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# Root growth and dry matter partitioning of cauliflower under drought stress conditions: measurement and simulation

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## Abstract

Field and container experiments were carried out in order to quantify root growth and dry matter partitioning of cauliflower under drought stress conditions. Drought stress did not influence allometric relationships between leaf and stem dry matter and shoot and tap root dry matter. Drought stress, however, had an impact on the sink strength of the curd, thereby curd growth was delayed and curd dry matter production was more seriously depressed by a limited water supply than total dry matter. Drought stress did not modify a linear relationship between shoot dry matter and total root length, however, the specific root length of cauliflower was lower under drought stress conditions leading to a higher dry matter deposition in the fine root fraction. Also the vertical increment of rooting depth per degree day almost doubled under drought stress conditions. An existing model for dry matter partitioning in cauliflower was adopted to include the effects of drought stress on dry matter partitioning to the curd. Therefore, the initial increase of the curd's sink strength was made dependent on the plants relative growth rate during the vernalisation period. Furthermore, a simple descriptive root growth model was adopted to include drought stress impact on root growth. For this purpose the increase of rooting depth per degree day and the specific root length were made dependent on the average soil water potential in the rooted soil profile. The modified model modules predicted dry matter partitioning and described the root length distribution of cauliflower sufficiently well using total dry matter production rate as input values.

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## 1. Introduction

Productivity of crops under drought stress condition is strongly related to the processes of dry matter partitioning in the plant and the spatial and temporal root

distribution. The development of crop leaf area is controlled by the amount of assimilates allocated to the leaves and determines radiation interception and therefore transpiration and assimilate production (Jones, 1992; Campbell and Norman, 1998). Water uptake may be limited by the amount of roots in a particular soil layer (Klepper et al., 1983; Klepper, 1990; Kage and Ehlers, 1996) and enhanced root growth can reduce drought stress. An optimal partitioning of dry matter between root and shoot, and the further separation of aboveground dry matter between the vegetative

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and generative organs therefore is of crucial importance for crop yield under drought stress conditions.

Prediction of crop performance and optimisation of crop management under limited water supply conditions consequently requires an accurate description of the partitioning processes and their adaptation to drought stress. Modifying influences of drought stress on the partitioning of dry matter were shown for many plant species (Cruz et al., 1986; Huck et al., 1986; Schulze, 1986; Li et al., 1994). Drought stress thereby mostly reduces leaf growth and increased at least relatively dry matter allocation into the root fraction, leading to a declining shoot/root-ratio (Brouwer, 1983; Wilson, 1988; Setter, 1990). The yield effect of this adaptation process, however, depends strongly upon time and extend of drought stress (Campbell and Turner, 1990).

There still exists a couple of contrasting approaches to model dry matter partitioning in crop growth models (see review Marcelis et al., 1998). Empirical (Kiniry et al., 1992; Chapman et al., 1993; Kleemola et al., 1996; Connor and Fereres, 1999) or allometric (Pearsall, 1927; Stützel and Aufhammer, 1991; Kage and Stützel, 1999) approaches which describe rather than explain developmental and external effects on dry matter partitioning are even now dominating. More rarely approaches are used which try to predict dry matter partitioning using either the concept of the functional equilibrium (Wilson, 1988) or allocate the assimilates with respect to the goal of maximizing the growth rate (Chen and Reynolds, 1997). The main reason for this is that the control mechanisms of partitioning and their feed back with the environmental conditions are not yet fully understood (Setter, 1990, Reynolds and Chen, 1996).

Also for cauliflower mainly empirical (Kage and Stützel, 1999; Kage et al., 2000a; Olesen and Grevsen, 2000) or at least partly empirical based partitioning rules are most widely used (Alt, 1999; Alt et al., 2000). The influence of drought stress on partitioning of dry matter, however, is still not considered in any of the mentioned models.

The aim of the presented work, therefore, was to quantify the influence of drought stress on the partitioning of dry matter, using container and field experiments and to summarize these data within a mathematical model of dry matter partitioning. Because drought stress responses strongly depend on

the spatial distribution of the roots in the soil profile (Klepper, 1990) also an existing root growth model for cauliflower (Kage et al., 2000), was adopted to include effects of drought stress.

## 2. Material and methods

### 2.1. Container experiments

Container experiments with different irrigation treatments were carried out during spring 1996 and 1997 within an unheated, glass roofed rainout shelter. Thereby, in 1997 containers of different size were used, the experiments were therefore designated as large container (0.222 m<sup>3</sup> volume) and small container (0.021 m<sup>3</sup> volume) experiments, LCE and SCE, respectively. In the preliminary 1996 experiment only large containers were used. The height of the containers was 0.95 and 0.3 m and the spacing between them was 1 m (LCE) and from 0.4 to 0.7 m (SCE, increasing during experiment due to intermediate harvest sampling). All containers were filled with a silt loam substrate (0.01 C/g soil) at a final bulk density of 1.35 g cm<sup>-3</sup> and planted with one transplant of cauliflower (*Brassica oleracea* convar. *botrytis* var. *botrytis* 'Fremont') on May 2. The dry weight of the transplants was 0.29 g/plant. The soil substrate of the upper 30 cm of the LCE was mixed with 62 g of a N, P, K, MgO fertilizer ((Flory 9: N 15, 7, P<sub>2</sub>O<sub>5</sub>, K<sub>2</sub>O 22, MgO, Planta Düngemittel GmbH, Regenstauf, Germany) per container. The plants of the SCE were fertilized weekly with 5 g 'Flory 9'/plant. In order to prevent evaporation losses the containers of the LCE and the SCE were covered with a 0.05 and 0.03 m thick layer of gravel.

The LCE had four irrigation treatments, thereby the total experimental time was divided into three phases, phase 1: transplanting to 20 DAP, phase 2: 21–42 DAP and phase 3: 43–68 DAP. Additionally to a control treatment without drought stress (LCE W1) three stress treatments (LCE W2, W3 and W4) were included which differed in the amount and time of drought stress influence. At the beginning of the experiment all treatments beside the fluctuating stress treatment (W3) were watered up to approximately 90% of the water holding capacity of the containers. The latter was estimated using previously determined water content/potential curves. The total amount of

water per container at beginning of the experiment was  $60 \times 10^3 \text{ cm}^3$ , from which about  $38 \times 10^3 \text{ cm}^3$  were plant available. The average soil water potential then was about  $-10 \text{ kPa}$ . Containers of the W3 were watered only up to about 75% of the container water capacity in order to ensure drought stress conditions during phase 2 of the experiment. The W1 treatment was watered daily when the soil water potential in 0.3 m depth was below  $-20 \text{ kPa}$  and received a total amount of irrigation water of 7.5, 24 and  $92 \times 10^3 \text{ cm}^3$  per plant in phase I, II and III, respectively. During the first phase of the experiment until 20 days after transplanting (DAP), all treatments were watered according to the watering regime of the W1 treatment to ensure a properly establishment of the plants. During the second phase of the experiment plants of the W2 treatment were watered with half the amount of the W1 treatment, W3 and W4 plants were not watered. In the third experimental phase the W3 treatment received the same amount of water as the W1 treatment and the W4 treatment again no water. There were four replications per treatment.

The small container experiment, SCE, had only two irrigation treatments, W1, without stress and W2, moderate stress. There were also four replications per treatment. The containers of the SCE W1 treatment were watered every morning during the experiment up to soil water potential of  $-10 \text{ kPa}$ . During phase 1 (0–20 DAP) all plants received an total amount of  $3 \times 10^3 \text{ cm}^3$  per plant and during phase 2 and 3 the W1 plants  $93 \times 10^3 \text{ cm}^3$  per plant and the W2 plants  $45 \times 10^3 \text{ cm}^3$  per plant. Until 31 DAP all containers in one treatment received the same amount of irrigation water, thereby the needed amount was calculated from the average weight of all containers. From 32 DAP on, however, irrigation amounts were calculated individually from the weight of the container. Irrigation water was given daily in the morning hours until 31 DAP, from then on a second irrigation was given at around noon on days with high potential evapotranspiration.

Transpiration of the plants ( $T_{\text{act}}$ ) was determined by weighting of the containers in intervals of 1–3 days. The accuracy of the weight (IS600, Sartorius AG, Göttingen, Germany) for the large container was 20 g. weighing was carried out from about 05:30 to 08:00 h. No correction was made for the increase of plant fresh matter.

Measurement of soil water potential,  $\Psi_s$ , was carried out in the LCE discontinuously every 1–3 days using insertion tensiometers with a septum and continuously in one container per treatment using tensiometers with electronic pressure transducers (LCI 10502, UP GmbH, Osnabrück, Germany). Tensiometers were placed in 0.30, 0.55, and 0.75 m depth. Furthermore TDR-probes (Trase, Soilmoisture Equipment Corp., Santa Barbara, USA) were installed horizontally in depths of 0.15, 0.30, 0.55 and 0.75 m. Volumetric soil water content was also used to calculate soil water potential for dry soil conditions when tensiometer were out of their measurement range ( $< -60 \text{ kPa}$ ). Within the SCE only average gravimetric soil water contents were determined every 1–3 days by weighting of the containers. Gravimetric soil water contents were transformed into volumetric soil water contents using the appropriate bulk density of the soil. Here, also soil water potential was calculated from volumetric soil water content when tensiometers were outside of their measurement range.

For determination of dry weight plants were harvested and divided into their functional subunits turgescent leaves, senescent leaves, stem and curd. This was done for the LCE only at the time of the last harvest (68 DAP) and for the SCE on 19, 31, 40, 47, 53, 60 and 60 DAP. In the LCE also curd diameter, CD, was determined non destructively on 58, 60, 61, 63, 65 and 66 DAP using a ruler. Curd weight  $W_c$  was estimated from curd diameter using an empirical regression equation derived from the destructive samplings of both experiments:

$$W_c = 26.75 \text{ CD}^{0.422} \quad r^2 = 0.98 \quad n = 40. \quad (1)$$

At the end of the experiment, on July 9, 68 DAP the tap roots of the plants were extracted from the soil down to 0.2 m, the attached soil was removed by washing and the dry matter was determined. In 1996 for every container two series of soil cores were extracted with a special root auger ( $\varnothing 80 \text{ mm}$ ; Fa. Eijkelkamp, Giesbeek, the Netherlands) down to a depth 0.8 m in vertical increments of 0.1 m. The roots were washed out over a 2 mm sieve and the length of the roots was determined using the line intersection method (Tennant, 1975) from which root length density could be calculated for every soil layer.

For the LCE the transpiration use efficiency (TUE) was obtained from the total dry matter of the plants and

the total amount of transpired water. Within the SCE the TUE was derived from the slope of a regression equation ( $y = \text{TUE} \cdot x$ ) between the above ground dry matter of the several intermediate harvests ( $y$ ) and the calculated cumulative transpiration up to the time of the respective intermediate harvest.

The drought stress status of the plants was in both experiments (LCE and SCE) characterised using an average soil water potential in the rooted soil volume,  $\Psi_{\text{RS}}$ . For the LCE this value was determined from the soil water potentials of the rooted soil layers. For the W3 treatment (fluctuating drought stress) only the upper soil layers were considered after re-wetting (43 DAP), because more than 95% of the water uptake of the plants was from this layer of the containers. The  $\Psi_{\text{RS}}$  values for the SCE was calculated from the average value of the soil water potential after rewetting ( $-10$  i.e.  $-80$  kPa) and the soil water potential measured or calculated on the next following morning before rewetting.

Global radiation ( $R_{\text{G}}$ ) relative humidity of the air (rH) and air temperature (Temp) were measured at a weather station located in a distance of approximately 20 m of the experiment. The photosynthetic active radiation (PAR) was calculated according to *Szeicz (1974)* thereby considering the transmissivity of the rainout shelter:

$$\text{PAR} = R_{\text{G}} \cdot 0.5 \cdot (1 - 0.333). \quad (2)$$

The air saturation deficit (SD) was calculated in hourly time steps according to *Smith (1992)*. The daily average saturation deficit of the air ( $\text{SD}_{\text{ave}}$ ) then was obtained from the average of the hourly saturation deficit values. Temperature sum (TS) and temperature sum during the generative phase ( $\text{TS}_{\text{gen}}$ ) were calculated from daily average temperature assuming a base temperature of  $0$  °C.

## 2.2. Field experiments

In 1995, 1996 and 1997 field experiments (FE95, FE96 and FE97) were carried out during the summer months with different irrigation treatments. In 1995 there were two treatments, irrigated (W1) and not irrigated from 14 DAP on (W2), in 1996 and 1997 there were three irrigation treatments, W1 (optimal), W2 (reduced) and W3 (not irrigated later than 14 DAP). For the optimal irrigated treatments (W1) irrigation

started when the soil water potential in 0.4 m soil depth became lower than  $-30$  kPa. For the reduced irrigated treatment the set point value of irrigation was  $-60$  kPa. The drought stress treatment (W3) was only once irrigated shortly after transplanting in order to ensure an optimal plant establishment and then received no further irrigation.

Irrigation was applied using a computer controlled line sprinkler system (Fa. Gierharke, Gütersloh, Germany). The sprinkler system was equipped with flat fan nozzles (LU 120-03 Fa. Lechler, Fellbach, Germany) and in 1996 and 1997 with 5-hole nozzles (FL 500; Fa. Lechler, Fellbach, Germany) in distances of 0.5 m. Every irrigation circle applied between 5 and 20 mm of water at an intensity of about 10 mm/h. Total amounts of applied irrigation water were 142 (1995 W1), 37.5 (1995 W2), 78 (1996 W1), 32 (1996 W2), 0 (1996 W3), 94 (1997 W1), 52 (1997 W2) and 38 (1997 W3)  $10^3 \text{ cm}^3 \text{ m}^{-2}$ .

The planting pattern was  $0.5 \times 0.5$  m in 1995 (4 plants  $\text{m}^{-2}$ ) and  $0.5 \times 0.6$  m in 1996 and 1997 (3.33 plants  $\text{m}^{-2}$ ). Transplants with weights of 0.24, 0.35 and 0.38 g DM per plant were planted on June 27, June 27 and July 9 in 1995, 1996 and 1997, respectively. There were always four replicated field plots per treatment. The experiments were located on the experimental field 'Herrenhausen' in Hannover, Germany ( $52.2^\circ$  North,  $9.4^\circ$  East, 54 m above sea level). The soil of the experimental field is a loamy sand with a 25 cm thick, humic A-horizon. The field capacity is around  $21 \text{ m}^3 \text{ m}^{-3}$ , and plant available field capacity is  $13 \text{ m}^3 \text{ m}^{-3}$ .

For the field experiments cauliflower cv. 'Fremont' was used. Nitrogen fertilizer (calcium ammonium nitrate) was applied to ensure optimal growth according to standard recommendations (300 kg N/ha minus soil mineral nitrogen from 0 to 60 cm). Plant nursery was as described in (Kage et al., 2003) for the 'Herrenhausen experiment'.

Volumetric soil water contents were determined gravimetrically in 1995 and 1996 in weekly intervals using a soil auger of 30 mm diameter down to a depth of 0.8 m in 1995 and 1.0 m in 1996 in 0.1 m increments using the known average soil bulk density of each depth. In 1997 volumetric soil water contents were measured using TDR-probes of 0.2 cm length (Trase, Soilmoisture Equipment Corp., Santa Barbara, USA) vertically installed at 0.0, 0.2, 0.4, 0.6

and 0.8 m soil depth. Volumetric water contents were converted to soil water potential values using previously determined, soil depth specific relationships between soil water potential and volumetric water content. Additionally, in all plots and in all experimental years two tensiometers per plot were installed in 0.2, 0.4, 0.6, and 0.8 m depth and matrix potential was recorded one to two times a week.

For determination of dry weight plants were harvested on DAP 24, 38, 51 and 77 in 1995, on DAP 19, 41, 54 and 62 in 1996 and on DAP 16, 31, 50 and 68 in 1997 and divided into their functional subunits turgescent leaves, senescent leaves, stem and curd. Leaf area was determined from sub samples (leaf area meter Li-3100; Licor Inc., Lincoln, USA).

Fresh matter, total leaf number and curd diameter were measured for each harvested plant individually. Water content and leaf area of the turgescent leaves was obtained from aliquots of all plant from one plot. In 1995 always six plants per plot were harvested for each intermediate and the final harvest. In 1996 and 1997 for the intermediate harvest 6 and for the final harvest 12 plants per plot were harvested.

Root growth was monitored within the field experiments only in the experimental year 1996 using the minirhizotron method. Details of the observation procedure are given in Kage et al. (2000). Root observations were carried out from August 2 (35 DAP) once a week. At the final harvest date (62 DAP) soil cores were extracted 0.2 m apart from the minirhizotron inspection tubes. The excavation of soil cores was carried out down to a depth of 1.0 m in 0.1 m increments. Measured root scores (sc) from 0.3 m soil depth on from the last observation before final harvest were correlated with the average root length density (RLD) per soil layer and treatment using Eq. (3) (Kage et al., 2000b) which includes two empirical parameters  $f_{1\text{RLD}}$  and  $f_{2\text{RLD}}$ .

$$\text{RLD} = \ln \left( \frac{1 - \text{sc}}{f_{1\text{RLD}}} \right) / f_{2\text{RLD}}. \quad (3)$$

The obtained parameters and correlation coefficients were:  $f_{1\text{RLD}}$ : 3.02(±0.739), 2.18(±0.480), 5.40(±0.776);  $f_{2\text{RLD}}$ : -3.24(±1.594), -4.59(±2.37), -2.68(±0.573);  $r^2 = 0.93, 0.71, 0.99$  for the W1, W2 and W3 treatment, respectively. Number of data pairs was six for each regression.

Weather data were collected using an automated weather station in hourly intervals. Obtained parameters were global radiation ( $R_G$ ) relative vapour saturation, wind speed ( $u$ ) and average day temperature. Hourly net radiation ( $R_n$ ) values were calculated from recorded global radiation values ( $R_G$ ) using the following empirical regression equation:

$$R_n = 0.6494 \times R_G - 18.417. \quad (4)$$

### 2.3. Statistical analysis

All statistical calculations were done using the SAS statistical software package (SAS/STAT, 1990). Thereby the procedures GLM, MEANS/DUNNET, NLIN and REG were used always at an error probability of  $P = 0.05$ .

## 3. Model modules

### 3.1. Root growth

The root growth module is essentially based on the approach presented by Kage et al. (2000), therefore only a brief description will be given here.

The root dry weight is divided into the dry matter of the tap root  $W_{\text{IR}}$  (g per plant) and dry matter of the fine roots  $W_{\text{FR}}$  (g per plant). It is further assumed that there is an allometric growth of the tap root dry matter ( $W_{\text{tr}}$ ) and the shoot dry matter ( $W_{\text{Sh}}$ ):

$$\ln(W_{\text{IR}}) = o \cdot \ln(W_{\text{Sh}}) + p, \quad (5)$$

with  $o$  (–) and  $p$  (–) as empirical parameters. Furthermore, a constant relation of fine root dry matter growth rate ( $f_{\text{FR}}$ ) and total dry matter growth rate ( $dW_t/dt$ ) is postulated:

$$\frac{dW_{\text{FR}}}{dt} = f_{\text{FR}} \cdot \frac{dW_t}{dt}. \quad (6)$$

Increase of fine root length,  $d\text{RRL}/dt$  (cm m<sup>-2</sup> per day) then is obtained from the product of  $dW_{\text{FR}}/dt$  with the specific root length SRL (cm g<sup>-1</sup>):

$$\frac{d\text{RRL}}{dt} = \text{SRL} \cdot \frac{dW_{\text{FR}}}{dt}. \quad (7)$$

Rooting depth ( $z_r$ ) is described using an expo-linear function of the accumulated temperature sum:

$$z_r = \begin{cases} z_r = z_{r0} \cdot e^{a_{zr} \cdot TS} & TS < TS_{zrcrit} \\ z_r = z_{rcrit} + b_{zr} \cdot (TS - TS_{zrcrit}) & TS \geq TS_{zrcrit} \end{cases} \quad (8)$$

with  $z_{r0}$ : rooting depth at planting (cm),  $a_{zr}$  ( $^{\circ}\text{C}^{-1}$  per day) and  $b_{zr}$  ( $\text{cm } ^{\circ}\text{C}^{-1}$  per day) empirical parameters. The value of  $z_{rcrit}$ , i.e. the rooting depth at the time of transition from exponential to linear increase of rooting depth is  $z_{rcrit} = b_{zr}/a_{zr}$  (cm) and the value of  $TS_{zrcrit}$ , i.e. the temperature sum at this time point is  $TS_{zrcrit} = \ln(z_{rcrit}/z_{r0})/a_{zr}$  ( $^{\circ}\text{C}$  day).

Assuming a negative exponential decline of RLD with depth,  $z$  (cm) the following equation holds:

$$RLD = RLD_0 \cdot e^{-k_r \cdot z}, \quad (9)$$

with  $RLD_0$  ( $\text{cm cm}^{-3}$ ): RLD at soil surface and  $k_r$  ( $\text{cm}^{-1}$ ): empirical Parameter. The average root length density in per soil layer,  $RLD_{av}$  ( $\text{cm cm}^{-3}$ ) then is given by:

$$RLD_{ave[i]} = \frac{RLD_0 \cdot (e^{-k_r \cdot z_1} - e^{-k_r \cdot z_2})}{k_r \cdot (z_2 - z_1)}, \quad (10)$$

with  $z_1$  and  $z_2$  as distances of the upper and lower boundary of the soil layer towards the soil surface (cm), respectively.

### 3.2. Model modifications for including effects of drought stress on root growth

It is postulated that adaptation processes of root growth are starting when the average soil water potential in the rooted soil volume,  $\bar{\Psi}_{WR}$ , is longer than 3 days below certain level,  $\Psi_{WRW}$ . The value of  $\Psi_{WRW}$  was set at a value of  $-63$  kPa based on the results of Jones et al. (1991).

In the presented version of the model adaptation of rooting depth increase is limited to the linear phase (Eq. (8)). Because drought stress is quite uncommon shortly after transplanting cauliflower, this is not a serious shortcoming. If drought stress occurs, the rate of rooting depth increase per unit temperature sum,  $b_{zr}$ , increases proportionally to the difference between the drought stress threshold for rooting depth increase and the actual average soil water potential in the rooted soil volume,  $\bar{\Psi}_{WR}$ :

$$b_{zr} = \begin{cases} b_{zr0} & \bar{\Psi}_{WR} \geq \Psi_{WRW} \\ b_{zr0} + f1_{bzr} \cdot (\log(|\Psi_{WRW}|) - \log(|\bar{\Psi}_{WR}|)) & \bar{\Psi}_{WR} < \Psi_{WRW} \end{cases} \quad (11)$$

thereby  $b_{zr0}$  is the vertical increment in rooting depth per degree day and  $f1_{bzr}$  is an empirical parameter ( $\text{cm } ^{\circ}\text{C}^{-1}$ ) increasing the downward growth of the root system under drought stress.

The model assumes that root length growth stops if soil water potential reaches the permanent wilting point. Therefore, the values of SRL is decreasing linearly starting from it's reference value  $SRL_0$  ( $\text{cm g}^{-1}$ ) above  $\Psi_{WRW}$  down to zero at the permanent wilting point,  $\Psi_{PWP}$ :

$$SRL = \min \left( SRL_0, \max \left( 0, \left( SRL_0 - \frac{SRL_0}{1.4} \cdot (\log(|\Psi_{WRW}|) - \log(|\bar{\Psi}_{WR}|)) \right) \right) \right) \quad (12)$$

It is furthermore assumed that ratio between shoot dry weight to total root length is constant. Therefore, and because SRL decreases under drought stress,  $f_{fr}$  increases reciprocally with SRL:

$$f_{fr} = \frac{1}{(W_{sh}/WL) \cdot SRL}. \quad (13)$$

Eq. (12) in combination with Eq. (13) gives an increased amount of assimilates allocated to the root system under drought stress used to produce thicker roots.

### 3.3. Partitioning of above ground dry matter

Shoot growth rate  $dW_{sh}/dt$  is the sum of the growth rates of the vegetative organs  $dW_v/dt$  and the generative organs (curd)  $dW_c/dt$ :

$$\frac{dW_{sh}}{dt} = \frac{dW_v}{dt} + \frac{dW_c}{dt}. \quad (14)$$

Curd growth starts with completion of vernalisation. The description of dry matter partitioning into the curd follows the approach of Kage and Stützel (1999):

$$\frac{dW_c}{dt} = f_c \cdot \frac{dW_{sh}}{dt}, \quad (15)$$

where  $f_c$  is a partitioning parameter (–) increasing logarithmically with accumulating temperature sum after completion of vernalisation,  $TS_v$  (°C per day):

$$f_c = \frac{f_0 \cdot f_f}{f_0 + (f_f - f_0) \cdot e^{(-r_f \cdot TS_v)}} \quad (16)$$

This partitioning approach, however, is now expanded, including effects of the stress conditions before the completion of vernalisation on the partitioning of assimilates to the curd. Therefore, based upon an empirical analysis the parameter  $r_f$  now was made dependent on the average relative growth rate of total dry matter during the vernalisation phase,  $rgv$  (per day):

$$r_f = f1_{rf} \cdot rgr_v + f2_{rf} \quad (17)$$

The values for the other parameters of Eq. (16),  $f_0$  and  $f_f$  were taken from Kage and Stützel (1999) ( $f_0 = 0.000215$ ,  $f_f = 0.815$ ).

The separation of  $dW_v/dt$  into growth rates of leaves  $dW_L/dt$  and stem  $dW_{St}/dt$  follows the allometric approach outlined by Kage and Stützel (1999):

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

$$\frac{dW_{St}}{dt} = \frac{dW_v}{dt} - \frac{dW_L}{dt} \quad (19)$$

### 3.4. Leaf initiation and vernalisation

Also leaf initiation and vernalisation were described analogously to Kage and Stützel (1999). Thereby, the number of visible leaves (> 1 cm) increases expo-linearly as a function of the accumulated temperature sum, TS. The two parameters  $k_1$  and  $k_2$  were estimated at  $0.00297(\pm 0.00481)$  and  $0.0374(\pm 0.00277)$  for the container experiments and  $0.00308(\pm 0.00494)$  and  $0.0329(\pm 0.00173)$  for the field experiments.

$$TUE = \begin{cases} TUE_0 & \Psi_{WR} > \Psi_{WRTUE1} \\ TUE_0 + f1_{TUE} \cdot (\log(|\Psi_{WR}|) - \log(|\Psi_{WRTUE1}|)) & \Psi_{WRTUE1} > \Psi_{WR} > \Psi_{WRTUE2} \\ TUE_{max} - f2_{TUE} \cdot (\log(|\Psi_{WR}|) - \log(|\Psi_{WRTUE2}|)) & \Psi_{WRTUE2} > \Psi_{WR} \end{cases} \quad (22)$$

### 3.5. Dry matter production

Modelling dry matter production under drought stress conditions is outside the scope of the presented

work. Alternatively, and in order to minimize possible errors of erratic mechanistic simulations of dry matter production on parameter estimates for the presented partitioning routines we used descriptive, empirical functions to interpolate shoot dry matter growth and to derive the corresponding growth rate.

For the field experiments this was achieved using fitted, temperature sum dependent expo-linear functions:

$$\frac{dW_s}{dt} = \begin{cases} f1_{WS} \cdot Temp \cdot W_{sh} & TS \leq TS_{W_{sh}} \\ f2_{WS} \cdot Temp & TS > TS_{W_{sh}} \end{cases} \quad (20)$$

with  $f1_{WS}$  (day °C<sup>-1</sup>) and  $f2_{WS}$  (g (°C day)<sup>-1</sup>) as Parameters. The transition point of exponential to linear growth  $TS_{W_{sh}}$  (°C day) can be calculated analogously to Eq. (8).

Dry matter production rates for the container experiments were calculated from the measured plant transpiration rates ( $T_{act}$ ) and a transpiration use efficiency (TUE) based approach (Campbell and Norman, 1998):

$$\frac{dW_{Sh}}{dt} = T_{akt} \cdot TUE \quad (21)$$

Here, a TUE rather than a light use efficiency based approach was used because transpiration rates of the container grown, isolated plant can be measured quite accurately whereas light interception is quite cumbersome to quantify under such experimental conditions.

It is, however, well known, that TUE depends beside other factors on the drought stress conditions the plants are growing in. Thereby a limited drought stress may increase TUE and severe drought stress then again depresses TUE. We found a similar response of instantaneous TUE in our LCE experiments based on gas exchange measurements on individual leaves (data not shown) and from a poor performance of a constant TUE approach for interpolating shoot dry matter data.

TUE of the container experiments therefore was calculated as a function of the average soil water potential in the rooted soil volume:

with  $TUE_0$ : transpiration use efficiency in absence of drought stress (set to a value of 4.2 g l<sup>-1</sup> based on the results of previous experiments),  $TUE_{max}$ : maximum possible transpiration use efficiency (g l<sup>-1</sup>),  $\Psi_{WRTUE1}$ : soil water potential where stomata closure starts and

TUE is beginning to increase,  $\Psi_{\text{WRTUE2}}$ : Soil water potential where  $\text{TUE}_{\text{max}}$  is reached and with  $f1_{\text{TUE}}$  ( $\text{g l}^{-1}$ ) and  $f2_{\text{TUE}}$  ( $\text{g l}^{-1}$ ) as parameters.

The value of  $\Psi_{\text{WRTUE2}}$  (kPa) is given by the following equation:

$$\Psi_{\text{WRTUE2}} = 10^{\left(\frac{\text{TUE}_{\text{max}} - \text{TUE}_0}{f1_{\text{TUE}}} - \log(\Psi_{\text{WRTUE1}})\right)}. \quad (23)$$

### 3.6. Water budget

The quantification and prediction of the impact of drought stress on dry matter partitioning relies on an adequate knowledge of the water supply and demand of the crop. For the container experiment data were directly available from measurements. For the field experiments, however, the lower frequency of the measurements made it necessary to use a water budget model to characterise water supply and demand.

The calculation of potential and actual evapotranspiration,  $\text{ET}_{\text{pot}}$  and  $\text{ET}_{\text{akt}}$ , was done in hourly

active root length weighted average of the soil water potential in the rooted soil layers:

$$\Psi_{\text{WR}} = \sum \Psi_{\text{B}[i]} \cdot \frac{\text{WL}[i]}{\text{WL}_{\text{ges}}}, \quad (24)$$

with  $\Psi_{\text{B}(i)}$ , Soil water potential within soil compartment  $i$  (kPa),  $\text{WL}(i)$ , root length in soil compartment,  $i$  ( $\text{cm cm}^{-2}$ ) and  $\text{WL}_{\text{ges}}$  total root length ( $\text{cm cm}^{-2}$ ).

Evapotranspiration was separated into transpiration,  $T$  ( $\text{g m}^{-2} \text{s}^{-1}$ ) and evaporation,  $E$  ( $\text{g m}^{-2} \text{s}^{-1}$ ), according to (Ritchie, 1972) using an extinction coefficient for global radiation,  $k_{\text{RG}}$ , of 0.52. Leaf area index was interpolated between measured values using and logistic growth equation with high accuracy ( $r^2 > 0.9$ ). Actual soil evaporation  $E_{\text{akt}}$  is determined analogously to Beese et al. (1978) using a dimensionless reduction factor  $f_{\text{evap}}$ , (0.1) calculated from the soil water potential within the upper 0.05 m of the soil profile,  $\Psi_{\text{B}(0-5)}$ :

$$f_{\text{evap}} = \begin{cases} 1 & -0.71 \log(|\Psi_{\text{B}[0-5]}|) + 2.99 \geq 1 \\ -0.71 \log(|\Psi_{\text{B}[0-5]}|) + 2.99 & 1 > -0.71 \log(|\Psi_{\text{B}[0-5]}|) + 2.99 > 0 \\ 0 & -0.71 \log(|\Psi_{\text{B}[0-5]}|) + 2.99 \leq 0 \end{cases} \quad (25)$$

time steps using the Penman–Monteith–Equation (Monteith, 1965) and additional equations for intermediate variables given by the FAO (Smith, 1992). Crop height of cauliflower was calculated from actual shoot dry matter according to Röhrig and Stützel (2001). The canopy resistance,  $rc_x$ , was derived from the average stomata resistance  $rs_x$  and the leaf area index, LAI (Stockle et al., 1994).

Because of the higher vertical heterogeneity of root length density in the field experiments the value of the average soil water potential in the rooted soil volume  $\Psi_{\text{WR}}$  was calculated in the field experiments as a rel-

Vertical soil water transport was calculated using a soil water diffusivity based form of the Richards–Equation. The hydraulic properties of the soil profile thereby were described using the functions suggested by van Genuchten (1980). The Parameters of these functions were estimated using the program RETC (Wösten and van Genuchten, 1988) and are summarised in Table 1. For this purpose data from Pagel (1990, personal communication) were used.

The water uptake of the plants from different soil layers was calculated as dependent on the average root length density and the volumetric water content in

Table 1

Parameters of the van Genuchten–Mualem equation for different soil layers of the field experiment site

Depth (m)	$\theta_r$ ( $\text{cm}^3 \text{cm}^{-3}$ )	$\theta_s$ ( $\text{cm}^3 \text{cm}^{-3}$ )	$\alpha$ ( $\text{cm}^{-1}$ )	$n$	$l$	$k_s$ (cm per day)
0–30	0.02	0.50111	0.10575	1.30101	0.5	121
30–60	0.02	0.36486	0.03661	1.29044	0.5	77
60–80	0.02	0.40866	0.10763	1.28845	0.5	191
80–100	0.02	0.42962	0.12133	1.29533	0.5	205
100–200	0.02	0.39300	0.02900	1.3100	0.5	221

$\theta_r$ , residual soil water content;  $\theta_s$ , saturation soil water content;  $\alpha$ ,  $n$  and  $l$ , parameters;  $k_s$ , saturated soil hydraulic conductivity. The additional parameter  $m$  is calculated by:  $m = 1 - 1/n$ .

a particular soil layer. Therefore, the single root approach of Nye and Tinker (1977) was used. The maximum water uptake of the roots,  $I_{\max}$  ( $\text{cm s}^{-1}$ ), for a particular soil layer is calculated according to

$$I_{\max,i} = \frac{(\theta_i - \theta_{\text{PWP}})2\pi D_{w,i}}{\ln((x_i/1.65)a)}, \quad (26)$$

with:  $I_{\max[i]}$ : maximum water influx rate of the roots in a particular soil layer, ( $\text{cm}^3 \text{cm}^{-1} \text{s}^{-1}$ ),  $a$ : average root radius, set to 0.02 (cm),  $\theta_{(i)}$ : volumetric soil water content ( $\text{cm}^3 \text{cm}^{-3}$ ),  $\theta_{\text{PWP}}$ : volumetric soil water content at permanent wilting point, ( $\text{cm}^3 \text{cm}^{-3}$ ),  $D_{w[i]}$ : soil water diffusivity in the soil compartment ( $\text{cm}^2$  per day) and  $x$  the mean half root distance (cm). The relative water water,  $I_{\text{rel},i}$  then is calculated:

$$I_{\text{rel},j} = \frac{I_{\max,i} \cdot \text{RLD}_i}{\sum I_{\max,i} \cdot \text{RLD}_i}. \quad (27)$$

Actual water uptake from a soil layer is proportional to the relative maximum water uptake and the actual transpiration rate:

$$S(t, z)_i = \begin{cases} I_{\text{rel},i} \cdot T_{\text{akt}} & T_{\text{akt}} \leq \sum I_{\max,i} \cdot \text{RLD}_i \\ I_{\text{rel},i} \cdot \sum I_{\max,i} & T_{\text{akt}} > \sum I_{\max,i} \cdot \text{RLD}_i \end{cases} \quad (28)$$

For the calculations the soil profile from 0 to 2 m depth was divided into 21 layers, the first two layers being 0.05 m and the other 0.01 m thick.

### 3.7. Model implementation and parameter estimation

The dynamic simulation model was implemented using the simulation software ModelMaker (Walker, 1997). Water transport and evaporation calculation routines were called from a dynamic link library

(DLL) generated from Pascal source code. Integration was performed using Euler's algorithm at a time step length of one day. Only the water balance calculations were internally integrated at a time step of 1 h. Some parameter values were estimated directly within the ModelMaker-Software package using parts of the available data and taking advantage of the built in Marquard-Algorithm (Marquardt, 1963). The data sources used for the estimation of the parameters are summarised in Table 2.

## 4. Results

Using either the TUE based approach (Eq. (21)) or the expo-linear function (Eq. (20)), a sufficient accurate description of the time course of dry matter production could be achieved (Fig. 1). The estimated parameter values for  $\text{TUE}_{\max}$ ,  $f1_{\text{TUE}}$  and  $f2_{\text{TUE}}$  were  $6.74 \text{ g l}^{-1} (\pm 0.049)$ ,  $14.6 (\pm 3.92)$  and  $5.23 (\pm 0.283)$ , respectively. Parameters estimated for the field experiments are summarized in Table 3. It is noticeable, that the limited root volume of the SC plant reduced final shoot weight for the W1 treatment relative to the W1 treatment of the LC experiment. Drought stress reduced shoot dry matter, depending on time and magnitude of drought stress. The 50% reduction of the water supply which started in the second phase of the experiment drastically reduced shoot dry matter in the SC experiment and only gradually and at later growth stages in the LC experiment (Fig. 1). The increase of the water supply rate in the third experimental phase of the LC W3 treatment resulted in shoot dry matter growth rates comparable to the LC W1 treatment. Generally the shoot dry matter per plant was lower in the field experiments compared to the container

Table 2  
Overview of the data used for estimation of parameter values

Parameter	Equation	Data source for parameter estimation
$f1_{\text{bzt}}$	Eq. (11)	Root data of FE96 W1, FE96 W2, FE96 W3
$\text{SRL}_0$	Eq. (12)	Root data of FE96 W1
$f1_{\text{rf}}, f2_{\text{rf}}$	Eq. (17)	Curd dry matter data from: LCE W1, LCE W2, LCE W3, LCE W4, SCE W1, SCE W2, FE96 W1, FE96 W2, FE96 W3
$g, h$	Eq. (18)	leaf- and stem dry matter data from: LCE W1, LCE W2, LCE W3, LCE W4, SCE W1, SCE W2, FE96 W1, FE96 W2, FE96 W3
$f1_{\text{ws}}, f2_{\text{ws}}$	Eq. (20)	Above ground dry matter within the treatments of the field experiments
$\text{TUE}_{\max}, f1_{\text{TUE}}, f2_{\text{TUE}}$	Eq. (22)	Shoot dry matter data of SCE W1, SCE W2

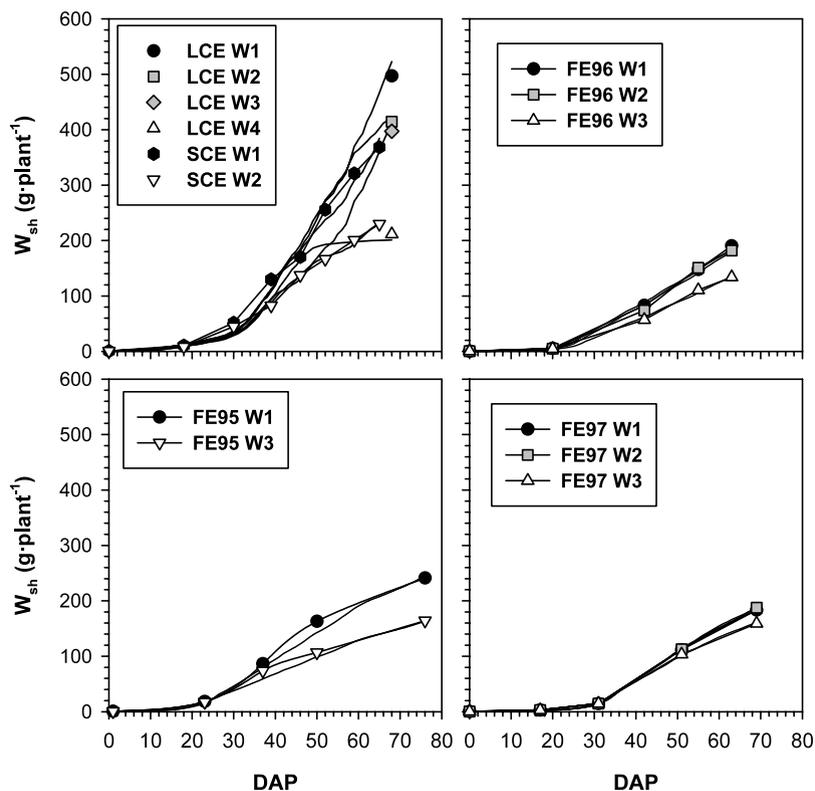


Fig. 1. Time course of shoot dry matter,  $W_{sh}$ , of the container and field experiments. Symbols: measured values, Lines: with Eq. (20) (field experiments) and Eq. (21) (container experiments) calculated shoot dry matter ( $r^2$  of fitted curves  $>0.98$  for all treatments). DAP, Days after transplanting;  $W_{sh}$ , shoot weight; LCE, large container experiment; SCE, small container experiment; FE, field experiment.

experiments, because of mutual shading of the plants under field conditions.

Natural rainfall resulted in variable drought stress conditions between years in the field experiments, with

Table 3

Estimated parameter values ( $\pm$  SE) of the expo-linear function for describing time series of shoot dry matter of the field experiments (Eq. (20))

Experiment	Treatment	$f1_{ws}$	$f2_{ws}$
FE95	W1	0.1222 ( $\pm 0.00324$ )	0.881 ( $\pm 0.053$ )
	W2	0.1311 ( $\pm 0.00684$ )	0.562 ( $\pm 0.053$ )
FE96	W1	0.1354 ( $\pm 0.00184$ )	0.854 ( $\pm 0.038$ )
	W2	0.1262 ( $\pm 0.00165$ )	0.874 ( $\pm 0.040$ )
	W3	0.1251 ( $\pm 0.00241$ )	0.616 ( $\pm 0.038$ )
FE97	W1	0.0093 ( $\pm 0.00036$ )	0.767 ( $\pm 0.012$ )
	W2	0.0092 ( $\pm 0.00035$ )	0.792 ( $\pm 0.012$ )
	W3	0.00963 ( $\pm 0.00045$ )	0.648 ( $\pm 0.011$ )

almost missing impacts on shoot dry matter in 1997, large impacts in 1995 and medium stress in 1996 (Fig. 1). The comparable large deficit of the soil water budget in the 1995 field experiment, W2 treatment resulted in an almost complete exhaustion of the soil water reserves in the upper soil layers, and later on to a still remarkable decline of soil water contents even at 80 cm soil depth. The soil water budget model modules were able to describe these time course of soil water contents in different depths (Fig. 2, 1996–1997 data: not shown, regression equations for all years in Table 4).

Rooting depth of cauliflower increased almost linearly between the measurements and reached 90 cm, the lower boundary of our observations at around 58 DAP. Drought stress increased the rooting depth during the later stages of the growth period (Fig. 3). Using the value 0.00394 for  $a_{zr}$  (Kage et al., 2000a) and slightly modifying parameter  $b_{zr}$  using Eq. (8) with the

Table 4

Slope,  $a$  ( $\pm$ SE), intercept,  $b$  ( $\pm$ SE), correlation coefficient,  $r^2$ , and number of observations,  $n$ , for the regression equations ( $Y=ax+b$ ) between measured and simulated volumetric soil water contents of the field experiments

Experiment	Treatment	$a$	$b$	$r^2$	$n$
FE95	W1	0.807( $\pm$ 0.0919)	0.041( $\pm$ 0.0116)	0.76	57
	W2	0.915( $\pm$ 0.0690)	0.004( $\pm$ 0.0108)	0.73	67
	all	0.947( $\pm$ 0.0729)	0.007( $\pm$ 0.0472)	0.77	124
FE96	W1	0.726( $\pm$ 0.0966)	0.081( $\pm$ 0.0193)	0.49	60
	W2	0.765( $\pm$ 0.0983)	0.045( $\pm$ 0.0187)	0.51	60
	W3	0.903( $\pm$ 0.0885)	0.014( $\pm$ 0.0163)	0.64	60
	all	0.898( $\pm$ 0.0639)	0.028( $\pm$ 0.0122)	0.53	180
FE97	W1	0.631( $\pm$ 0.1407)	0.072( $\pm$ 0.0339)	0.35	38
	W2	0.733( $\pm$ 0.1116)	0.040( $\pm$ 0.0260)	0.54	38
	W3	0.735( $\pm$ 0.1139)	0.038( $\pm$ 0.0264)	0.53	38
	all	0.733( $\pm$ 0.0679)	0.044( $\pm$ 0.0159)	0.50	116

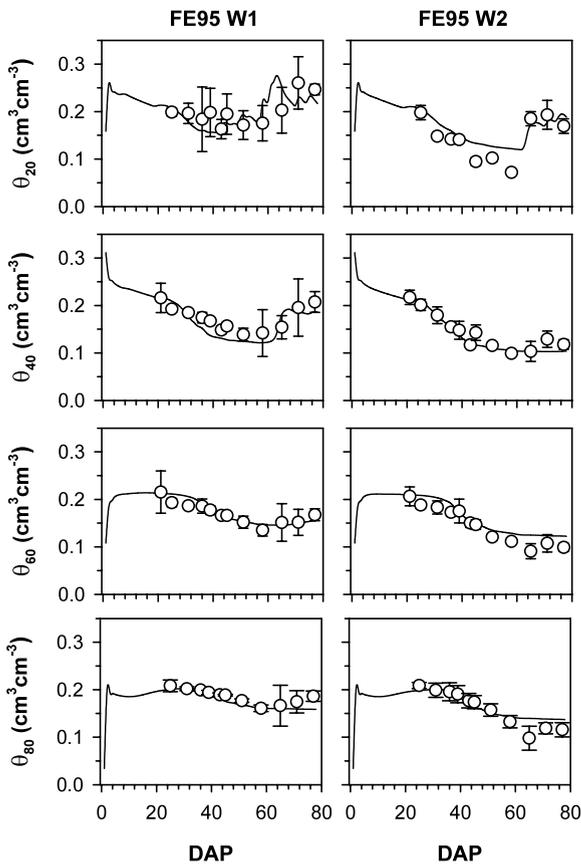


Fig. 2. Volumetric soil water content during the field experiment in 1995 for different irrigation treatments in 0.2, 0.4, 0.6, and 0.8 m depth ( $\theta_{20}$ ,  $\theta_{40}$ ,  $\theta_{60}$ , bzw.  $\theta_{80}$ ); Symbols: Measured values, Error bars: SE of measured values, Lines: Simulated values.

parameter values  $b_{zr0} = 0.107$ , for unstressed plants (Kage et al., 2000a) and  $f2_{bzr} = 0.4404(\pm 0.24336)$  rooting depth increase could be appropriately described for the treatments FE96 W1 and FE96 W3 (Fig. 3). For the treatment FE96 W2, however, the correlation coefficient was only 0.24 (data not shown).

There was an almost constant relationship between shoot dry matter and total root length for plants from the large container experiment (Fig. 4a) and the specific root length decreased under drought stress conditions (Fig. 4b). The specific root length values found in the container experiment, however, were

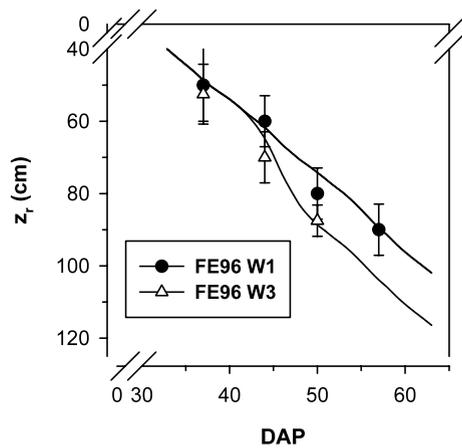


Fig. 3. Rooting depth development ( $z_r$ ) of the irrigated (FE96 W1) and nonirrigated (FE96 W3) treatments of the field experiment in 1996. Symbols: Measured values, Error bars: SE of measured values, Lines: Simulated values.  $r^2 = 0.96$  and  $0.92$  for FE96 W1 and FE96 W3.

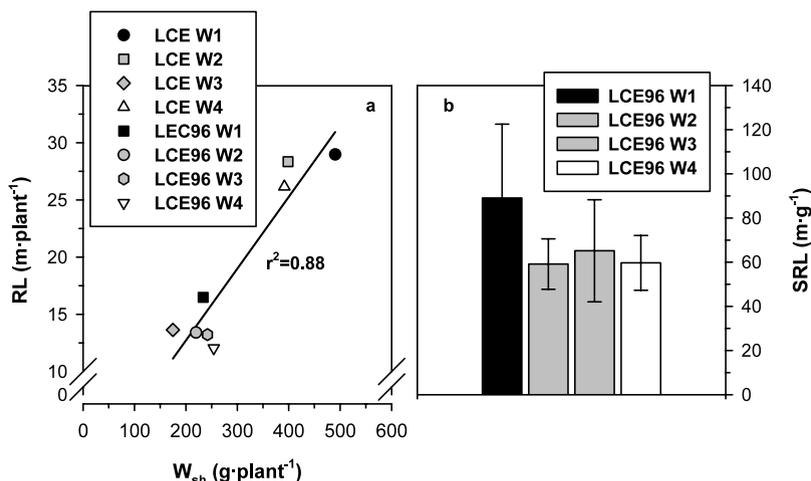


Fig. 4. (a) Relationship between total root length  $RL_{ges}$  and shoot dry weight,  $W_{sh}$ , of all treatments of the large container experiments at final harvest. (b) Measured specific root length (SRL) at final harvest of the preliminary large container experiment from 1996.

not appropriate in describing the root length density data of the field experiment (data not shown). Using the root length data of the control treatment FE96 W1 and a value for  $f_{fr} = 0.117$  (Kage et al., 2000) the value of  $SRL_0$  was estimated at  $64.34(\pm 3.70)$  ( $m\ g^{-1}$ ). The relationship  $W_{sh}/WL_{ges}$  therefore was  $0.1328$  ( $g\ m^{-1}$ ). Using these parameter values and the model approach outlined in (Eqs. (6)–(13)) the vertical root distribution of the field experiments was properly described (Table 5) even for the FE W2 treatment where rooting depth was relatively poorly described. The values of the parameters  $o$  and  $p$  were left unchanged according to Kage et al. (2000) at  $0.9501$  and  $-2.221$ , respectively. There was a good correlation between measured and simulated data of tap root dry matter ( $r^2 = 0.75$ ) and there were no indications of a drought stress impact on the allometric

Table 5

Slope,  $a$  ( $\pm$  SE), intercept,  $b$  ( $\pm$  SE), correlation coefficient,  $r^2$ , and number of observations,  $n$ , for the regression equation between measured and simulated root length density values of the soil layers below 0.3 m from the field experiments 1996

Treatment	$a$	$b$	$r^2$	$n$
FE96 W1	$0.954(\pm 0.0581)$	$0.000(\pm 0.0134)$	0.86	35
FE96 W2	$0.683(\pm 0.0983)$	$0.043(\pm 0.0623)$	0.75	35
FE96 W3	$0.868(\pm 0.0849)$	$0.024(\pm 0.0153)$	0.79	35
All	$0.831(\pm 0.0396)$	$0.023(\pm 0.0085)$	0.80	105

relationship between shoot and tap root dry matter (data not shown) (Table 6).

Drought stress seriously reduced curd dry matter in the container and the field experiments (Fig. 5). Remarkably, the curd dry matter of the LC W3 treatment was comparable to the W1 treatment, despite the reduced shoot dry matter (Fig. 1) in this treatment. The obtained differences in curd dry matter ( $W_c$ ) for the different drought stress treatments (Fig. 5) could not be explained by the reduced shoot growth rate alone (data not shown), because also the relative portion of dry matter allocated to the curd was reduced under drought stress. Therefore, the parameter  $r_f$  of Eq. (16)

Table 6

Estimated parameter values of  $r_f$  (Eq. (16)), and average relative growth rates during the vernalisation period,  $rg_{rv}$ , for the parameterisation data set (LCE, SCE FE96)

Experiment	Treatment	$r_f$	$rg_{rv}$
SCE	W1	$0.01745 (\pm 0.00052)$	0.142857
	W2	$0.02002 (\pm 0.00065)$	0.146481
LCE	W1	$0.01552 (\pm 0.00014)$	0.103369
	W2	$0.01629 (\pm 0.00011)$	0.105235
	W3	$0.01665 (\pm 0.00027)$	0.0955603
	W4	$0.01595 (\pm 0.00350)$	0.103044
FE96	W1	$0.02357 (\pm 0.00077)$	0.105235
	W2	$0.02554 (\pm 0.00154)$	0.0955603
	W2	$0.02483 (\pm 0.00016)$	0.103044

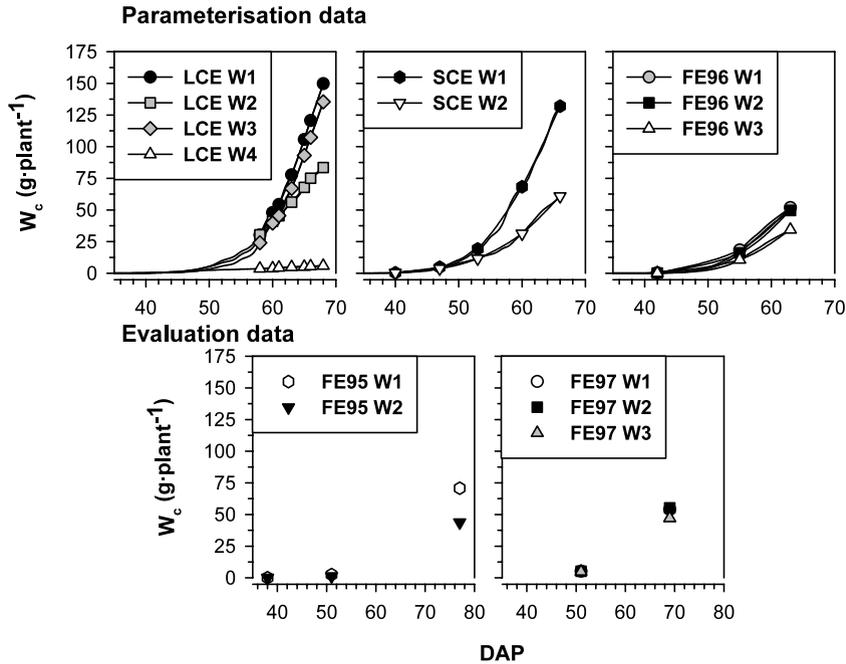


Fig. 5. Time course of curd dry weight,  $W_c$ , for different irrigation treatments in the container and field experiments: Symbols: measured values, lines: simulated values using parameter values of  $r_f$  (Eq. (16)) shown in Table 6.

was estimated for all treatments of the parameterisation data set individually. The estimated parameter values were decreasing with increasing drought stress and were closely correlated to the relative growth rate of

the plant during the vernalisation period,  $rgr_v$  (Fig. 6). Using this relationship the time course of curd dry matter could be described for all drought stress treatments with high accuracy (Table 7).

Despite the strong drought stress the plants were exposed to, there still was a unique allometric relationship for all treatments of the FE96 and the container experiments between leaf and stem dry matter (Fig. 7). This relationship could successfully be used to describe and predict partitioning of vegetative dry matter into stems and leaves (Table 7).

### 5. Discussion

The aim of the presented work was to elaborate a model for the prediction of dry matter partitioning and root growth of cauliflower considering the influences of drought stress. For this purpose data from container and field experiments were used to adopt and expand existing model approaches for dry matter partitioning and root growth (Kage and Stützel, 1999; Kage et al., 2000).

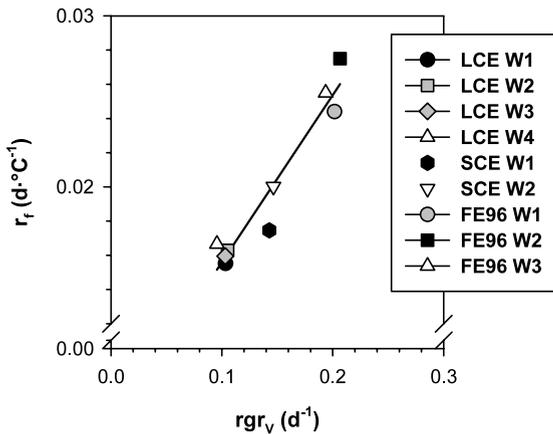


Fig. 6. Fitted values of parameter  $r_f$ , Eq. (16) (initial increase of the dry matter fraction allocated to the curd) as dependent on the relative growth rate of the plants during the vernalisation phase,  $rgr_v$  for the parameterisation experiments. Regression line shown is:  $r_f = f1_{rf} \cdot rgr_v + f2_{rf}$ ,  $r^2 = 0.93$ ,  $n = 9$ ; with  $f1_{rf} = 0.9789$  ( $\pm 0.01006$ ) and  $f2_{rf} = 0.0058$  ( $\pm 0.00152$ ).

Table 7

Slope,  $a$  ( $\pm$ SE), intercept,  $b$  ( $\pm$ SE), and correlation coefficient,  $r^2$ , number of observations,  $n$ , of the regression equation between measured and simulated dry matter of the aboveground organs

Experiment	Organ	$a$	$b$	$r^2$	$n$
Parameterisation data	Curd	0.943( $\pm$ 0.0275)	0.959( $\pm$ 1.9630)	0.96	47
	Leaf	1.016( $\pm$ 0.0209)	0.759( $\pm$ 4.6961)	0.99	30
	Stem	0.899( $\pm$ 0.0476)	0.966( $\pm$ 1.3560)	0.93	30
Evaluation data	Curd	1.057 ( $\pm$ 0.0421)	-6.542( $\pm$ 5.4697)	0.98	12
	Leaf	0.976( $\pm$ 0.0354)	-0.986( $\pm$ 10.6502)	0.98	20
	Stem	1.091( $\pm$ 0.0563)	-2.958( $\pm$ 2.5414)	0.95	20

Parameterisation data: LCE, SCE and FE96, Evaluation data: FE95 and FE97.

During the drought stress period of the treatment FE96 W3 the increase of rooting depth almost doubled from 0.107 to 0.228 ( $\text{cm } ^\circ\text{C}^{-1}$  per day). Such an increase of the vertical expansion rate of the root system, however, is in agreement with observations of Hoogenboom et al. (1987) and Asseng et al. (1997). Whereas in the LCE the bulk density of the soil substrate was constantly  $1.35 \text{ (g cm}^{-3}\text{)}$  over all depths, the soil bulk density in the field experiment increased to values of about  $1.7 \text{ (g cm}^{-3}\text{)}$  from 0.3 m below the soil surface on (Kochler, unpublished data). A higher bulk density leads to a higher soil strength and therefore decreases SRL (Klepper, 1990). Also under drought stress conditions soil strengths increases and similarly SRL (Cruz et al., 1986; Klepper, 1990; Klepper and Rickman, 1990; Benjamin et al., 1996). Our assumption of a linear decrease of SRL with decreasing  $\Psi_{\text{WR}}$

(Eq. (12)) is of course an oversimplification, but seems to be sufficient to describe our data (Table 5). Indirectly, this supports the assumption of Jones et al. (1991) that at soil water potentials below  $\Psi_{\text{PWP}}$  root growth ceases completely. The coupling of SRL via  $W_{\text{S}}/W_{\text{L}_{\text{ges}}}$  with  $f_{\text{fr}}$  (Eq. (13)) leads to an increased portion of dry matter increase allocated to the roots. This lowers the shoot/root-ratio under drought stress, a common observation for many crop species (McCoy et al., 1990; Chartzoulakis et al., 1993; Li et al., 1994; Rodrigues et al., 1995; Rabha and Uprety, 1998) and mimics the principle of the functional equilibrium between root and shoot (Wilson, 1988). Potential water uptake in a certain soil layer depends on the soil water content and the root length density and for the whole soil profile on the rooting depth and total root length (Klepper, 1990). An decrease of SRL under drought stress conditions therefore has to be compensated by an increased transfer of assimilates into the root system but leads not necessarily to an increase of total root length because the decrease in SRL compensate this (Huck et al., 1986). The missing impact of drought stress on the relationship between shoot and tap root growth, however, is in accordance with the concept of functional equilibrium. The tap root mainly plays the role of anchoring the plant within the soil and is needed for the upward transport of water and the downward transport of assimilates. A similar conclusion holds for the constant allometric relationship between leaf and stem dry matter (Fig. 7).

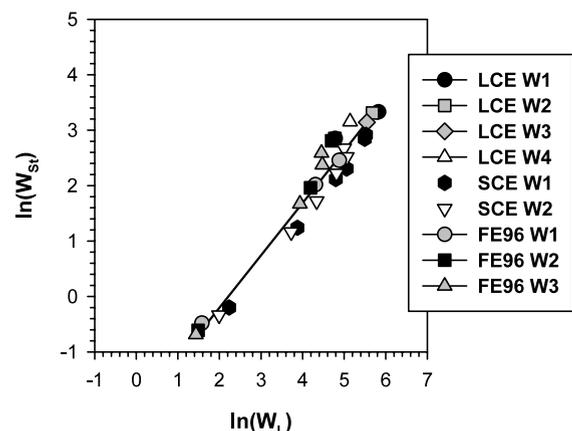


Fig. 7. Relation between the logarithms of leaf,  $\ln(W_{\text{L}})$  and stem weights,  $\ln(W_{\text{St}})$  of the parameterisation experiments. The regression line is:  $\ln(W_{\text{St}}) = g \cdot \ln(W_{\text{L}}) + h$ ,  $r^2 = 0.96$ ,  $n = 28$ ; with  $g = 0.944(\pm 0.0389)$  and  $h = -2.091(\pm 0.1729)$ .

The found dependence of  $r_{\text{f}}$  and the average relative growth rate during the vernalisation period,  $\text{rg}_{\text{rv}}$ , (Eq. (17)) may be explained by a higher amount of generative cells established during the curd induction phase for fast growing plants. A higher number of growing generative cells may increase the relative sink

strength and lead to a relative increase of assimilates allocated to the curd (Alt, 1999).

## 6. Conclusion

The presented model approaches were able to describe and predict drought stress impacts on dry matter partitioning and root growth of cauliflower for our experimental data. The presented model modules may further be used for evaluating possible cost/benefit ratios of adaptation processes on cauliflower crop yield under conditions of limited water supply and to derive optimised irrigation schedules in combination with modules describing leaf area development and dry matter production under drought stress.

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