995) and LUE (Manrique et al., 1991; Stützel and Aufhammer, 1991b; Hammer and Wright, 1994) may vary considerably for a particular cultivar even under optimal nutrient and water supply as a result of light and temperature regimes under which the crops are grown. For the purpose of this study, both parameters were therefore estimated using a least squares fit of simulated to measured total dry matter data for every single experiment of the parameterisation and validation group. This was done with the Marquardt method (Marquardt, 1963) using the algorithm from Press et al. (1986). For some test functions results from this fitting routine were compared with the outcome of the procedure NLIN of the statistical software package SAS (SAS Institute, 1988) which resulted in a good agreement. All other parameters of the model were kept constant.

## 4. Results

### 4.1. *Parameterisation*

The simple approach used in this study for interpolating total dry matter was able to describe the data of all experiments with a sufficient degree of accuracy. In all but one case the correlation coefficient between observed and calculated total dry matter was higher than 0.9 and the slope and intercept of the linear regression were close to one and close to zero, respectively (Tables 2 and 3).

Table 2

Estimated values of light use efficiency (LUE) ( $\text{g MJ}^{-1}$ ) ( $\pm\text{SE}$ ) and specific leaf area (SLA) ( $\text{cm}^2 \text{g}^{-1}$ ) ( $\pm\text{SE}$ ), the correlation between both parameters,  $C$  the coefficient of determination of the dry matter production model,  $r^2$ , and the number of data points,  $n$ , of the cauliflower experiments used in the derivation of the model parameters

Year	Cultivar	Experiment	LUE	SLA	$C$	$r^2$	$n$
1994	Fremont	1	2.85 ( $\pm 1.7$ )	143.1 ( $\pm 125.3$ )	-0.99	0.83	4
1994	Fremont	2	2.06 ( $\pm 0.18$ )	169.2 ( $\pm 22.5$ )	-0.99	0.99	5
1994	Linday	1	1.94 ( $\pm 0.25$ )	252.4 ( $\pm 56.3$ )	-0.98	0.99	4
1994	Linday	2	2.41 ( $\pm 0.43$ )	129.2 ( $\pm 34.4$ )	-0.99	0.98	6
1995	Fremont	2	3.30 ( $\pm 0.18$ )	106.3 ( $\pm 7.7$ )	-0.99	1.00	7
1995	Fremont	3	2.30 ( $\pm 0.67$ )	227.5 ( $\pm 133.1$ )	-0.97	0.90	7
1995	Fremont	4	4.68 ( $\pm 1.41$ )	71.0 ( $\pm 27.0$ )	-0.99	0.98	7
1995	Linday	2	3.19 ( $\pm 0.17$ )	109.2 ( $\pm 7.9$ )	-0.99	1.00	7
1995	Linday	3	2.40 ( $\pm 0.31$ )	205.3 ( $\pm 50.0$ )	-0.97	0.98	7
1995	Linday	4	3.35 ( $\pm 0.40$ )	105.1 ( $\pm 19.4$ )	-0.99	0.99	9

Table 3

Estimated values of light use efficiency (LUE) ( $\text{g MJ}^{-1}$ ) ( $\pm\text{SE}$ ) and specific leaf area (SLA) ( $\text{cm}^2 \text{g}^{-1}$ ) ( $\pm\text{SE}$ ), the correlation between both parameters,  $C$  the coefficient of determination of the dry matter production model,  $r^2$ , and the number of data points,  $n$ , of the cauliflower experiments used in the validation of the model

Year	Cultivar	Experiment	LUE	SLA	$C$	$r^2$	$n$
1994	Fremont	1	2.79 ( $\pm 0.97$ )	146.4 ( $\pm 84.3$ )	-0.98	0.93	4
1994	Fremont	2	4.57 ( $\pm 1.59$ )	117.3 ( $\pm 55.8$ )	-0.99	0.96	5
1995	Fremont	1	2.17 ( $\pm 0.04$ )	148.0 ( $\pm 4.4$ )	-0.99	1.00	4
1995	Fremont	2	3.32 ( $\pm 0.01$ )	131.0 ( $\pm 0.1$ )	-0.99	1.00	3
1995	Fremont	3	1.98 ( $\pm 0.48$ )	339.6 ( $\pm 185.6$ )	-0.99	0.99	3
1996	Fremont	1	3.82 ( $\pm 0.17$ )	91.0 ( $\pm 5.4$ )	-0.99	1.00	5
1996	Fremont	2	4.40 ( $\pm 0.17$ )	110.2 ( $\pm 6.1$ )	-0.99	0.99	5
1996	Fremont	3	5.03 ( $\pm 2.00$ )	87.5 ( $\pm 43.4$ )	-0.99	0.97	4

The estimated values for the parameter LUE, however, were quite variable for the different cauliflower experiments ranging from 1.94 to 4.68  $\text{g MJ}^{-1}$  in the parameterisation experiments and from 1.98 to 5.03  $\text{g MJ}^{-1}$  in the validation experiments (Tables 2 and 3). A high variability was also found for the estimated values of SLA ranging from 71 to 252  $\text{cm}^2 \text{g}^{-1}$  and from 91 to 340  $\text{cm}^2 \text{g}^{-1}$  in the parameterisation and validation experiments, respectively. However, the asymptotic standard errors of the parameter values for some experiments were quite high and there was a highly negative correlation ( $>0.97$ ) between both parameters (Tables 2 and 3).

The values obtained for the parameters  $k_1$  and  $k_2$  of the leaf development model are presented in Table 4. Despite some differences between the experiments, it

Table 4

Parameters  $k_1$  (leaf leaf<sup>-1</sup> °C<sup>-1</sup> day<sup>-1</sup>) and  $k_2$  (leaf °C<sup>-1</sup> day<sup>-1</sup>) ( $\pm$ SE), correlation coefficient,  $r^2$  and number of observations,  $n$  of the non-linear regression between temperature sum after transplanting and number of leaves (>1 cm) for two different cultivars of cauliflower in 2 experimental years

Cultivar	Year	$k_1$	$k_2$	$r^2$	$n$
Fremont	1994	0.00382 ( $\pm$ 0.000175)	0.0525 ( $\pm$ 0.00552)	0.99	8
Fremont	1995	0.00379 ( $\pm$ 0.000723)	0.0348 ( $\pm$ 0.00624)	0.90	13
Linday	1994	0.00351 ( $\pm$ 0.000168)	0.0536 ( $\pm$ 0.00398)	0.99	9
Linday	1995	0.00333 ( $\pm$ 0.000246)	0.0454 ( $\pm$ 0.00751)	0.94	13
Both	Both	0.00352 ( $\pm$ 0.000155)	0.0460 ( $\pm$ 0.00353)	0.94	43

Table 5

Slope ( $\pm$ SE), intercept ( $\pm$ SE), correlation coefficient  $r^2$ , and number of observations  $n$ , of the linear regression between the logarithms of leaf and stem dry weight for two different cultivars of Cauliflower in 2 experimental years

Cultivar	Year	Slope	Intercept	$r^2$	$n$
Fremont	1994	1.163 ( $\pm$ 0.133)	-2.056 ( $\pm$ 0.683)	0.92	9
Fremont	1995	0.878 ( $\pm$ 0.025)	-0.986 ( $\pm$ 0.111)	0.98	21
Linday	1994	1.129 ( $\pm$ 0.094)	-1.461 ( $\pm$ 0.487)	0.94	11
Linday	1995	0.920 ( $\pm$ 0.020)	-0.910 ( $\pm$ 0.096)	0.99	23
Both	Both	0.941 ( $\pm$ 0.022)	-0.974 ( $\pm$ 0.105)	0.97	64

was possible to describe all leaf number data with a single parameter set. From the initially exponential increase of leaf number follows that a small difference of 0.5 in number of leaves at transplanting resulted in a comparable high difference of visible leaves during the linear leaf development phase of 2 (Fig. 1).

In all parameterisation experiments a linear relationship between the logarithms of leaf and stem dry matter could be found (Table 5). Therefore, the assumption of an allometric growth of stem and leaves seems to be valid for the cauliflower crops analysed. Despite the fact that the slopes and intercepts of this relationship were somewhat variable between the experiments, indicating an effect of the experimental year, the fit to all data of the parameterisation experiments resulted in a coefficient of determination of 97% (Fig. 2).

The growth of the curd fraction was described well for all plants with a logistic function of the temperature sum since the end of the vernalisation period (Eq. (21), Fig. 3). The curd starts to become an important sink about 400°C day<sup>-1</sup> after curd initiation and approaches its maximum fraction on total growth rate around 800°C day<sup>-1</sup> after curd initiation. However, there is considerable variation in the curd fraction of about 400–800°C day<sup>-1</sup> after curd initiation (Fig. 3).

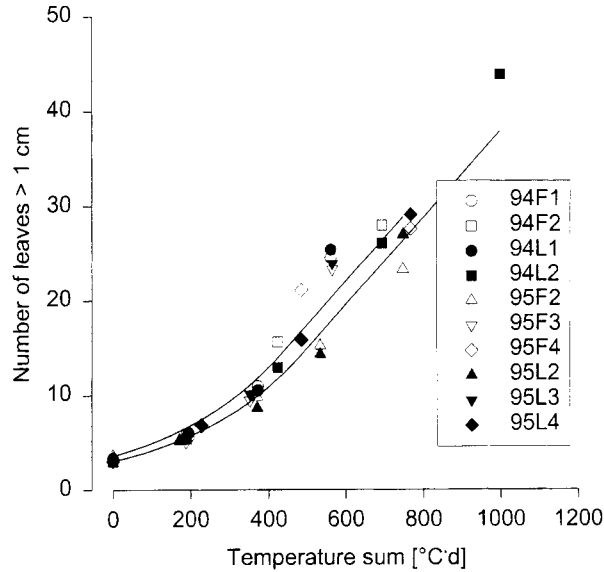


Fig. 1. Number of leaves >1 cm of two cauliflower cultivars as dependent on the temperature sum after transplanting into the field. First two digits in the legend designate the year (1994 or 1995) the next digit the cultivar (F = Fremont, L = Linday) and the last one the experiment. The two curves represent the predicted leaf number when assuming either a leaf number at transplanting of 3 (upper curve) or 3.57 (lower curve).

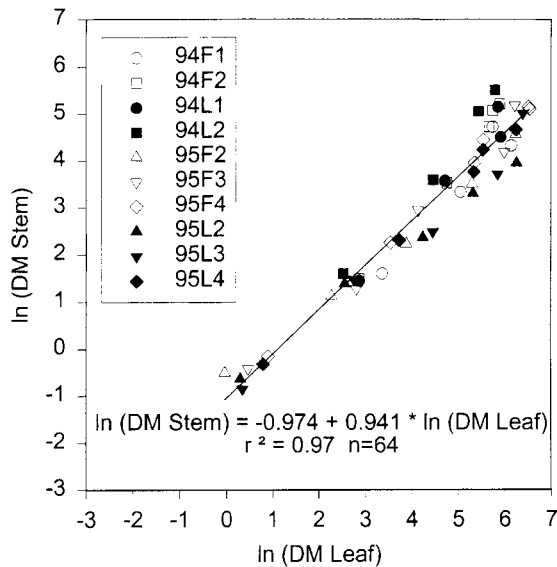


Fig. 2. Relationship between the logarithms of leaf and stem dry matter for two cultivars of cauliflower grown in 2 years. First two letters designate the year (1994 or 1995) the next letter the cultivar (F = Fremont, L = Linday) and the last one the experiment.

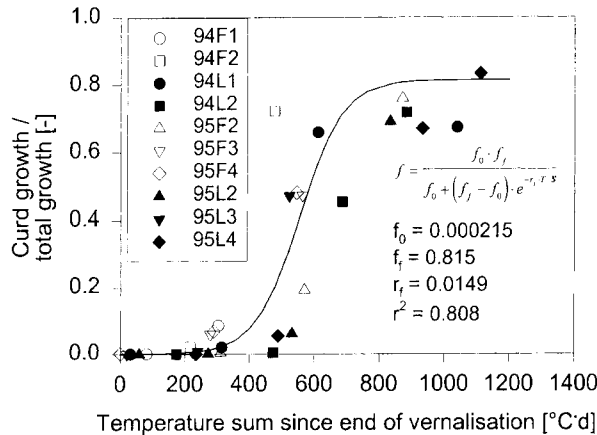


Fig. 3. Fraction of the curd growth on total growth of cauliflower as a function of the temperature sum since end of the vernalisation process and the results of the fit of a logistic growth equation to the data.

#### 4.2. Validation

The overall model performance is demonstrated for an arbitrarily chosen validation experiment in Fig. 4. The measured increase of leaf number follows the model until the last leaf appears, which was initiated before the vernalisation process is completed (Fig. 4(a)). The dry matter production over time is properly interpolated by the model (Fig. 4(b)). At the end of the growing period the dry matter production rate of leaves decreases, the growth of stem dry matter almost stops and about all dry matter increase is attributed to curd growth. This results in a steadily decreasing fraction of leaf mass on total plant mass, a more or less constant fraction of stem mass and a steadily increasing proportion of curd mass on total plant mass (Fig. 4(c)).

The application of the model on the validation experiments resulted in a coefficient of determination of 0.73 between observed and predicted leaf number (Fig. 5). It has to be noticed that in contrast to Fig. 1 where only leaf numbers before the end of vernalisation were shown in this case all measurements were included. Errors in estimating the vernalisation process are therefore also contributing to the scatter of the data.

The comparison of the simulated and measured fractions of the individual organs on total dry matter shows for the parameterisation and the validation experiments that over all organs the model predicted the dry matter fractions quite well (Fig. 6). It must be noticed, however, that much of the variation in the dry matter fractions is between rather than within the different organ groups. The correlation between simulated and measured dry matter fractions calculated separately for the different organs, was poor especially for the

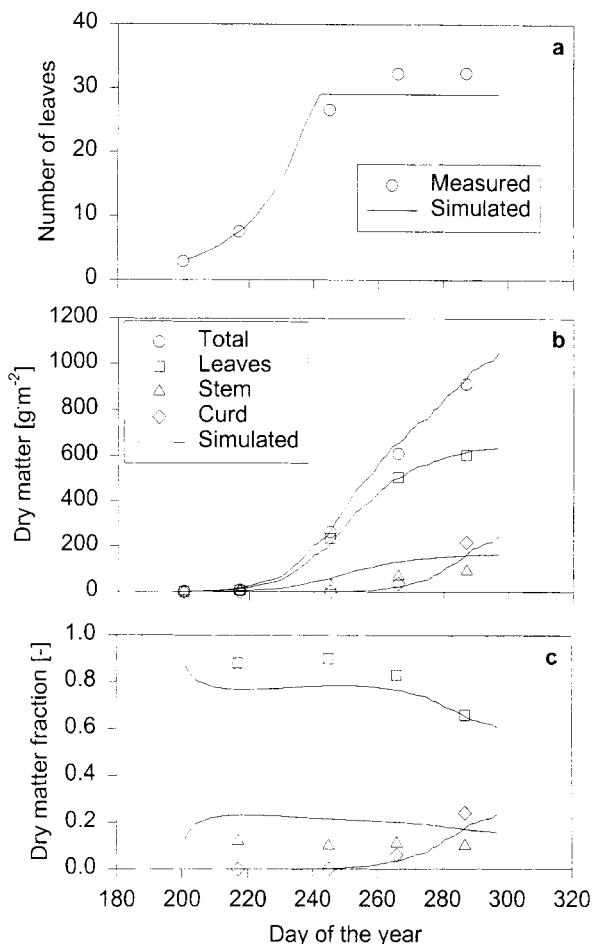


Fig. 4. Simulated vs. measured parameters for an arbitrarily chosen cauliflower experiment from the validation group (year 1996, experiment 2). Light use efficiency and specific leaf area were fitted, all other parameter values are from independent estimations from the parameterisation data. (a) Simulated vs. measured number of leaves, (b) simulated vs. measured total dry matter of plants and dry matter of leaves, stems and flowers, (c) simulated vs. measured fraction of single organs on total dry matter.

stem fraction (Table 6). This may be due to only little variation of the stem fraction during the growing period. For the curd fraction, which shows a much higher variation, a much closer relationship could be found. The prediction of the model with respect to the dry matter fractions is of similar quality for the validation experiments as for the parameterisation experiments.

The measured length of the growing period ranged from 66 to 112 day from transplanting to maturity. About 69% of this variation could be described with the model (Fig. 7).

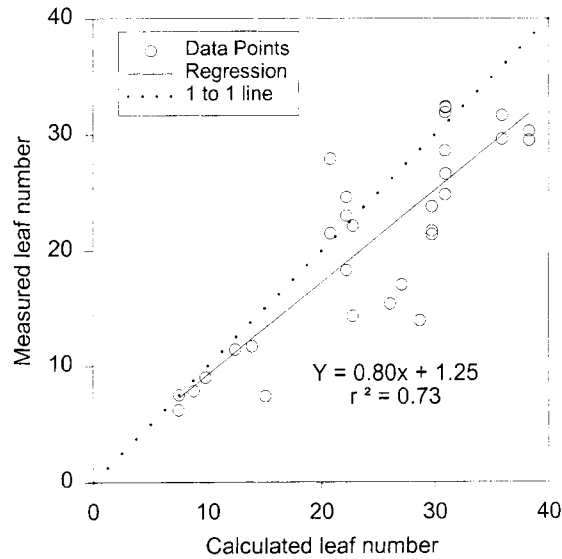


Fig. 5. Simulated vs. measured leaf numbers for the cauliflower crops (cv. 'Fremont') from the independent validation experiments.

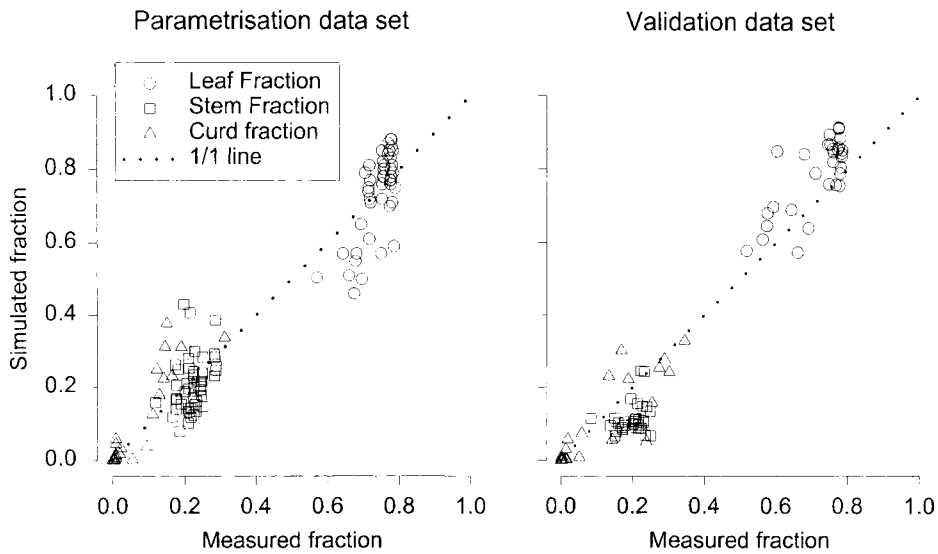


Fig. 6. Simulated vs. measured dry matter fraction (organ mass/total plant mass) for the cauliflower crops cv. 'Fremont' and 'Linday' from the parameterisation experiments (left graph) and for cauliflower crops cv. Fremont from the validation experiments (right graph).

## 5. Discussion

The purpose of this paper is to present a model for development and vernalisation of cauliflower. Therefore, the dry matter production part of the

Table 6

Intercept ( $a$ ) slope ( $b$ ) and correlation coefficient ( $r^2$ ) of the linear regression equation between simulated and measured dry matter fractions of different cauliflower organs in the parameterisation and the validation group of experiments

Experiment group	Organ	$a$	$b$	$r^2$
Parameterisation	Leaves	-0.7579	2.0129	0.4984
Parameterisation	Stem	0.0394	0.7614	0.109
Parameterisation	Curd	-0.0022	1.6629	0.8774
Validation	Leaves	0.1206	0.9356	0.5448
Validation	Stem	0.0334	0.3942	0.0823
Validation	Curd	0.0044	0.8707	0.7668

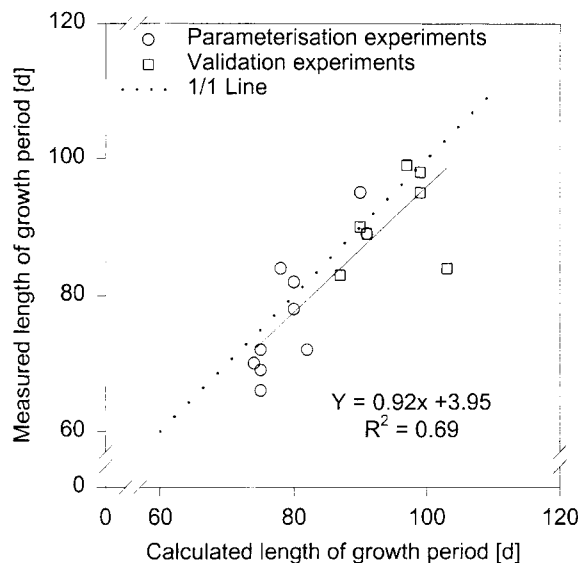


Fig. 7. Calculated vs. measured length of the growth period all experiments from the parameterisation and validation group of experiments. The shown regression line is for both types of experiments.

model is at this stage purely descriptive and used simply as an interpolation tool. However, the parameters were chosen such that they were biologically meaningful. The values for SLA found by the fitting procedure are indeed with some exceptions in the range of measured values for cauliflower ranging from 300 to 40  $\text{cm}^2 \text{g}^{-1}$  in the report of Olesen and Grevsen (1997) and of 240  $\text{cm}^2 \text{g}^{-1}$  in Aikman and Scaife (1993). This is also true for the LUE where values of 2.8, 3.2, 4.1 and 4.4  $\text{g MJ}^{-1}$  were reported for cauliflower by Aikman and Scaife (1993), Olesen and Grevsen (1995, 1997) and Wheeler et al. (1995), respectively. However, due to the strong correlation between both parameters and their high standard errors (Tables 2 and 3), the estimated values of LUE and SLA have to be interpreted very carefully.



Grevsen and Olesen (1994a) used an exponential model for leaf development, and found a value of about 0.003 (leaf leaf<sup>-1</sup> °C<sup>-1</sup> day<sup>-1</sup>) for the specific leaf initiation rate. This results in a leaf initiation rate of about 0.06 (leaf °C<sup>-1</sup> day<sup>-1</sup>) for leaf number 20 which is in good agreement with the value found for  $k_2$  from Eq. (3) (Table 5). A recalculation of data from Booij (1990) resulted in values of  $k_2$  of 0.084 (°C day<sup>-1</sup>) for his 22°C treatment and 0.0225 for his 14°C treatment, respectively.

With the data available from this study the accuracy of the vernalisation part of the model can be evaluated only indirectly. The indicator parameters we measured were the leaf number and length of the growing period. The poor prediction of leaf number (Fig. 5) may be the result of insufficient prediction of the vernalisation rate. However, due to the high variability of the vernalisation rate of cauliflower (Booij, 1990) in conjunction with the limited number of plants analysed, it is likely to have results of a high experimental error.

The simple allometric approach of leaf/stem partitioning in combination with an empirical temperature sum based approach for relative curd growth was able to describe the data from the parameterisation experiments (Table 6 and Fig. 2) and to predict the dry matter partitioning pattern of cauliflower under optimal nutrient and water supply adequately (Fig. 6). The poor prediction of stem fraction (Table 6), is not critical, since there is only a small variation in the stem fraction during the growth period of cauliflower and the absolute value of this fraction is small.

Marcelis (1993) distinguishes in his review empirical allometric, functional equilibrium and several transport and sink strength based approaches of modeling dry matter partitioning in plants. He infers that descriptive allometric partitioning approaches may have only a limited explanatory value but are usually more easily parameterised. They have proven their usefulness in many cases as for guar (*Cyamopsis tetragonoloba*) (Stützel et al., 1988) and faba beans (*Vicia faba* L.) (Stützel and Aufhammer, 1991a). However, it remains to be proved whether this approach is also valid under restricted nutrient and water supply. For more variable environmental conditions more mechanistic approaches of modelling partitioning based on relative sink strength (Marcelis, 1996) or optimisation principles (Johnson and Thornley, 1987) may be desirable.

The model presented here differs from other models of cauliflower development (Wiebe, 1975; Wurr et al., 1990; Grevsen and Olesen, 1994b; Pearson et al., 1994; Wheeler et al., 1995), mainly in its simulation of the length of the generative phase directly as a consequence of curd dry matter growth rate which is a function of total dry matter increase and partitioning to the curd. It can be expected that the implicit assumption of source limited curd growth is valid at least during the second-half of the curd growth phase, when the curd becomes the dominant sink.

More simple temperature sum based approaches have also proved their usefulness at least for practical purposes like planning market supply (Wiebe, 1979). They also have the advantages of more widely available input data and a smaller number of parameters. However, for the second main problem of cauliflower production, nitrogen management, a dry matter based production model for cauliflower is indispensable.

For a precise prediction of cauliflower growth an exact estimation of the model parameters LUE and SLA is necessary. Further analysis is therefore needed to identify the main factors that may cause a variation in LUE and SLA. Olesen and Grevsen (1997) have shown that LUE in cauliflower depends on the level of radiation intensity and on temperature. Incorporating such relationships in the dry matter production model may explain the variation in LUE between the experiments. In a further model development also root growth has to be considered in order to predict nitrogen uptake under variable and sub-optimum nitrogen supply.

A principal problem in cauliflower crops is the high variation in the development rates between individual plants within a crop (Booij, 1990). This is the reason for multiple harvests in practical farming. For the prediction of the length of the harvest period it is necessary to include explicitly the plant to plant variation in the development and growth processes into the model.

## **6. Conclusions**

The model presented was able to predict leaf number, the fraction of the dry matter of single organs to total dry matter and the length of the growing season of independent experiments sufficiently well when dry matter production was calculated based on LUE and SLA values fitted for each experiment. The functional relationships for the reaction of these parameters on changing environmental conditions have to be evaluated.

## **Acknowledgements**

The technical assistance of E. Diedrich and M. Kling is gratefully acknowledged. The authors debt credit to Prof. H. Wiebe for valuable discussions and detailed information about his cauliflower development model.

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