

Predicting dry-matter partitioning between individual cauliflower leaves using a source limitation/sink hierarchy model

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SUMMARY

Data from a container and two field experiments were used to construct a model which describes dry-matter partitioning between individual leaves of cauliflower. Thereby a combined source limitation/sink hierarchy approach is applied, assuming early sink-limited exponential growth followed by a source-limited growth phase. Increasing competition for assimilates from newly formed leaves with higher sink priority then decreases the availability of assimilates and determines the end of the growth phase of an individual leaf. Leaf senescence is assumed to start when the growth rate of an individual leaf approaches zero. The end of senescence, i.e. the time of leaf death, is described using an empirical temperature sum function. The model was able to describe ($r^2 = 0.97$) and predict ($r^2 = 0.90$ and 0.87) the partitioning of dry matter between classes of leaves consisting of three and five individuals for the container and the field experiments, respectively. The parameter estimates obtained indicate that 2–3 leaves are growing simultaneously with high growth rates. The potential growth rate of sequentially newly formed individual leaves decreased during the growth period of cauliflower, probably due to assimilate competition from the initiated curd. The model presented may serve as a background for analysing and predicting translocation processes, which determine nitrogen harvest index and therefore nitrogen use efficiency.

Crop growth models may calculate leaf dry matter and leaf area production either at the level of the whole canopy using only one state variable for leaf dry matter and leaf area (Jones and Kiniry, 1986; Williams *et al.*, 1989) or they may aim to predict leaf growth at the scale of individual leaves (Carberry *et al.*, 1993; Porter, 1984). The latter approach offers the possibility of describing the growth and senescence of the leaf fraction more mechanistically, since local environmental conditions and the age of an individual leaf are decisive for growth and senescence rates (Ackerly, 1999; Rousseaux *et al.*, 1999). Nitrogen content (Field, 1983) and photosynthetic capacity (Wolfe *et al.*, 1988) of leaves declines during their life time, because of an adaptation to shading by newly formed leaves, but also due to increasing portions of structural leaf components and as a consequence of a genetically predetermined ageing process (Hikosaka *et al.*, 1994). These processes at the individual leaf level determine nitrogen distribution within the canopy and thereby the productivity of a crop.

Existing models for leaf growth at the individual leaf level (Carberry *et al.*, 1993; Lecoeur *et al.*, 1996; Porter, 1984) are still descriptive rather than explanatory, since final leaf sizes are input values (Porter, 1984), derived from empirical functions (Carberry *et al.*, 1993) or only simulate relative leaf area (Lecoeur *et al.*, 1996). Such approaches are not truly satisfying because stress factors like drought (Randall and Sinclair, 1988) or insufficient nitrogen supply (Biemond, 1995) clearly affect maximum mass and area of individual leaves.

The aim of the presented work is to derive and evaluate a model for dry matter between individual leaves, based on a sink hierarchy approach and therefore avoiding the use of predetermined maximum leaf sizes. Such a model should therefore be applicable over a wider range of environmental conditions. Leaf area expansion of individual leaves is linked directly to dry-matter increase via the conversion factor specific leaf area, SLA.

MATERIALS AND METHODS

The data used within this study were obtained from one container experiment carried out in 1997 in a rain-out shelter at the Faculty of Horticulture in Hannover, Germany and in two field experiments in 1996 and 1997 on an experimental farm located about 20 km south of Hannover.

Container experiment

The container experiment was carried from 2 May to 7 July (Table I) using the cauliflower cultivar 'Fremont' at two irrigation levels. Seeds were sown in seed plates and transplanted after germination into peat cubes of 4 cm edge length until about six leaves were visible. The average plant dry weight at transplanting was 0.65 g.

Plants were grown in containers of 0.025 m³ volume with an average diameter of 0.33 m and a height of 0.30 m which were filled to a height of 0.25 m with loess loam at a density of 1.35 g cm⁻³. After transplanting one plant per container, an additional layer of coarse quartz sand of 0.03 m in height was placed upon the loess layer

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TABLE I
Dates of sowing, transplanting and harvesting of container and field experiments

Experiment	Year	Sowing date	Transplanting date	Harvest dates (days after transplanting)
Container	1997	14 March	2 May	19, 31, 40, 47, 53, 60, 66
Field	1996	23 May	18 June	28, 49, 69
Field	1997	3 June	9 July	26, 47, 68*, 82

*Final harvest of N-fertilized treatments of unshaded light environment.

to minimize soil evaporation. Nutrients were given once a week to ensure an optimal supply. The containers were placed at distances of 0.4 m up to the last week. During the last week the distances were altered to 0.7 m. There were two irrigation treatments, seven harvests with three plants each, resulting in 42 containers arranged randomly within three blocks (replications). The two irrigation treatments were called "optimal supply" (W1) and sub-optimal supply (W2). The optimal supply treatment was irrigated daily to restore an average soil water potential of -10 kPa. The sub-optimal supply treatment was irrigated in the same way as the optimal supply treatment until 20 d after planting (dap) and from then on received every day an amount of water to re-establish an average soil water potential of -80 kPa. Both treatments received $3,000$ cm³ of water per container during the first 20 d. From day 21 to the end of the experiment the W1 treatment received $93,000$ cm³ and the W2 treatment $45,000$ cm³ (Figure 1). Amounts of irrigation water were calculated from daily determined container weights. From 31 dap onwards, plants of the W1 treatment were irrigated twice a day when transpiration demand was high.

Daily transpiration was calculated from the differences of container weights corrected for plant growth which was determined from an interpolated growth curve. Weather data were collected at an automatic weather station located near the rain-out shelter.

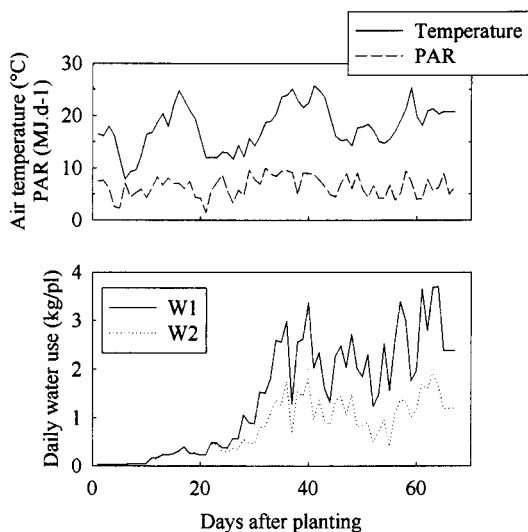


FIG. 1
Average daily air temperature ($^{\circ}$ C), photosynthetic active radiation (PAR) ($\text{MJ PAR m}^{-2} \text{d}^{-1}$) and daily water use of cauliflower plants (kg pl^{-1}) grown in containers with either high (W1) or low (W2) water supply.

Field experiment

The field experiments used in this study have already been described (Alt, 1999) and (Alt *et al.*, 2000), so only a brief description will be given here. Two independent field experiments with cauliflower (*Brassica oleracea* L. *convar. botrytis* var. *botrytis* L. 'Fremont') were conducted on the institute's experimental farm 15 km south of Hannover, Germany, on a typical loess derived hapludalf soil. When the plants had developed an average of 3.25 and 3.5 visible leaves in 1996 and 1997, respectively, they were transplanted into the field (Table I). The initial dry weight at that time was 0.34 g plant^{-1} in 1996 and 0.39 g plant^{-1} in 1997. The average plant density was 3.5 plants m^{-2} . Irrigation was given whenever needed.

The experiments were laid out as split plots with two light environments, i.e. shaded and unshaded, as main plots and four nitrogen-fertilizer levels as sub-plots. There were three replications for each treatment. In the analysis presented here, only the highest two N fertilization treatments are considered. Shaded main plots were covered one meter above the ground with a net absorbing 40% of the photosynthetically active radiation (PAR) either immediately after transplanting (1996) or two weeks after transplanting (1997) until the end of experiment. Nitrogen fertilization was given as ammonium nitrate at transplanting. Soil nitrate content of 10 – 15 kg N ha^{-1} in 1996 and 1997 in 0 – 60 cm were subtracted from the 300 (N2) and 450 kg ha^{-1} (N3) target values.

Plant growth analysis

On several intermediate harvests in both years, six plants per plot in the field experiment and three containers with one plant each in the container experiment were collected and separated into stem, leaf including petioles, and the curd. Stems were cut 1 cm below field level and at the onset of inflorescence. The leaf fraction was subdivided into groups of three or five consecutive leaves (1–5, 6–10, etc.). Leaves were considered and counted down to a size of approximately 1 cm². If more than 80% of a leaf area showed a senescent colour, it was classified as 'senescent'. Leaf area of every leaf group was measured with a LICOR 3100 leaf area meter (LI-COR Inc., Lincoln, NE, USA). The samples of all plant compartments were oven dried at 70°C and 105°C until weight constancy and weighed.

MODEL

Dry-matter partitioning between individual leaves

Growth of individual leaves can be described in terms of phyllochrone, i.e. the time between the appearance of two consecutive leaves, the leaf growth rate and the leaf growth duration (Bos and Neuteboom, 1998). Under the simplifying assumption of a constant leaf growth rate,

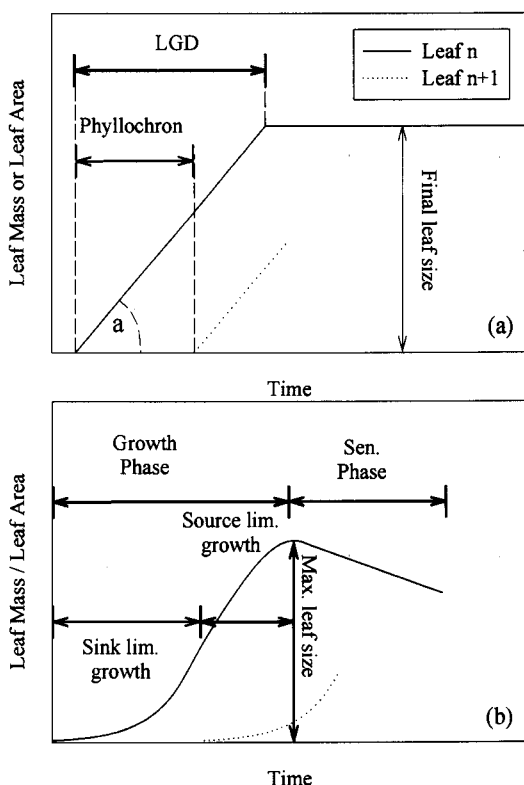


FIG. 2

Schematic representation of different approaches for describing and calculating growth of individual leaves. Upper graph (a) shows an approach used by Bos and Neuteboom (1998), describing leaf growth in terms of phyllochron, leaf growth duration (LGD) and leaf growth rate ($= \tan \alpha$). Lower graph shows the approach used in this study dividing the leaf life cycle into a growth and a senescence phase and the growth phase further into a sink- and source-limited growth phase.

the final leaf area or leaf mass is determined by the product of leaf growth duration and the leaf growth rate (Figure 2a). The growth of individual leaves is, however, more realistically described by a sigmoid growth pattern (Stewart and Dwyer, 1994; Tardieu *et al.*, 1999), which may be followed by a senescence phase (Figure 2b).

Our model hypothesizes that such behaviour may best be explained by early exponential growth during which potential growth rates are limiting (sink-limited growth) followed by a phase during which assimilate availability is limiting (source-limited growth). Increasing competition for assimilates from newly formed leaves with higher sink priority then decreases the availability of assimilates which determines the end of the growth phase. Dominance of dissimilatory processes at least commences the senescence phase.

Sink-limited potential growth rate is calculated from the product of a relative growth rate parameter, rg_{SL} ($d^{-1} C^{-1}$), temperature, T ($^{\circ}C$), and the actual dry matter of the individual leaf, WSL_i ($g DM pl^{-1}$). The availability of assimilates for the growth of a particular leaf, i , is calculated from the amount of assimilates for total leaf growth, dW_L/dt ($g DM pl^{-1} d^{-1}$), left over by younger leaves (central brackets of Eqn. 1), which are assumed to have higher sink priority. However, only a certain

fraction of assimilates, f_{av} (-), is available for a particular leaf, since the next following, only little older leaves still have a comparably high sink strength. Furthermore, a translocation term, dT_{wsl}/dt ($g pl^{-1} d^{-1}$), is introduced which accounts for the loss of dry matter from individual leaves during senescence.

The growth rate of an individual leaf then is calculated from:

$$\frac{dWSL_i}{dt} = \min \left(rgr_{SL} \cdot T \cdot WSL_i, f_{av} \left(\frac{dW_L}{dt} - \sum_{n_i}^{i-1} \frac{dWSL_{n_i}}{dt} \right) - \frac{dT_{wsl}}{dt} \right) \quad (1)$$

Here, n_i denotes the youngest visible leaf with the highest index.

The partitioning of assimilates to an organ is not only dependent on its potential to attract assimilates, i.e. its sink strength, but depends also on the sink strength of other organs (Marcelis, 1996). During the generative phase of cauliflower the curd becomes the dominating sink as more than 80% of net dry-matter increase is allocated to the curd during the last weeks of growth (Kage and Stützel, 1999b). To follow the philosophy of the above outlined hypothesis in a strict sense, the initiation and the growth of the individual inflorescence parts has to be simulated. To avoid this cumbersome approach, an alternative, more simple approach is included at the present stage of development. The relative growth rate parameter rg_{SL} is decreased linearly with temperature sum after the end of vernalization and the initiation of the final generative organ:

$$rg_{SL} = rgr_0 - rgr_{dec} TS3 \quad (2)$$

Here rgr_0 (d^{-1}) is the relative growth rate until vernalization, rgr_{dec} ($^{\circ}C^{-1} d^{-2}$) is the decrease of rg_{SL} with increase of temperature sum since end of vernalization, $TS3$ ($^{\circ}C d$). For $TS3$ a base temperature of $0^{\circ}C$ is assumed.

Until the stage presented here, the whole model therefore contains three parameters, rgr_0 , rgr_{dec} and f_{av} for describing the growth dynamics of all individual leaves of the canopy.

Leaf senescence

The number of senescent leaves may, to a first approximation, be described by a linear increase of the number of senescent leaves with temperature sum after a lag phase:

$$\frac{dn_{Ls}}{dt} = \begin{cases} 0 & TS < TS_{sen} \\ s_r \cdot T & TS \geq TS_{sen} \end{cases} \quad (3)$$

Here, dn_{Ls}/dt (d^{-1}) is the increase in senescent leaves per time (d^{-1}), TS ($^{\circ}C d$) is the temperature sum since transplanting, s_r ($leaf^{\circ}C^{-1} d^{-1}$) is a senescence parameter and TS_{sen} ($^{\circ}C d$) is a lag phase without senescence.

During the process of senescence total nitrogen content of fully expanded leaves decreases from about 4.5% to about 0.5% (unpublished results). Further assuming that 0.5% of this decrease is attributed to nitrate N this gives an re-translocation of 3.5% N as proteins or amino acids corresponding to approximately 22% re-translocation of dry matter if an N fraction of 6.25% for proteins is adopted. Translocation of soluble

carbohydrates is thought to be of minor importance, since much of this pool may be lost due to respiration. Therefore a pool of translocatable dry matter, TLW (g DM pl⁻¹), is defined which is initialised with 25% of the leaf dry matter at the beginning of the senescence process.

The build up and breakdown of proteins and other cell components are processes which occur simultaneously. Growth defined by the increase of mass in a certain time period therefore occurs when assimilatory processes overcompensate dissimilatory processes and senescence starts in the opposite case.

As our analysis relies on data for leaf weight only, we assume for simplicity that senescence starts when the relative growth rate of an individual leaf averaged over a time period of 5 d falls below a value of 0.1% of the initial growth rate rg_{SL} or as an alternative condition 250°C d before the leaf is expected to be senescent as calculated from Eqn. 3.

The translocation rate of dT_{SLW}/dt (g DM pl⁻¹ d⁻¹) is given by the amount of translocatable dry matter divided by the temperature sum needed for a complete exhaustion of this pool times the increment of the temperature sum:

$$\frac{dT_{SLW_i}}{dt} = \max \left(0, \frac{TLW_i}{\left(TS_{sen} + \frac{i}{s_r} \right) - TS_{senstart}} \frac{dT}{dt} \right) \quad (4)$$

Here, dT_{SLW}/dt (g DM pl⁻¹ d⁻¹) is the translocation rate from an individual leaf, i is the leaf number and $TS_{senstart}$ is the value of the temperature sum when the senescence process of the individual leaf starts and s_r is an senescence parameter (°C⁻¹ d⁻¹).

As a crude estimation of leaf loss, the assumption was introduced that leaves are dropped 40°C d after the pool of translocatable dry matter is exhausted.

The dry matter of newly formed leaves are initialized with 1/50 g pl⁻¹, expressing the assumption that leaves become visible when they have an area of 1 cm² and that newly formed leaves have a specific leaf area (SLA) of 50 cm² g⁻¹.

Leaf area expansion

The specific leaf area of cauliflower, SLA (cm² g⁻¹), depends on several plant internal and external factors like temperature (Olesen and Grevsen, 1997) and the intensity of incident radiation (Alt *et al.*, 2000). Because during the container experiment neither temperature nor radiation intensity was changing systematically (Figure 1) it was assumed that for the data analysed here these factors did not affect SLA seriously. It is postulated that SLA depends linearly on leaf number, i , and on the actual size of the leaf, expressed as leaf weight WSL_i :

$$SLA_i = SLA_0 + a_{SLA} \times i + b_{SLA} \times WSL_i \quad (5)$$

where a_{SLA} (cm² g⁻¹) and b_{SLA} (cm² g⁻¹ pl) are parameters.

In the field experiment, the net shading introduced a severe change of the radiation environment. We therefore expanded Eqn. 5 and introduced according to Alt *et al.* (2000) an average value of the radiation intensity during the last 10 d, \bar{I} (MJ m⁻² d⁻¹), as an influence factor for SLA:

$$SLA_i = SLA_0 + a_{SLA} \times i + b_{SLA} \times WSL_i + c_{SLA} \times \bar{I} \quad (6)$$

with c_{SLA} (cm² g⁻¹ MJ⁻¹ m⁻² d) as an additional parameter.

The model calculates leaf area expansion from the increases in leaf mass of the actual growing leaves and their individual, actual specific leaf area, SLA_i . Because the value of SLA_i is dependent on leaf weight, the change of SLA_i with change of weight of the individual leaf, $dSLA_i/dWSL_i$ (cm² g⁻² pl) has also to be considered for:

$$\frac{dSLA_i}{dt} = \frac{dWSL_i}{dt} \left(SLA_i + WSL_i \frac{dSLA_i}{dWSL_i} \right) \quad (7)$$

Estimation of total leaf dry-matter production

Total leaf dry-matter production rate is needed as an input value of Eqn. 1. The prediction of this quantity is not the main subject of this paper, although a high accuracy in the description of the time course of total leaf dry-matter production is a prerequisite for an accurate prediction of the growth of the individual leaves.

Therefore, the total leaf dry-matter production was described for the container and the field experiments with simple empirical models. Simple radiation interception models (Monsi and Saeki, 1953) assume randomly distribution and horizontal homogeneity of leaf area, a condition which clearly does not hold for the isolated grown plants of the container experiment. A light-use efficiency approach was therefore not applicable here. Instead we calculated the growth rate of shoot dry matter, dW_{sh}/dt (g pl⁻¹ d⁻¹), of the plants from the container experiment from the amount of transpired water, T_{act} (kg pl⁻¹ d⁻¹), and the transpiration use efficiency i.e. the dry-matter production per unit of transpired water, TUE (g DM kg⁻¹):

$$\frac{dW_{sh}}{dt} = T_{act} \times TUE \quad (8)$$

Such an approach seems to be justified as the amount of transpired water is a good measure of radiation interception and therefore of dry-matter production if the vapour pressure deficit of the air is not changing substantially (Bierhuizen and Slatyer, 1965).

For the field experiment a light-use efficiency approach was used (Kage *et al.*, 2001). Here, a value of 0.75 was taken for the extinction coefficient, k , and a correction was introduced accounting for uneven leaf area distribution during growth phases with incomplete ground cover (Röhrig and Stützel, 2001). Therefore, the equation for calculating the amount of intercepted radiation Q (MJ PAR m⁻² d⁻¹) now reads:

$$Q = Clf \times I \times (1 - e^{-kLAI}) \quad (9)$$

The correction factor, Clf (-), was calculated (Röhrig and Stützel, 2001) from the relative ground cover, rgc (-):

$$\text{Clf} = 0.77 + 0.28 (1 - e^{-1.65\text{rgc}}) \quad (10)$$

The relative groundcover again is derived from the plant diameter D (m) and the planting density PD (m^{-2}), assuming near isometric plant distribution:

$$\text{rgc} = \min\left(D^2 \frac{\pi}{4} 1.0\right) \quad (11)$$

Plant diameter is derived from the vegetative dry matter of cauliflower plants, W_v , (gm^{-2}) using the empirical equation of Röhrig and Stützel (2001):

$$D = \frac{0.656 W_v}{46.31 + W_v} \quad (12)$$

To describe total leaf weight growth rate over time from total dry-matter growth rate, the newly formed dry matter has to be partitioned. During the vegetative phase this is done between leaves and stem and after curd initiation between leaves, stem and curd.

Two approaches for the partitioning of dry matter between the vegetative plant parts of cauliflower i.e. leaves and stem, have been developed (Alt, 1999; Kage and Stützel, 1999b), where the first approach was validated for conditions without water and nitrogen stress and the second includes a further refinement accounting for effects of nitrogen shortage and effects of low light intensity. We used the first approach for the container experiment and the second one for the field experiments from which it was originally derived. A slight re-parameterization of the first approach was necessary to achieve a good description of total leaf growth rate and to minimize erratic growth rates of individual leaves. The values of the changed parameters are summarized in Table II. For the second approach, used in the field experiment, the original parameters as presented in Alt (1999) were taken.

For the partitioning between generative and vegetative organs the approach of Kage and Stützel (1999b), Eq. 21 was used, in which the portion of dry-matter increase attributed to the curd is increasing following a logistic growth pattern after curd initiation. However, also in this case the growth-rate parameter r_f of the logistic equation, describing the rapidity of increase in the portion of assimilates allocated to the curd was estimated separately for all treatments of the field experiment to minimize the effect of biased curd dry-matter predictions on the prediction of individual leaf weight growth rates.

TABLE II

Values and standard error (SE) of parameters which were adjusted using the data of the container experiment (TUE = transpiration use efficiency, r_f parameter for describing increase in dry-matter partitioning to the curd, g, h = parameters for stem/leaf-partitioning; k_1, k_2 : parameters describing leaf initiation rate)

Parameter	Units	Value	SE
TUE	(g l^{-1})	4.45 (W1) 5.22 (W2)	0.12 0.10
r_f	($^{\circ}\text{C d}^{-1}$)	0.0161	0.00025
g	(-)	0.900	0.16
h	(-)	-2.121	0.83
k_1		0.00253	7.96E-5
k_2		0.0508	0.005

Parameter estimation and regression analysis

The parameters of equations 3 and 5 were estimated by linear regression using the experimental data of the container and the 1996 field experiment with the statistical package SAS (PROC REG) (SAS Institute, 1988).

The other parameters were estimated using the Levenberg-Marquardt algorithm (Marquardt, 1963) implemented within the HUME modelling environment (Kage and Stützel, 1999a). Thereby unweighted sums of squares of differences between measured and simulated data were used as the objective function. The parameters determining crop productivity LUE and TUE (Eqn. 8) and those determining partitioning (Eqn. 1, 2 and 4) were estimated separately and in an iterative way until no significant change in parameter values could be detected. The parameters SLA_0 and c_{SLA} of Eqn. 6 were estimated also within the HUME environment from the total leaf area data of the 1996 field experiment.

The data of the 1997 field experiment, however, were not used for calibration of the model for predicting dry-matter partitioning between individual leaves.

RESULTS

Growth rates and final dry weight of cauliflower differed substantially between the container and the field experiments and was influenced by irrigation regime and net shading, respectively (Figure 3). Total dry-matter production and partitioning between leaves, stem and curd was described with high accuracy (Figure 3) using the TUE and LUE approach with the adjusted parameter values shown in Table II and Table III. However, dry-matter production during the last days of the container experiment was slightly overestimated but this affected predominantly predicted curd dry matter and not leaf dry matter. Leaf shedding was simulated as a discrete event and therefore reduced leaf and total shoot weight in a discontinuous manner (Figure 3). TUE was higher for the W2 than for the W1 treatment and LUE was higher for the shaded treatments. The value of the growth rate parameter r_f determining the speed of increase in the partitioning of dry matter to the curd was lower for the shaded treatments (Table III).

The number of visible leaves increased expo-linearly until the curd was initiated (Kage and Stützel, 1999b, Figure 4a), however, leaf formation especially during the linear phase was faster in the container experiment. The estimated parameter value for the parameter k_2 was therefore considerably higher (Table II) than the value of 0.0353 leaves per degree day from Alt (1999) which was used in the field experiment. The number of senescent leaves increased in the container and in the field experiment approximately linearly with temperature sum after a certain lag phase (Figure 4b), but in the container experiment leaf senescence started later and the number of senescent leaves increased more slowly. Neither net shading nor restricted water supply enhanced the senescence rate significantly (Figure 4b).

The time course of dry weight for the leaf groups in both irrigation treatments showed similar behaviour, however, at a lower level for the W2 treatment (Figure 5). Maximum leaf weights were found for the 10–12 and 13–15 groups, earlier and later formed groups were

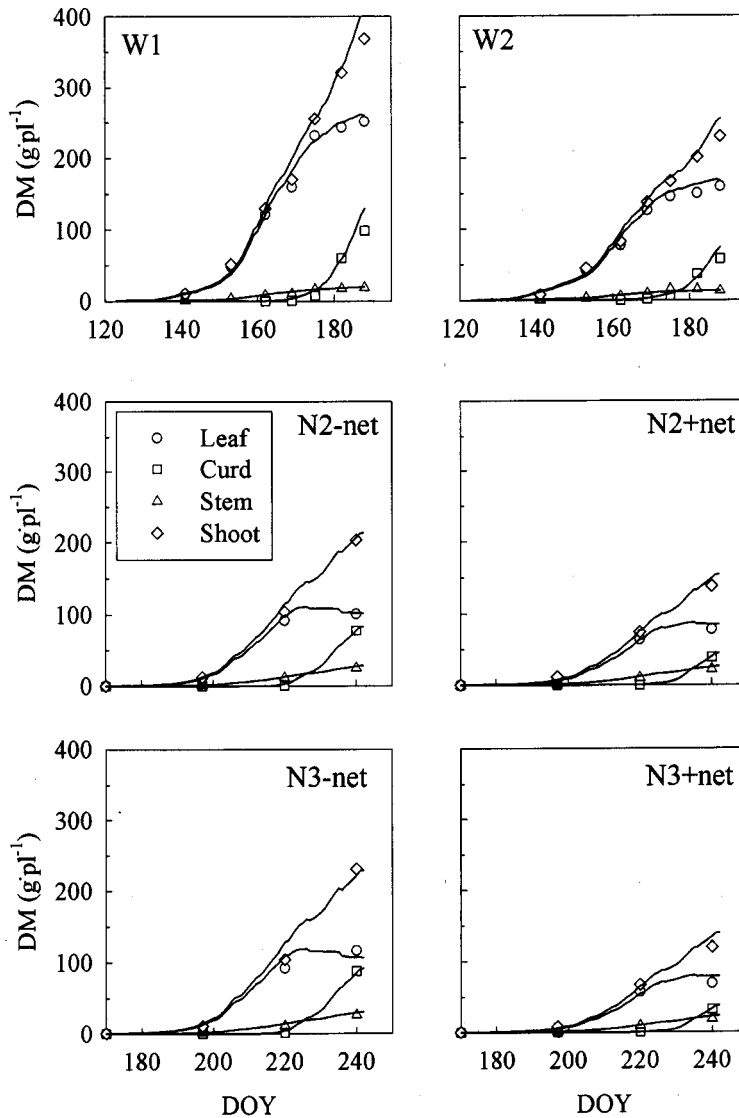


FIG. 3

Comparison of simulated and measured dry matter leaf, stem, curd and whole shoot of cauliflower plants grown in containers under two water supply regimes (W1 and W2) and 1996 in the field with 300 kg N ha^{-1} N supply (N2) or 450 kg N ha^{-1} N supply (N3) and with (+net) or without net shading (-net).

approaching lower maximum values. Even at the aggregated level of groups consisting of three leaves, the s-shaped growth dynamics postulated in Eqn. 1 become obvious. The model outlined in Eqn. 1 and 2 successfully described the leaf mass of leaf groups

consisting of three individual leaves from both irrigation treatments of the container experiment (Figure 5). The estimated value for the parameter f_{av} (Table IV) indicates that during the source-limited growth phase, one leaf is able to attract about one third of the

TABLE III

Estimated values and standard errors (SE) of light use efficiency (LUE) and growth rate parameter r_f (describing increase in dry-matter partitioning to the curd, of Eqn. 21 from (Kage and Stützel, 1999b))

Year	N	Net shading	LUE (g MJ^{-1})	r_f ($^{\circ}\text{C}^{-1} \text{d}^{-1}$)
96	2	no	2.75 (± 0.02)	0.026 (± 0.0014)
96	3	no	2.96 (± 0.09)	0.027 (± 0.0053)
96	2	yes	3.50 (± 0.04)	0.019 (± 0.0012)
96	3	yes	3.42 (± 0.06)	0.018 (± 0.0018)
97	2	no	3.09 (± 0.07)	0.030 (± 0.0075)
97	3	no	3.13 (± 0.05)	0.022 (± 0.0023)
97	2	yes	3.18 (± 0.02)	0.016 (± 0.0007)
97	3	yes	3.17 (± 0.02)	0.018 (± 0.0009)

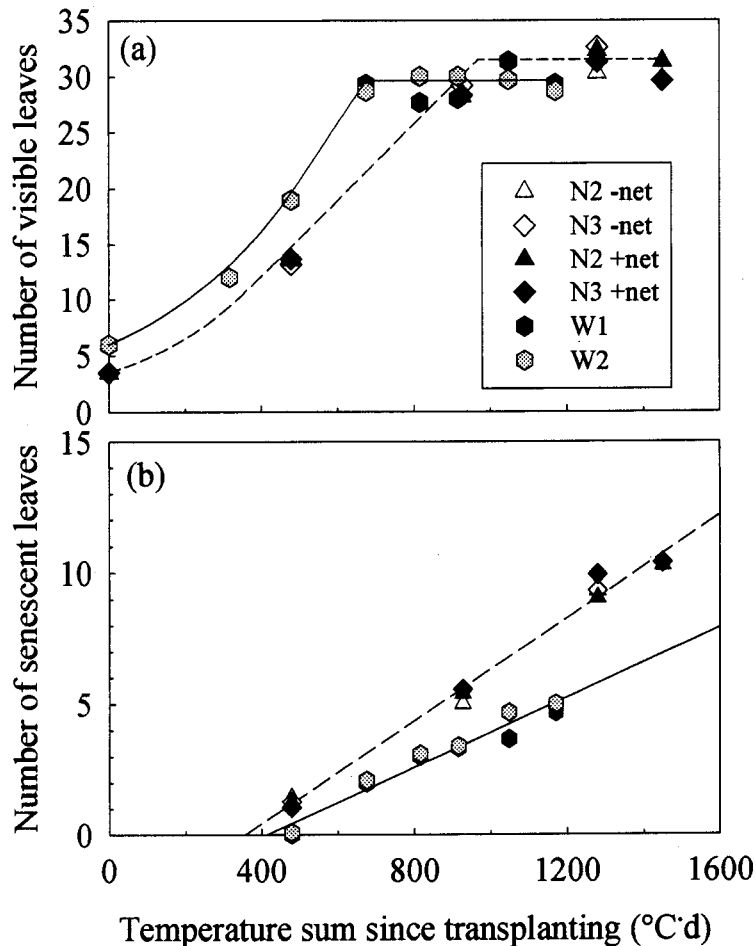


FIG. 4

Number of visible (a) and senescent (b) leaves of container grown cauliflower plants cultivated under high (W1) or low water supply (W2) and of field-grown cauliflower plant under optimum (N2) and super-optimum (N3) N supply and with and without net shading as a function temperature sum since transplanting. Visible leaves were calculated using an exponential equation (for parameters see text). The regression line for senescent leaves for both water supply levels of the container experiment is $y = -2.74 (\pm 0.42) + 0.0067 (\pm 0.0005) \text{ TS}$, $r^2 = 0.95$, $n = 12$. The regression line for the field experiment is $y = -2.916 (0.313) + 0.00901 (0.000296) \text{ TS}$, $r^2 = 0.97$, $n = 29$.

assimilates available for total leaf growth. From the value of rgr_0 it is straightforward to calculate that an individual leaf will achieve a potential growth rate of $0.5 \text{ g DM pl}^{-1} \text{ d}^{-1}$ after about 260°C d since initiation, and of $1.5 \text{ g DM pl}^{-1} \text{ d}^{-1}$ after about 315°C d since initiation. These values may mark the range of the length of the sink limited growth phase, depending on the assimilate supply of the plants. The value of rgr_{dec} (Table IV) is significantly different from zero, which corroborates our hypothesis that curd initiation delays the growth of individual leaves.

A multiple linear regression analysis of the SLA values from the W1 treatment (Figure 6) indicated that most of the variation found ($r^2 = 0.78$) in this parameter could be explained using only leaf number and leaf weight as independent parameters. The estimated parameters predict that SLA is decreasing with leaf number and with leaf dry weight. SLA values of the W2

treatment were higher than of the W1 treatment (data not shown).

The observed dynamics of leaf area in the W1 treatment (Figure 7) was quite similar to the dynamics of leaf dry matter (Figure 5). The combination of this descriptive SLA model and the dry-matter partitioning model was able to reproduce the leaf area development of the W1 treatment quite precisely (Figure 7). The most obvious discrepancy between measured and simulated leaf areas are for the leaf group 4–6, due to an overestimation of leaf area which is relatively higher than the overestimation of leaf mass for this group and is therefore a consequence of SLA values being too high (Figure 5).

The evaluation of the model using the data from the field experiment indicates a good predictive quality of the model regarding the simulated dry matter for groups of five leaves in both evaluated years (Figure 8a, c). The

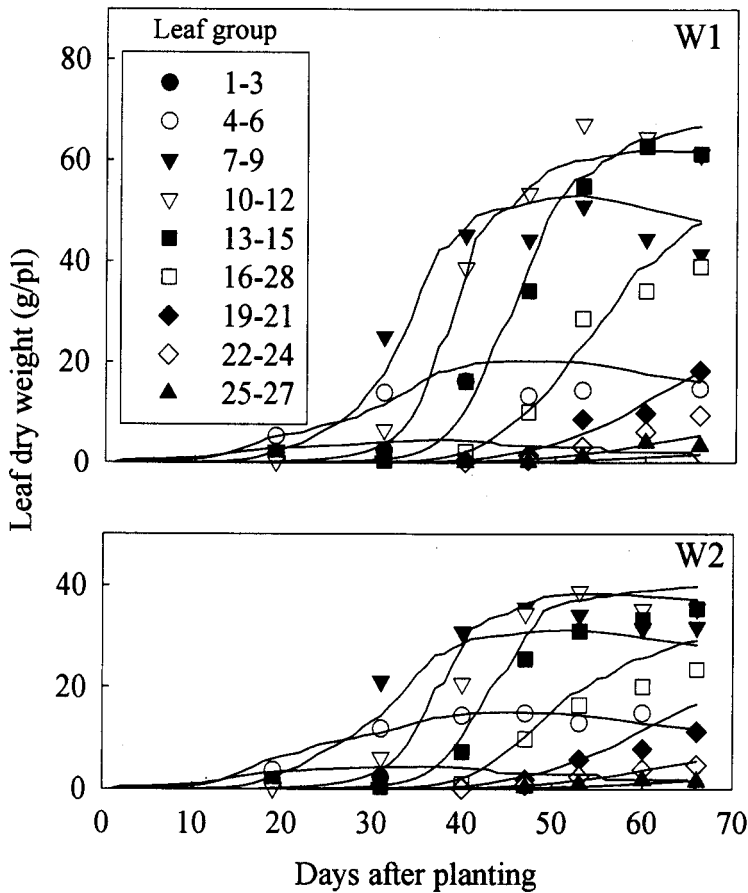


FIG. 5

Comparison of simulated and measured leaf dry weight of leaf groups consisting of three consecutive leaves from container-grown cauliflower plants under two water-supply regimes. For estimated parameter values see Table IV. The linear regression equation between simulated and measured values is $y = -0.08 (\pm 0.45) + 0.994 (\pm 0.0182) x$, $r^2 = 0.97$, $n = 80$.

values of parameters SLA_0 and c_{SLA} were estimated to be $242.18 (\pm 6.29) (\text{cm}^2 \text{g}^{-1})$ and $-12.61 (\pm 0.916) (\text{cm}^2 \text{g}^{-1} \text{MJ}^{-1} \text{d})$, respectively. With these parameter values the descriptive value for leaf area was quite good (Figure 8b), the predictive value, however, is only of moderate quality (Figure 8d), due to an underestimation of small leaf area and an overestimation of high leaf area values. The descriptive and predictive value of the model regarding leaf area development at the canopy level, however, is less critical. Linear regression between measured (y) and simulated (x) total leaf area expresses as LAI are in 1996: $y = -0.099 (\pm 0.198) 1.032 (\pm 0.070)x$, $r^2 = 0.956$, $n = 12$, and in 1997: $y = -0.279 (\pm 0.278) 1.215 (\pm 0.096)x$, $r^2 = 0.931$, $n = 14$.

DISCUSSION

The aim of the present work was to derive a model which is able to predict dry-matter partitioning between individual leaves. This is a prerequisite for any mechanistic approach of modelling leaf senescence as well as for assimilate and nitrogen translocation during leaf senescence.

Dry-matter production and partitioning parameters were calibrated for every treatment of the experiments separately, to achieve the best possible description of total leaf dry-weight increase. The effects of radiation intensity on LUE we found (Table III) further substantiate the results of Kage *et al.* (2001) and are also confirmed by Olesen and Grevsen (2000). The smaller effect in 1997 may be explained by the fact that net shading was applied in this experiment two weeks after planting. Higher TUE values of drought stressed plants (Table II) are a consequence of increasing stomatal resistances which affect transpiration more than photosynthesis (Jones, 1992).

There were marked differences between the container and the field experiments regarding leaf development

TABLE IV
Estimated values and standard errors (SE) of the parameters of Eqn. 1, describing the growth of individual leaves of cauliflower obtained by adjustment to the leaf weight data of the container experiment

Parameter	Value	SE
f_{av}	0.366	0.027
rgT_0	0.0211	0.00027
rgT_{dec}	$2.59E-5$	$1.02E-6$

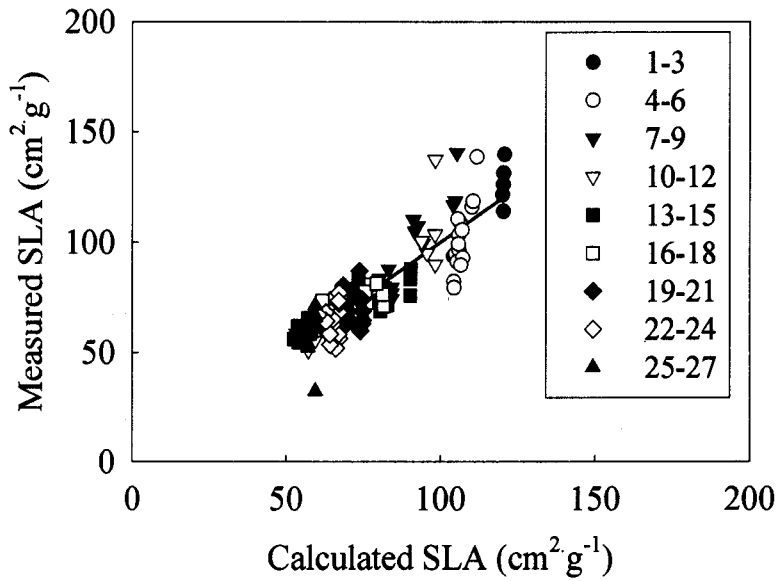


FIG. 6

Calculated vs. measured specific leaf area, SLA, of cauliflower leaves from plant grown in containers under high water supply. The multiple linear regression equation is: $SLA = 125.47 (2.32) + 2.59 (0.125)n_L - 1.705 (0.1185) WSL$, $r^2 = 0.78$, $n = 141$.

and senescence (Figure 4). The reason for the more rapid increase of visible leaf number in the container experiment compared with the field experiment (Figure 4a) may be seen in a better establishment of the transplants in the container situation and lower light competition resulting in an increased growth rate of these plants (Dale and Milthorpe, 1983). However,

because the net shading in the field experiment affected the growth rate but not leaf appearance (Figure 4a), this argument remains weak.

The higher assimilate supply of the container-grown plants, a consequence of the missing light competition, may also explain the differences in the relationship between the temperature sum since transplanting and

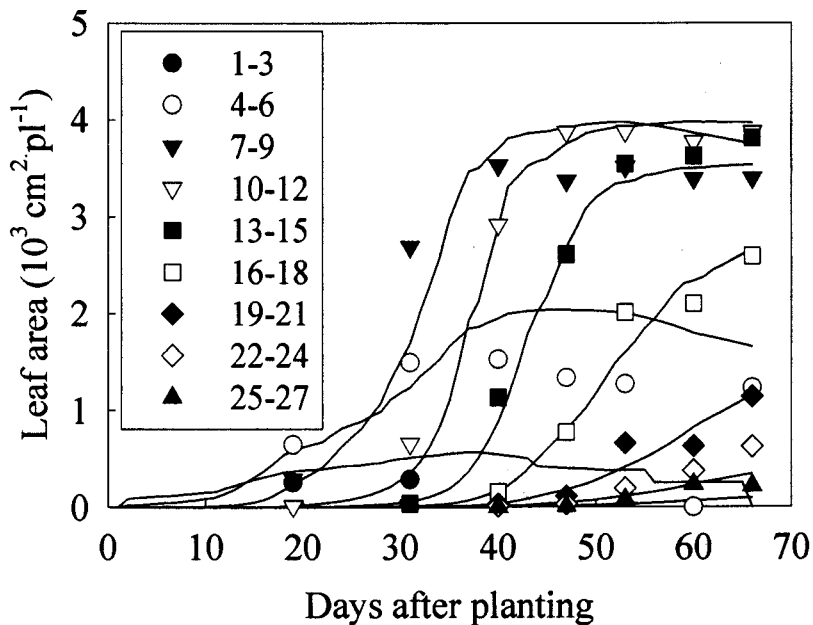


FIG. 7

Measured and simulated leaf area of leaf groups consisting of three consecutive leaves of container-grown cauliflower plants under high water supply. The modelling efficiency is 0.95 and the linear regression equation between simulated and measured values is $y = 38.68 (63.21) + 0.96 (0.031)x$, $r^2 = 0.96$, $n = 40$.

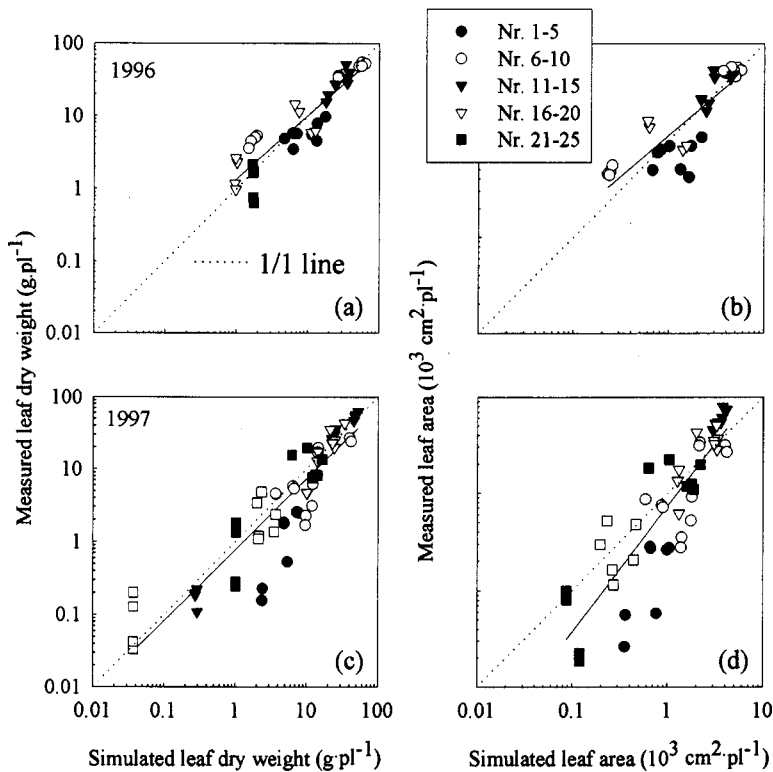


FIG. 8

Simulated vs. measured dry weight (a and c) and area (b and d) of leaf groups consisting of five leaves each from cauliflower plants grown in two years (1996: a and b, 1997: c and d) in a field experiment. The regression equation shown are: 1996: $y = 0.826 (\pm 1.238) + 0.9401 (\pm 0.0491)x$, $r^2 = 0.90$, $n = 40$ leaf DM $y = -39.21 (\pm 247.26) + 1.087 (\pm 0.083)x$, $r^2 = 0.85$, $n = 32$ leaf area. 1997: $y = -1.2296 (1.0021) + 1.0831 (0.0527)x$, $r^2 = 0.87$, $n = 63$ (leaf DM) $y = -467.8 (239.3) + 1.463 (0.111)x$, $r^2 = 0.77$, $n = 55$ (leaf area).

the number of senescent leaves between the field and the container experiment (Figure 4b). The delayed curd growth of the shaded plants (Figure 3, Table II) may thereby explain the missing influence of shading on the number of senescent leaves.

The senescence process may be modelled more mechanically considering explicitly the balance between photosynthesis and respiration depending on the local environmental conditions of the leaf. Furthermore import and export rates of assimilates and soluble nitrogen compounds into individual leaves depend on the source-sink relationships within the whole plant. However, leaf age seems to be of comparable importance to local environmental conditions and their influence on the carbon budget of an individual leaf (Hikosaka *et al.*, 1994). This may explain that our approach, which ignores effects of the carbon balance, was able to describe the number of senescent leaves and thereby the end of the senescence process.

Bell shaped curves for maximum leaf area and leaf mass as we found for cauliflower (Figures 5, 7) were reported by Wolfe *et al.* (1988) and Carberry *et al.* (1993). Such growth patterns are sufficiently described by the model, because maximum leaf area and mass is according to our assumptions closely coupled to the total assimilate flow in the "total leaf fraction". This flow also follows a bell shaped pattern, since an early increase of

assimilates available for leaf production is counteracted by increasing amounts of assimilates allocated to the curd after its initiation. As the level of assimilate supply neither alters the phyllochrone (Figure 4) nor seems to influence the leaf growth duration seriously (Figure 5), the model elegantly explains differences in final leaf mass during the development of the single plant and between treatments.

Despite the good quality of our fit regarding total leaf dry matter (Figure 3), influences of erratic estimation of total leaf dry matter on the prediction of the weight of individual leaves still can be substantial. A prediction error of 10 g pl^{-1} on total leaf DM level (Figure 3) is equivalent to a relative error of about 5–10% but may cause errors of more than 30% at the single-leaf level. Considering this fact, the descriptive and predictive value of our model seems satisfactory. However, erratic estimations of the time course of total leaf production or errors in the leaf initiation rate can cause quite large errors in the estimations of dry matter and area of individual leaves. Such errors are not necessarily critical, since according to our approach estimations of total leaf weight and area are not seriously influenced by an altered partitioning of dry matter between individual leaves.

Approaches for dry-matter partitioning between plant organs used in crop growth models may be grouped into descriptive allometric, functional equilibrium and sink

regulation approaches (see Marcelis *et al.*, 1998 for review). Approaches from the latter group may be further classified into sink hierarchy and relative sink strength based.

Relative sink strength is defined according to Marcelis *et al.* (1998) as the sink strengths of a particular organ S_i relative to the sum of the sink strength of all other organs ΣS and assumed to be directly proportional to the fraction of assimilates allocated to a particular organ, f_i :

The term sink strength itself is not precisely defined (Marcelis, 1996) and sometimes questioned (Farrar, 1993). It may be postulated that it is the product of sink size and sink activity (Warren Wilson, 1972). However, it is still debatable whether sink size is better characterized by cell number or by organ size (see Marcelis, 1996 for discussion). A sink strength calculated from the product of organ size and relative growth rate is, however, in conflict with our results, since the ceasing growth of individual leaves clearly demonstrates a decreasing sink activity.

Alternatively, a Michaelis-Menten kinetic may be used to describe sink strength (Minchin *et al.* 1993; Patrick, 1988; Marcelis, 1996). According to this concept, different or changing sink activities may be explained by different or changing K_m values. Differing K_m values, however, should result in altered partitioning patterns under a changing assimilate supply (Marcelis, 1996). In our study it was, however, possible to describe dry-matter partitioning between individual leaves for plants growing with quite different growth rates using the same parameter values (Table II, Figures 5, 8).

Therefore, both the above outlined approaches for defining sink strength may give a satisfying description and prediction of our data only after a considerable refinement. The approach presented here describes sink hierarchy more algorithmic rather than based on fundamental physiological processes. However, the main hypotheses outlined in Eq. 1, that assimilates are allocated to the leaf pool, are portioned successively top down from the youngest to older leaves and only a fixed portion of assimilates is available for an individual leaf are in accordance with accepted concepts like apical dominance and sink priority (Fick *et al.*, 1973; Marcelis, 1996; Minchin *et al.*, 1993) and were not falsified by our data.

We followed in this study the still most frequently used approach to calculate leaf area expansion directly coupled to the amount of available assimilates. Thereby, the specific leaf area SLA ($\text{cm}^2 \text{g}^{-1}$) or the inverse leaf mass per area LMA (g cm^{-2}) were used for conversion of dry matter into leaf area. It is well known that this conversion ratio is not constant and underlies many environmental influences. Mild water stress affects leaf area expansion but not photosynthesis, thus resulting in a decreased SLA (Tardieu *et al.*, 1999), whereas higher temperatures increase leaf expansion more than photosynthesis thereby increasing SLA (Olesen and Grevsen, 1995). Changes in SLA may be explained by morphological changes during the growth of an individual leaf or between different leaf age classes. But the SLA is also affected by different levels of soluble carbohydrates, which may accumulate under high assimilate supply conditions and may decrease under low assimilate

supply, see (Tardieu *et al.*, 1999 and Bertin and Gary, 1998 for discussion).

Leaf area development may be simulated by a more physiological foundation as a process which is, within certain limits, independent of dry-matter accumulation. Such approaches may also explicitly distinguish between cell division and cell expansion (Lecoeur *et al.*, 1996; Randall and Sinclair, 1988). Advantages of this concept may arise under conditions of temporal drought stress, making it possible to simulate drought stress effects during the cell division phase predetermining maximum leaf sizes (Lecoeur *et al.*, 1995).

CONCLUSIONS

The approach outlined in this paper successfully described and predicted partitioning of dry matter between individual leaves of cauliflower growing under quite contrasting environmental conditions. It may serve as a base for further elaboration of concepts describing and predicting senescence and translocation processes. These processes are of crucial importance for determining nitrogen harvest index and thereby nitrogen use efficiency.

Such further refinements should include the effect of soil water potential on leaf area expansion. This may be possible via the incorporation of an additional influence factor for changes of SLA depending on the leaf water potential or may be achieved by calculating leaf area expansion as an independent process.

The technical assistance of E. Diedrich is gratefully acknowledged.

ABBREVIATIONS

Symbol	Meaning
WSL	weight of an individual leaf
W_L	weight of the total leaf fraction
rgr_{SL}	relative growth rate parameter for individual leaves
T	mean daily air temperature
f_{av}	fraction of assimilates which can be attracted by an individual leaf
T_{wsl}	Translocated leaf dry matter
rgr_0	initial relative growth rate parameter
rgr_{dec}	decrease of relative growth rate parameter per unit temperature sum
TS3	temperature sum accumulated during the generative plant development phase
n_{LS}	number of senescent leaves
s_r	senescence parameter
TS	temperature sum since transplanting
TS _{scn}	lag phase temperature sum before leaf senescence starts
TLW	pool of translocatable leaf dry matter when senescence of an individual leaf starts
TS _{scnstart}	accumulated temperature sum when senescence of an individual leaf start
SLA	specific leaf area
SLA_0	parameter for calculation of specific leaf area
a_{SLA}	parameter for calculation of specific leaf area
b_{SLA}	parameter for calculation of specific leaf area
c_{SLA}	parameter for calculation of specific leaf area
\bar{I}	ten day running average radiation intensity
ASL	area of an individual leaf
Wsh	weight of the shoot
Tact	actual transpiration rate
TUE	transpiration use efficiency
Q	amount of intercepted radiation
Clf	clustering factor affecting efficiency of radiation interception
I	radiation intensity
rgc	relative ground cover
D	plant diameter
Wv	weight of the vegetative plant organs

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