Simulation modelling for improving nitrogen use efficiency in intensive cropping systems

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Abstract

The presented thesis deals with the problem of low nitrogen use efficiency (NUE) of unprotected, intensive vegetable cropping systems. Thereby a system based approach is used and the combination of simulation modelling together with data from field experiments gives the foundation of the presented work. The thesis is organised within 12 chapters, after a short introduction before the final discussion 10 chapters are dealing with different aspects and foundations of nitrogen use efficiency in intensive vegetable cropping systems.

Chapter 2

An empirical model derived from data of field experiments is presented that predicts development and dry matter partitioning in cauliflower under conditions of unrestricted nutrient and water supply. The model is a combination of an empirical relationship between temperature sum and leaf number, a vernalisation model, an allometric approach of dry matter partitioning between leaf and stem and an empirical logistic function describing the fraction of dry matter allocated to the curd depending on the temperature sum after the end of the vernalisation process. This model was incorporated in a simple dry matter production model which calculated dry matter production using the product of intercepted photosynthetic active radiation and light use efficiency. However, the parameter values light use efficiency and specific leaf area of the model had to be fitted to every experiment in order to get an acceptable description of cauliflower dry matter production.

Applied to an independent data set the model was able to predict measurable parameters like leaf number ($r^2 = 0.73$), the proportion of leaf, stem and curd on total dry matter ($r^2 = 0.55, 0.08$ and $0.77$) and the length of the growing season ($r^2 = 0.69$).

Chapter 3

Measurements of CO$_2$-exchange of cauliflower leaves were carried out in a field experiment which included two nitrogen fertilisation rates. Irradiance and CO$_2$ concentration were varied at the leaf level within a leaf cuvette and additionally a temperature treatment was applied to field grown plants moved into climate chambers. These measurements were used to estimate parameter values of a rectangular hyperbola describing cauliflower leaf CO$_2$ exchange as a function irradiance and CO$_2$ concentration. The obtained parameter estimates were used to derive empirical regression equations with temperature and nitrogen content of the leaves as independent variables. The resulting relationships were applied within a simple photosynthesis-respiration based dry matter
production model in order to derive functional relationships between light use efficiency and irradiance, leaf area index and temperature.

The rectangular hyperbola was able to describe the gas exchange data as varied by irradiance and CO$_2$ concentration on the single leaf level with sufficient accuracy, but estimates of initial light use efficiency (about 25 µg J$^{-1}$) were too high because of the bias emanating from the limited flexibility of this model. Light saturated photosynthesis rate ($P_{\text{max}}$) showed an optimum response to temperature and an increase with increasing nitrogen content of leaves. The initial slope $\alpha$ of the rectangular hyperbola showed no consistent responses to ambient temperature and nitrogen content of leaves. The respiration per unit leaf area $\beta$ increased exponential with increasing temperature, resulting in a $Q_{10}$ value of 1.86. Because only a limited number of plants evaluated in this study, additionally work is needed to further substantiate the results of the gas exchange measurements.

The model analysis demonstrated that LUE is only independent on the light integral over a range of 5 to 10 MJ m$^{-2}$d$^{-1}$ photosynthetically active radiation if one assumes an adaptation of $P_{\text{max}}$ within the canopy and over time according to the incident irradiance. Acclimatisation within the canopy and higher leaf area indices, LAI, reduce the decrease of LUE with irradiance but a substantial decline remains even for LAI values of 4.

## Chapter 4

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

The results indicate that an estimated constant LUE (3.15 (±0.04) gMJ$^{-1}$) is only poorly able to predict total dry matter production for cauliflower (modelling efficiency $EF = 0.69$) of an independent data set. Using a linear decline of LUE with $I$ ($LUE = 6.66 (±0.80) - 0.36 (±0.08) I$) drastically
increased the predictive value \((EF = 0.88)\) of the LUE approach. The descriptive and predictive value of the photosynthesis based modules was higher when assuming that \(P_{\text{max}}\) declines within the canopy. Then the predictive value of the photosynthesis-respiration based approach was better than the simple LUE approach but not generally better than the LUE approach assuming a linear decrease of LUE with increasing daily radiation sum.

Chapter 5

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 3 and 5 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.

Chapter 6

Data from field experiments carried out in 3 consecutive years under contrasting N supply and radiation environment were used analyse the decline of nitrogen contents in cauliflower at different levels of morphological aggregation. Radiation environment was varied in two of three years using a net shading, reducing radiation intensity by 40\%. The decline of average shoot nitrogen contents, \(N_c\), \(\%\text{N DM}\) with shoot dry matter, \(W_{\text{sh}}\) \((\text{t ha}^{-1})\) for cauliflower \((N_c = 4.84 (0.071) W_{\text{sh}}^{-0.089(0.011)}\), \(r^2=0.67\)\) is much less than as described for some arable crops. Radiation environment had no significant influence on total nitrogen concentrations of leaves and only a small influence on protein nitrogen contents in lower
layers of the canopy. Total nitrogen content of leaf groups consisting of 5 leaves, $N_{LC}$, under optimal N supply could be described using a multiple linear regression on leaf weight of the leaf group, $W_{5L}$, (g dm$^{-5}$ leaves$^{-1}$) and the average leaf number of the leaf group, $n_{L}$, (-) $N_{LC} = 7.58 - 0.82W_{5L} - 0.074n_{L} + 0.024W_{5L}n_{L}$, $r^{2} = 0.76$, $n = 76$. Fractions of leaf nitrate nitrogen to total nitrogen, $f_{Nitr}$, (-) could linearly related to the average irradiance incident on different leaf layers, $I_{av}$ (W PAR m$^{-2}$) ($f_{Nitr} = 0.2456 (±0.0188) - 0.0023(±0.0004)I_{av}$, $r^{2} = 0.67$.

Reference N concentrations were obtained from the N dilution curves and used to identify critical soil nitrate values, $N_{min_{crit}}$, where nitrogen content of cauliflower organs begin to decline because of a limited N supply. Linear response plateau functions were fitted using log transformed values of soil nitrate values from 0-60 cm as independent variables. $N_{min_{crit}}$ values for total nitrogen were estimated at 85, 93 and 28 kg N ha$^{-1}$ for leaves, stem and curd, respectively. Within the canopy, $N_{min_{crit}}$ values for total N of leaves increased from the top to the bottom from 44 to 188 kg N ha$^{-1}$. $N_{min_{crit}}$ values for protein N in leaves from different layers of the canopy were much lower at around 30 kg N ha$^{-1}$, without a large gradient within the canopy.

Chapter 7

Root observations were carried out on cauliflower using the minirhizotron and the soil core method in two years on two locations with different soil types, a loess loam and a humic loamy sand. Total root length (RL) (cm cm$^{-2}$) of cauliflower was correlated to total shoot dry weight ($W_{sh}$) (g m$^{-2}$) $RL = 0.0124(±0.005)W_{sh}$, $r^{2} = 0.76$. There was an acceptable correlation ($r^{2} = 0.88$) between the minirhizotron and the soil core methods for the subsoil data, whereas the minirhizotron method underestimated rooting intensity for the top soil. Changes in rooting depth over time could be described for both soil types using a segmented function of temperature sum, consisting of an early exponential and a later linear phase. The increase of rooting depth during the linear phase was $0.107(±0.01)\text{ cm } °\text{C}^{-1} d^{-1}$.

A simple descriptive root growth model based on the assumptions of a negative exponential decline of root length density (RLD) with soil depth, of a fixed ratio of RLD at the top of the soil profile and at rooting depth ($r_{RLD}$) and of a fixed fraction of dry matter increase allocated to fine-roots ($f_{fr}$) was formulated and used to describe the temporal and spatial variation of RLD found in the field. Slightly different estimates of $f_{fr}$ and of $r_{RLD}$ could be found for the different soil types, indicating a higher fraction of fine-root dry matter for the loess loam soil and a somewhat deeper root system for the humic loamy sand soil. A cross validation using the parameter values obtained from adjusting to the rooting data of one soil
type for predicting RLD values of the other soil type, however, indicated that still quite satisfactory estimates ($r^2 = 0.91$ and 0.95) of RLD could be obtained.

**Chapter 8**

Data from two annual and a long term field experiment summing up to 8 crops grown under a differentiated nitrogen supply on a loess loam soil are used for a simulation modelling based analysis of nitrogen availability of cauliflower. The model was built out of components describing root growth, nitrate transport to the roots and the vertical nitrate transport within the soil. Net nitrogen mineralisation was input to the model and was derived from the initial amounts and change of N in plant and soil. N uptake of the plants was derived from a plant growth model described in second part of this paper.

The root observations obtained in two years indicated an increased fraction of dry matter allocated to the fine roots under N deficiency. An adopted version of the root growth model for cauliflower presented in chapter 7 taking this into account described the rooting data with sufficient accuracy ($r^2=0.75$ and 0.80). Based upon a acceptable description of the soil water budget as indicated by agreement between measured and simulated soil water tensions, vertical nitrate movement during the growth period of cauliflower was correctly described. The magnitude of this movement, however, was limited to soil depths of about 60 cm even after periods of high rainfall, because of a high soil water holding capacity. An analysis of the factors determining nitrate availability indicated that apparent mass flow was only of high importance for overfertilised conditions when high amounts of nitrate nitrogen remain in the soil up to the end of the growing season. Otherwise, the dominating fraction of nitrate has to be transported to the roots by diffusion. The single root model for calculating maximum nitrate transport to roots overestimated N availability as indicated by a too low estimated level of soil nitrate N when transport to roots limited N uptake of the plant. The introduction of an restricted uptake activity period of the roots was used to bridge the gap between theoretical calculations and empirical results. However, a probably too short uptake period was needed to give a good agreement between measurements and simulations. Scenario calculations were carried out to obtain functional relationships between N supply and residual soil nitrate levels. Thereby also hypothetical conditions for a sandy soil and possible benefits of split N applications were investigated.
Chapter 9

Based on previously presented studies concerning dry matter partitioning, dry matter production, root growth, N contents of cauliflower organs and soil nitrate availability (first part of the paper) an integrated simulation model for the cauliflower/soil system is constructed, parameterised and evaluated using data from field grown crops.

Dry matter production of cauliflower was described and predicted using a simple light use efficiency, LUE, based approach assuming a linear decrease of light use efficiency with increasing differences between actual, NCA\textsubscript{Prot}, and 'optimal', NCA\textsubscript{optProt} area based leaf protein concentrations. For two experimental years the decline of LUE with decreasing leaf area was estimated by model adjustment to be 0.82 and 0.75 (g DM MJ\textsuperscript{-1}g N \textsuperscript{-1}m\textsuperscript{2}). Using this approach and the parameters obtained from the first experimental year shoot dry matter production data of cauliflower from 5 independent experiments with varied N supply containing intermediate harvests could be predicted with an residual mean square error (RMSE) of 72 g m\textsuperscript{-2}. Nitrogen uptake and partitioning of cauliflower was simulated using functions describing an organ size dependent decline of N content. Leaf nitrate was considered explicitly as an radiation intensity dependent pool, mobilised first under N deficiency. The curd was assumed to have a sink priority for nitrogen. The model predicted shoot N uptake including data of intermediate harvest with a RMSE of 2.4 g m\textsuperscript{-2}. N uptake of cauliflower at final harvest was correlated to final leaf number.

A long term scenario simulation analysis was carried out to quantify seasonal variation of N uptake cauliflower cultivars under unrestricted N uptake. Due to variations of the vernalisation phase simulated shoot N uptake varied from about 260 kg N ha\textsuperscript{-1} for spring planted crops to about 290 kg for summer planted crops of the cultivar 'Fremont'. The cultivar 'Linday', which shows a more severe delay under high temperatures, shows on average a higher shoot N uptake for summer planted crops of about 320 kg N ha\textsuperscript{-1} and a much higher variation of shoot N uptake.

Chapter 10

Root observations on winter wheat grown on a loess loam soil during three consecutive years were carried using the minirhizotron and the soil core method. There was a good (r\textsuperscript{2}=0.92) correlation between the minirhizotron and the soil core method for the sub-soil data (>30 cm soil depth), whereas the minirhizotron method gave unrealistically low values of rooting intensity for the top soil. Rooting depth development could be described using a linear function of temperature sum with an increase of rooting depth of 0.11 (+0.01) cm °C\textsuperscript{-1}d\textsuperscript{-1}. 
A simple descriptive root growth model based on the assumptions of a negative exponential decline of root length density (RLD) with soil depth, and of a fixed ratio of RLD at the top of the soil profile and at rooting depth \( f_{RLD} \) was used to describe the temporal and spatial variation of RLD found in the field. Two hypotheses on the allocation of dry matter into the fine root fraction thereby were proven. Hypothesis H1 postulated a constant and hypothesis H2 a linearly with temperature sum decreasing fraction of dry matter allocated to fine roots. The H2 hypothesis performed much better than the H1 hypothesis and explained about 90% of the total variance found for RLD values from all years and all soil depths.

Chapter 11

Results from four years of a long term crop rotation experiment on a loess loam soil in northern Germany are presented where late harvested cauliflower is followed by winter wheat under two contrasting crop rotations and fertilisation regimes. The N uptake of cauliflower at final harvest was about 300 kg N ha\(^{-1}\) if curds reached a marketable size and N supply was optimal. About two thirds of this nitrogen was contained in unharvested plant material. Additionally about 80 kg nitrate N ha\(^{-1}\) was left in the soil from 0-120 cm, with large variations between years.

Experimental results indicate that only in one of four years winter rainfalls translocated substantial amounts of residual soil nitrate and mineralised nitrate from crop residues deeper than the final rooting depth of the following winter wheat. The winter wheat exhausted the sub soil very effectively from nitrate during ear emergence to grain filling if no late N dressings were applied.

A simulation model consisting of modules describing crop N uptake, mineralisation of soil organic matter and crop residues, the soil water balance and vertical nitrate movement was used to further analyse the dynamics of soil mineral nitrogen. The model was also used to estimate the N leaching losses of a cauliflower/winter wheat sequence on a sandy soil and N-losses of an alternative sequence of cauliflower followed by two lettuce crops in the succeeding year. N-losses on the sandy soil were higher than on the loess loam soil and higher for two lettuce crops than for wheat succeeding the late harvested cauliflower. Sowing winter wheat reduced N-losses on the sandy soil compared to the cropping sequence cauliflower/lettuce/lettuce.
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Chapter 1

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1. Introduction

'Pflanzenbauwissenschaft' or 'agronomy' is an applied science. This simple and self-evident truth implies that the mission of this academic discipline is to resolve practical problems using scientific methods. This science should create the knowledge about possible management options available to achieve a pre-defined goal and to give an understanding of their possible consequences and risks (Baeumer, 1992).

Every progress of science is closely coupled to the availability of appropriate methods. The development of methods and the improvement of theory therefore is often the key for resolving practical problems. This thesis summarises work concerning a practical problem, the low nitrogen use efficiency of intensive vegetable cropping systems. Thereby, a rapidly developing methodological approach, simulation modelling is widely used. The work presented here strives to contribute to the increase of knowledge about options for solving this practical problem and about potentials of simulation modelling as a heuristic tool.

1.1. Problem

Intensive production systems are characterised by a high level of external resource input per unit area and per unit time. Vegetable production systems thereby mark the upper limit of production intensity in field crop production because of the high economic value of the produced crops. Nitrogen fertilizer today is a comparably cheap external production factor in developed countries. Therefore, and due to a lack of knowledge about the actual fertilization optimum agricultural practice often applies too high amounts of nitrogen to vegetable crops in order to avoid deficiencies. Furthermore, vegetable crops often leave high amounts of crop residues in the field (Alt and Wiemann, 1990; Rahn et al., 1992), which further complicates estimations of N supply through mineralisation.

A recent survey of residual nitrate values at harvest time of cauliflower in the main region of cauliflower production in Germany showed that in 48% of the investigated fields the residual soil nitrate level (0-60 cm) was higher than 200 kg N ha\(^{-1}\) (Strohmeyer, 2000). In only 4% of the fields the residual soil nitrate contents (0-60 cm) were lower than 80 kg N ha\(^{-1}\). Long term cultivation of vegetable crops consequently leads to increased nitrate concentrations in the sub-soil (Hähndel and Dressel, 1996;
Hähndel and Isermann, 1993) which exceeds drastically allowed levels for drinking water (BMG, 1986). Overfertilisation practices as cited above (Strohmeyer, 2000) are partly an extension problem as the use of current knowledge (Scharpf, 1991; Lorenz et al., 1989) should avoid much of such obvious misuse of nitrogen fertilisers. However, further progress in the scientific basis for fertilisation recommendations and better knowledge about agronomic practices which reduce potentially harmful losses of nitrogen from the production system are urgently needed to match future needs for profitable and environmentally safe production systems in intensive crop production.

1.2. Nitrogen use efficiency

The term nitrogen use efficiency, NUE, is widely used within agronomic research to cover problems nitrogen productivity. It describes nitrogen input / output ratios at different scales, ranging from the primary processes of plant productivity, i.e. photosynthesis and respiration, to farm and regional levels (Novoa and Loomis, 1981; Moll et al., 1982; Huggins and Pan, 1993). An analysis of the term NUE may be helpful to analyze possible options for improving nitrogen use efficiency and to classify the work presented in this thesis. Here, a distinction is made between the systems levels 'crop' and 'cropping systems'.

Nitrogen use efficiency at the crop scale may be in a first step defined by the ratio between the yield and the nitrogen uptake of the crop. This ratio is sometimes also called the physiological nitrogen use efficiency (Novoa and Loomis, 1981) or utilisation efficiency. High NUE values can be achieved by a high harvest index and a high productivity of dry matter production per unit nitrogen uptake. For vegetable crops which are marketed on a fresh weight base, the dry matter content is inversely related to the nitrogen use efficiency.

A second component of NUE at the crop scale is the ratio of plant nitrogen uptake to potentially available nitrogen. This ratio is called uptake efficiency or available N use efficiency (Huggins and Pan, 1993). Enhancing the uptake efficiency of the crop may be possible through enhancing the physiological uptake efficiency of roots (Dempsey et al., 1988), enhancing root length density (Kage, 1997; Wiesler and Horst, 1994a) and 'simply' matching N supply and demand of a particular crop (Everaarts, 1993b; Greenwood et al., 1989).
At the cropping system level a useful definition of NUE is the ratio of the long term yield to the amount of nitrogen fertilized to a certain field over the longer periods. In addition to the components of NUE at the crop level this definition of NUE includes two further components of NUE: The first is the ratio of potentially available N for crops to the total N supply. This ratio may be called the nitrogen loss ratio or available N efficiency (Huggins and Pan, 1993) and comprises effects of N-losses from the production system by processes like leaching, denitrification and erosion. A second component can be identified as the ratio of nitrogen supply to nitrogen fertilized. Changes in the amount of soil organic matter may result in nitrogen immobilisation or net mineralisation, decreasing or increasing this ratio. Also all nitrogen inputs into the system additional to N fertilisation, namely by biologically nitrogen fixation increase this ratio.

The components of NUE at crop and cropping system level are closely interrelated. If the uptake efficiency at the crop level is low, residual soil nitrate levels are may be comparably high. This could increase the ratio of N-supply to N fertilised, a component of NUE at the cropping system level but also the losses from the system possibly will rise. Similarly, if the physiological utilization efficiency at the crop level is low, the amount of nitrogen in crop residues and the rate of mineralisation should be higher, which may increase nitrogen supply to the following crop but also N-losses.

Therefore, a low NUE at the crop level only determines a low NUE of the production system if this predetermines substantial N-losses from the system. Designing cropping systems with high NUE can therefore be achieved by using crops which make effective use of residual nitrogen in soil and crop residues and other measures which reduce the N-loss from the system.

1.3. Methodological aspects

The different ratios at crop and cropping system level presented in the above analysis are useful in defining terms. However, beside the fact that NUE is per definition a static entity it is the result of dynamic processes. The type of analysis presented above therefore hampers from the fact that these processes and their time scale are not explicitly considered. Simulation modelling offers the possibility to overcome these shortcomings and was therefore used throughout this thesis to analyse aspects of nitrogen use efficiency in intensive cropping systems.
Since its introduction in the late sixties systems theory and simulation modeling have become an increasingly important scientific method for analyzing agricultural production systems (de Wit, 1965; Duncan et al., 1967; see Bouman et al., 1996 for review). With this approach any dynamic change of a system can be described as the consequence of the change of the systems state variables from the knowledge of their initial values by integrating their rates of change according to the boundary conditions using mathematical descriptions of the processes causing this change (de Wit, 1982).

The mathematical formulation of an hypothesis, i.e. the construction of a model, offers by comparison of the model output with experimental data a very efficient and quantitative test of an hypothesis (Philip, 1991). However, the final goal of the scientific process is not simply to obtain a 'yes/no' type of information about the possibility of reject a hypothesis. Because 'science is concerned with prediction' (Thornley and Johnson, 1990), quantitative information about parameter values is needed which allows a sufficient description and prediction of the system behavior. This holds especially for applied or engineering sciences (see Hauhs, 1990, Passioura, 1996 and Hammer, 1998 for further discussion about scientific and engineering approaches in simulation modeling).

The model modules presented in the different chapters of this thesis describing different sub-systems of the soil-plant-system were all implemented within a generic, object oriented class library for building simulation models (Kage and Stützel, 1999). Part of this class library is a method for parameter estimation and for determining parameter uncertainty from experimental data based on the Marquardt algorithm (Marquardt, 1963).

Applying parameter adjustment procedures to crop simulation models is not trivial. The amount and quality of the available data and computational limitations usually restrict the application of such techniques to a small sub set of the usually large number of model parameters in crop growth models. This may be critical if high correlations between estimated and the 'fixed' parameters of a model have to be expected and if the values of the 'fixed' parameters are also subject to severe uncertainty. Also, technical difficulties may arise due to discontinuous changes of model output caused by parameter changes (see Metselaar, 1999, for a further discussion).
1. Introduction

However, parameter estimation procedures incorporated into dynamic modeling environments allows to test hypotheses about processes directly affecting only difficult or not measurable traits by their indirect effects on measurable quantities. The information content of experimental data may therefore be used more efficiently. Examples for this approach are given in several chapters of this thesis.

1.4. Outline of the thesis

This thesis covers NUE at the crop and at the cropping system scale. Cauliflower is used as an example crop to investigate aspects and components of NUE at the crop scale (Chapters 2 to 9). The final N uptake which quantifies N demand of the crops and the partitioning of nitrogen between harvested and residual plant parts is a consequence of the dynamic processes of dry matter production as well as dry matter and nitrogen partitioning. The first part of this thesis therefore elaborates the necessary prerequisites for a process oriented analysis of NUE.

In chapter 2 a simple empirical approach for predicting development and dry matter partitioning in cauliflower is presented.

Chapters 3 and 4 deal with the problem of predicting crop dry matter production, thereby comparing photosynthesis-respiration and light use efficiency based approaches of different complexity.

In chapter 5 the dry matter partitioning model module for cauliflower is refined by introducing a concept for calculating dry matter partitioning between the individual leaves of cauliflower.

In chapter 6 the influence of the factors organ size, radiation environment and N supply on the protein and nitrate content of cauliflower organs are analysed using empirical regression equations. Thereby, also critical soil nitrate values for sustaining optimal nitrogen contents are empirically derived.

In chapter 7 a simple root growth model is presented, giving the base for a mechanistic calculation of nitrogen supply rates for cauliflower.

The chapters 8 and 9 are a synthesis of the work presented in Chapters 2 to 6 and of a formerly presented model approach for calculating soil water budget as well as nitrogen transport in the soil profile and to the roots (Kage, 1992; Kage, 1997). This integrated
soil-crop model is used to analyse 'below ground' (chapter 8) and 'above ground' (chapter 9) processes affecting the **NUE at crop level** for the example crop cauliflower.

The fate of residual soil nitrate and nitrogen in crops residues of cauliflower is studied in chapter 10-11. There, experimental and simulation modelling results are presented from the sequence cauliflower/ winter wheat to study possible positive effects of deep rooting cereal crops on the **NUE at the cropping systems scale**.

Some aspects and prospects of simulation modelling and of nitrogen use efficiency research are discussed in chapter 12, the final discussion.

The experimental basis for this thesis consists of a number of 10 experiments, 9 field and 1 pod experiment (Table 1-1). The field experiments were carried out on two different locations with distinct soil types, a humic loamy sand at the campus of the faculty of horticulture in Hannover and at the experimental station 'Ruthe' situated 10 km south of Hannover on a loess loam soil.

Whenever possible a part of the available data was used for the parameterisation and another independent part was left for evaluation of the predictive quality of the model modules.

Chapter 2 was previously published in *Scientia Horticulturae* (1999) 80, 19-38. The chapters 3 and 4 are accepted for publication also in *Scientia Horticulturae*. Chapter 7 is accepted for publication in *Plant and Soil*. All other chapters are also organised to be suitable for an independent publication in scientific journals.
Table 1-1: Experimental data used for parameterisation (P.) and evaluation (E.) of the model modules presented in this thesis. Exp. No. = experiment number, Location (Loc.) R= experimental station Ruthe with loess loam soil and Location H= Campus of the faculty of horticulture in Hannover with humic, loamy sand soil.

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<td>Cultivar, Planting date</td>
<td>2, 4</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Annual, field/climate chamber</td>
<td>H</td>
<td>1995</td>
<td>2</td>
<td>Irrigation</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Annual, field</td>
<td>H</td>
<td>1996</td>
<td>1</td>
<td>Irrigation (not considered)</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>10</td>
<td>Pod experiment</td>
<td>H</td>
<td>1997</td>
<td>1</td>
<td>Irrigation</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>
Chapter 2

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

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Abstract

An empirical model derived from data of field experiments is presented that predicts development and dry matter partitioning in cauliflower under conditions of unrestricted nutrient and water supply. The model is a combination of an empirical relationship between temperature sum and leaf number, a vernalisation model, an allometric approach of dry matter partitioning between leaf and stem and an empirical logistic function describing the fraction of dry matter allocated to the curd depending on the temperature sum after the end of the vernalisation process. This model was incorporated in a simple dry matter production model which calculated dry matter production using the product of intercepted photosynthetic active radiation and light use efficiency. However, the parameter values light use efficiency and specific leaf area of the model had to be fitted to every experiment in order to get an acceptable description of cauliflower dry matter production.

Applied to an independent data set the model was able to predict measurable parameters like leaf number ($r^2 = 0.73$), the proportion of leaf, stem and curd on total dry matter ($r^2 = 0.55$, $0.08$ and $0.77$) and the length of the growing season ($r^2 = 0.69$).
2.1. Introduction

Two problems have been identified to be of major importance in the production of cauliflower: The first is the high variability in the length of the growing season (Booij, 1990a; Wiebe, 1980) which is a consequence of the vernalisation requirement of this crop. High summer temperatures e.g. can delay vernalisation and thus lengthen the growing period. The second problem is the high nitrogen leaching risk that is attributed to the usually high intensity of nitrogen fertilisation and low nitrogen use efficiency of cauliflower (Everaarts, 1993a; Rahn et al., 1992). Both problems are interrelated, the uncertainty of the length of the growing period also introduces a serious additional uncertainty in the estimation of the crop nitrogen demand. Of further importance in this context is the partitioning of the plant nitrogen between the harvested product and the crop residues, as the amount of nitrogen in crop residues has to be known for an accurate fertilisation of the subsequent crop (Everaarts, 1993b).

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

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

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

2.2.1. Development

During the juvenile phase the plant is not sensitive to the cold stimulus that is causing the vernalisation process (Fujime, 1983; Wiebe, 1972a). The end of the juvenile phase can be determined by a characteristic number of initiated leaves, which may vary with cultivars (Booij, 1990c; Grevsen and Olesen, 1994a; Hand and Atherton, 1987, december; Wiebe, 1972a; Wurr et al., 1994). For the cultivars 'Fremont' and 'Linday', used in this study we assumed that 16 leaves have to be initiated before the juvenile phase is completed (Wiebe 1998, personal communication, Wiebe, 1972).

2.2.2. Development of leaves

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

\[
\frac{dn_L}{dt} = k_1 \cdot T \cdot n_L \tag{2-1}
\]

where \( n_L \) is the number of leaves larger than 1 cm diameter, \( T \) is the temperature (°C) and \( k_1 \) is an empirical constant. Integration of Eqn. 2-1 yields the well-known exponential growth equation:

\[
n_L = n_{L0} \cdot e^{k_1 \cdot TS} \tag{2-2}
\]

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

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

\[
\frac{dn_L}{dt} = k_2 \cdot T \tag{2-3}
\]
In order to obtain a continuously derivable function the exponential and the linear part of the function have to predict the same leaf initiation rate at the switching point from one part to the other. Therefore, by combining the right hand sides of equations 2-1 and 2-2 and solving for \( n \) the leaf number at this switching point, \( n_{lc} \), where maximum leaf initiation rate is reached can be calculated:

\[
n_{lc} = \frac{k_2}{k_1}
\]  

(2-4)

The temperature sum at which the leaf development rate switches from the exponential to the linear phase, \( TS_c \), is obtained by substituting \( n_{lc} \) from Eqn. (2-4) for \( n \) in Eqn. 2-2. Rearranging gives:

\[
TS_c = \frac{\ln \left( \frac{n_{lc}}{n_{l0}} \right)}{k_1}
\]  

(2-5)

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

\[
n_L = n_{lc} + k_2 \cdot (TS - TS_c)
\]  

(2-6)

In order to calculate the number of leaves initiated, \( n_L \), from the number of visible leaves, \( n_L \), the empirical regression equation of Booij and Struijk (1990) was used:

\[
n_L = 186 \cdot n_L + 1.24
\]  

(2-7)

2.2.3. Vernalization

The vernalisation process is calculated according to Wiebe (1972b) using a daily vernalisation rate, \( dV/dt \), which itself is an optimum function of mean daily temperatures, \( T \).
This optimum function is defined by 4 cardinal temperatures, T1-T4, and the maximum vernalisation rate, $V_{\text{max}}$.

\[
\frac{dV}{dt} = \begin{cases} 
0 & T \leq T1 \\
V_{\text{max}} \frac{V_{\text{max}}}{T2 - T1} (T2 - T) & T1 < T < T2 \\
V_{\text{max}} \frac{V_{\text{max}}}{T3 - T2} (T3 - T2) & T2 \leq T \leq T3 \\
0 & T > T4 
\end{cases}
\]  

(2-8)

The 4 cardinal temperatures T1 to T4 are assumed to be 0°C, 10°C, 13°C and 28°C for the cultivar 'Fremont', for 'Linday' T4 is 23°C. The maximum vernalisation rate for the cultivars used was set to a value of 0.11 (d$^{-1}$) (Wiebe, 1998, pers. communic).

The vernalisation process is completed when the sum of the daily vernalisation rates has reached a value of one. The parameters of the vernalisation temperature are cultivar dependent (Wiebe 1997, personal communic.). However, it is possible to summarise the actual cultivars of cauliflower in different groups and to use a unique parameter set for this group (Wiebe 1997, personal communic.).

2.2.4. Dry matter production

Approaches to calculate the dry matter production rate of a plant stand range from quite detailed models upsampling from the leaf level (Spitters, 1990) to more comprehensive models on the crop scale (Amir and Sinclair, 1991; Jones and Kiniry, 1986) mostly based on the concept of light use efficiency, LUE, (Monteith, 1977). One of the main advantages of the comprehensive models is their more simple parameterisation. Since the focus of this study is on development and on dry matter partitioning aspects in cauliflower, we used at this step of analysis the simple LUE based approach for calculating net dry matter production rate of a cauliflower crop.

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

\[
\frac{dW}{dt} = Q \cdot \text{LUE}
\]  

(2-9)
The amount of absorbed photosynthetically active radiation is calculated from the intensity of radiation incident on the plant canopy, I, and the leaf area index LAI (Monsi and Saeki, 1953):

\[ Q = I \cdot (1 - e^{-kLAI}) \]  

(2-10)

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

### 2.2.5. Leaf-stem partitioning

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

The growth rate of total dry matter for the whole plant, \( \frac{dW_t}{dt} \), is the sum of the growth rate of the vegetative organs, \( \frac{dW_v}{dt} \), and the growth rate of the curd, \( \frac{dW_c}{dt} \):

\[ \frac{dW_t}{dt} = \frac{dW_v}{dt} + \frac{dW_c}{dt} \]  

(2-11)

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

\[ W_v = W_L + W_S \]  

(2-12)

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

\[ \frac{dW_v}{dt} = \frac{dW_L}{dt} + \frac{dW_S}{dt} \]  

(2-13)
If allometric growth of stem and leaf dry matter is assumed, which implies that the ratio of the relative growth rates of leaves and stem are constant (Thornley and Johnson, 1990), the relationship between the natural logarithms of leaf and stem dry matter is linear:

\[
\ln W_S = h + g \cdot \ln W_L
\]  \hspace{1cm} (2-14).

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

\[
W_s = e^h W_L^g
\]  \hspace{1cm} (2-15)

Differentiation of Eqn. 2-15 with respect to \(W_L\) yields:

\[
\frac{dW_s}{dW_L} = e^h g W_L^{g-1}
\]  \hspace{1cm} (2-16)

Applying the chain rule to the left hand side of Eqn. 2-16 and rearranging one gets:

\[
\frac{dW_s}{dt} = \frac{dW_S}{dW_L} \frac{dW_L}{dt}
\]  \hspace{1cm} (2-17)

Combining equations 2-16 and 2-17 and introducing the resulting relationship into equation 2-13 yields:

\[
\frac{dW_L}{dt} = \frac{dW_v}{dt} \frac{1}{1 + e^h g W_L^{g-1}}
\]  \hspace{1cm} (2-18)

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

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

\[
\text{LAI} = W_L \cdot \text{SLA}
\]  \hspace{1cm} (2-19)
The key parameters SLA and LUE are assumed to be constant over one growing period. However, we were not able to describe all experiments with the same values of SLA or LUE. We therefore fitted the values of SLA and LUE to the total dry matter data of every single experiment. This implies that the dry matter production part of the model is at this stage of development of purely descriptive nature.

### 2.2.6. Curd growth

The curd dry matter growth rate, \( \frac{dW_c}{dt} \), may be expressed as a fraction \( f \) of the total dry matter growth rate, \( \frac{dW_t}{dt} \):

\[
\frac{dW_c}{dt} = \frac{dW_t}{dt} \cdot f
\]

(2-20)

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

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

\[
f = \frac{f_0 \cdot f_1}{f_0 + (f_1 - f_0) \cdot e^{-r_f \cdot TS_3}}
\]

(2-21)

were \( TS_3 \) is the temperature sum the plants accumulated after the end of the vernalisation, i.e. in stage 3 of their growth period, \( f_0 \) is the fraction of curd dry matter increase to total dry matter increase when \( TS_3 = 0 \), \( f_1 \) is the maximum fraction of dry matter growth allocated to the curd and \( r_f \) is a growth rate parameter of \( f \).

The crop is assumed to be marketable when the curd has reached a diameter of 200 mm. An empirical regression equation derived from unpublished data was used to calculate the curd diameter \( CD \) (mm) from the curd weight \( W_c \) (g/pl.).
\[ \text{CD} = 33.82 \cdot W_c^{0.422} \]  \hspace{1cm} (2-22)

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

### 2.3. Material and Methods

#### 2.3.1. Field experiments

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

The parameterisation experiment set was a series of field experiments without replications using two different cauliflower cultivars, 'Fremont' and 'Linday'. In 1994 and 1995 three and five experiments were conducted, respectively. The last experiment in 1994 and the first and the last experiment in 1995 were discarded from further analysis, because of too big transplants which caused problems in plant establishment or severe plant damages due to bird attacks. The dates of planting for both groups of experiments used in the analysis are summarised in Table 2-1.

The second group of experiments is a part of a long-term field trial were effects of crop rotation, nitrogen fertilisation rate and soil tillage on nitrogen use efficiency on the cropping system level are studied. In this experiment only the cultivar 'Fremont' was used. This field trial has a three factorial split-plot design with three replications. For the analysis presented here, only data from plots with optimal nitrogen fertilisation and conventional, mould board plough tillage system were used. Both groups of field experiments were conducted on the same experimental farm located 15 km south of Hannover, Germany, on a typical loess derived hapludalf soil.

Seeds of cauliflower were germinated in planting plates filled with peat and transplanted by hand in peat cubes with 4 cm edge length after about 3-5 days. When the plants had about 2 to 4 visible leaves they were transplanted in the field. The average planting density was 4 plants/m². Before planting in the field prophylactic applications of chlorfenvinphos (Birlane™) against cabbage fly, and of molybdenum sulphate were applied to the peat cubes. Nitrogen was given as ammonium nitrate according to the
"Development and dry matter partitioning"

Table 2-1: Planting dates of the experiments which were used for model parameterisation and validation. Abbreviation ‘P’ in the column ‘usage’ stands for used for Parameterisation, ‘V’ used for Validation.

<table>
<thead>
<tr>
<th>Year</th>
<th>Experiment</th>
<th>Planting Date</th>
<th>Usage</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>1</td>
<td>May 5</td>
<td>P</td>
</tr>
<tr>
<td>1994</td>
<td>2</td>
<td>June 1</td>
<td>P</td>
</tr>
<tr>
<td>1995</td>
<td>2</td>
<td>May 2</td>
<td>P</td>
</tr>
<tr>
<td>1995</td>
<td>3</td>
<td>May 17</td>
<td>P</td>
</tr>
<tr>
<td>1995</td>
<td>4</td>
<td>June 13</td>
<td>P</td>
</tr>
<tr>
<td>1994</td>
<td>1</td>
<td>April 7</td>
<td>V</td>
</tr>
<tr>
<td>1994</td>
<td>2</td>
<td>July 26</td>
<td>V</td>
</tr>
<tr>
<td>1995</td>
<td>1</td>
<td>April 4</td>
<td>V</td>
</tr>
<tr>
<td>1995</td>
<td>2</td>
<td>July 19</td>
<td>V</td>
</tr>
<tr>
<td>1995</td>
<td>3</td>
<td>July 26</td>
<td>V</td>
</tr>
<tr>
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<td>1</td>
<td>April 9</td>
<td>V</td>
</tr>
<tr>
<td>1996</td>
<td>2</td>
<td>July 18</td>
<td>V</td>
</tr>
<tr>
<td>1996</td>
<td>3</td>
<td>July 24</td>
<td>V</td>
</tr>
</tbody>
</table>

\(N_{\text{min}}\)-fertilisation schedule (Scharpf and Wehrmann, 1975). For cauliflower this defines a target supply level of 300 kg N/ha including soil nitrate from 0 to 60 cm depth that has to be adjusted by fertilisation. Insecticides and irrigation were given whenever needed.

In the parameterisation experiments a number of 10 plants in 1994 and of 14 plants 1995 were harvested every two weeks and divided into leaves including petioles, stem and curd. In the validation experiment 6 plants per plot were analysed in 34 week sampling intervals. Leaf number was counted from a diameter > 1 cm considering bases of already aborted leaves. For determination of dry weight sub-samples of the plant organs were oven dried starting with a temperature of 60 °C and followed by a drying temperature of 105 °C until a constant weight was reached.
Crops were harvested when about 50% of the plants had reached a curd diameter of 200 mm.

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

**2.3.2. Parameter estimation**

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

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

**2.4. Results**

**2.4.1. Parameterisation**

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

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

The values obtained for the parameters \(k_1\) and \(k_2\) of the leaf development model are presented in Table 2-4. Despite some differences between the experiments, it was possible to describe all leaf number data with a single parameter set. From the initially exponential increase of leaf number follows that a small difference of 0.5 in number of leaves at transplanting resulted in a comparable high difference of visible leaves during the linear leaf development phase of 2 (Fig. 2-1).
In all parameterisation experiments a linear relationship between the logarithms of leaf and stem dry matter could be found (Table 2-5). Therefore, the assumption of an allometric growth of stem and leaves seems to be valid for the cauliflower crops analysed. Despite the fact that the slopes and the intercepts of this relationship were somewhat variable between the experiments, indicating an effect of the experimental
year, the fit to all data of the parameterisation experiments resulted in a coefficient of determination of 97% (Fig. 2-2).

The growth of the curd fraction was described well for all plants with a logistic function of the temperature sum since the end of the vernalisation period (Eqn. 2-21, Fig. 2-3). The curd starts to become an important sink about 400 °C·d after curd initiation and approaches its maximum fraction on total growth rate around 800 °C·d after curd initiation. However, there is considerable variation in the curd fraction about 400 to 800 °C·d after curd initiation (Fig. 2-3).

Table 2-3: Estimated values of light use efficiency (LUE) (g MJ⁻¹) (± SE) and specific leaf area (SLA) (cm²·g⁻¹) (± SE), the correlation between both parameters, C, the coefficient of determination of the dry matter production model, r², and the number of data points, n, of the cauliflower experiments used in the validation of the model.

<table>
<thead>
<tr>
<th>Year</th>
<th>Cultivar</th>
<th>Experiment</th>
<th>LUE</th>
<th>SLA</th>
<th>C</th>
<th>r²</th>
<th>n</th>
</tr>
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<tr>
<td>94</td>
<td>Fremont</td>
<td>1</td>
<td>2.79</td>
<td>146.4</td>
<td>-0.98</td>
<td>0.93</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(± 0.97)</td>
<td>(± 84.3)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>94</td>
<td>Fremont</td>
<td>2</td>
<td>4.57</td>
<td>117.3</td>
<td>-0.99</td>
<td>0.96</td>
<td>5</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>(± 1.59)</td>
<td>(± 55.8)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>95</td>
<td>Fremont</td>
<td>1</td>
<td>2.17</td>
<td>148.0</td>
<td>-0.99</td>
<td>1.00</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(± 0.04)</td>
<td>(± 4.4)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>95</td>
<td>Fremont</td>
<td>2</td>
<td>3.32</td>
<td>131.0</td>
<td>-0.99</td>
<td>1.00</td>
<td>3</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>(± 0.01)</td>
<td>(± 0.1)</td>
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</tr>
<tr>
<td>95</td>
<td>Fremont</td>
<td>3</td>
<td>1.98</td>
<td>339.6</td>
<td>-0.99</td>
<td>0.99</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(± 0.48)</td>
<td>(± 185.6)</td>
<td></td>
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</tr>
<tr>
<td>96</td>
<td>Fremont</td>
<td>1</td>
<td>3.82</td>
<td>91.0</td>
<td>-0.99</td>
<td>1.00</td>
<td>5</td>
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<td></td>
<td></td>
<td></td>
<td>(± 0.17)</td>
<td>(± 5.4)</td>
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</tr>
<tr>
<td>96</td>
<td>Fremont</td>
<td>2</td>
<td>4.40</td>
<td>110.2</td>
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<td>0.99</td>
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<td></td>
<td></td>
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<td>(± 0.17)</td>
<td>(± 6.1)</td>
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<tr>
<td>96</td>
<td>Fremont</td>
<td>3</td>
<td>5.03</td>
<td>87.5</td>
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<td>0.97</td>
<td>4</td>
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<td></td>
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<td>(± 2.00)</td>
<td>(± 43.4)</td>
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</tr>
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</table>
2.4.2. Validation

The overall model performance is demonstrated for an arbitrarily chosen validation experiment in Fig. 2-4. The measured increase of leaf number follows the model until the last leaf appears, which was initiated before the vernalisation process is completed (Fig. 2-4a). The dry matter production over time is properly interpolated by the model (Fig. 2-4b). At the end of the growing period the dry matter production rate of leaves decreases, the growth of stem dry matter almost stops and about all dry matter increase is attributed to curd growth. This results in a steadily decreasing fraction of leaf mass on total plant mass, a more or less constant fraction of stem mass and a steadily increasing proportion of curd mass on total plant mass (Fig. 2-4c).
Table 2-5: Slope (± SE), intercept (± SE), correlation coefficient, $r^2$, and number of observations, n, of the linear regression between the logarithms of leaf and stem dry weight for two different cultivars of Cauliflower in two experimental years.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Year</th>
<th>Slope</th>
<th>Intercept</th>
<th>$r^2$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fremont</td>
<td>1994</td>
<td>1.163 (±0.133)</td>
<td>-2.056 (±0.683)</td>
<td>0.92</td>
<td>9</td>
</tr>
<tr>
<td>Fremont</td>
<td>1995</td>
<td>0.878 (±0.025)</td>
<td>-0.986 (±0.111)</td>
<td>0.98</td>
<td>21</td>
</tr>
<tr>
<td>Lindsay</td>
<td>1994</td>
<td>1.129 (±0.094)</td>
<td>-1.461 (±0.487)</td>
<td>0.94</td>
<td>11</td>
</tr>
<tr>
<td>Lindsay</td>
<td>1995</td>
<td>0.920 (±0.020)</td>
<td>-0.910 (±0.096)</td>
<td>0.99</td>
<td>23</td>
</tr>
<tr>
<td>Both</td>
<td>Both</td>
<td>0.941 (±0.022)</td>
<td>-0.974 (±0.105)</td>
<td>0.97</td>
<td>64</td>
</tr>
</tbody>
</table>

The application of the model on the validation experiments resulted in a coefficient of determination of 0.73 between observed and predicted leaf number (Fig 2-5). It has to be noticed that in contrast to Fig. 2-1 where only leaf numbers before the end of vernalisation were shown in this case all measurements were included. Errors in estimating the vernalisation process are therefore also contributing to the scatter of the data.
Fig. 2-1 Number of leaves > 1 cm of two cauliflower cultivars as dependent on the temperature sum after transplanting into the field. First two digits in the legend designate the year (1994 or 1995) the next digit the cultivar (F = Fremont, L= Lindsay) and the last one the experiment. The two curves represent the predicted leaf number when assuming either a leaf number at transplanting of 3 (upper curve) or 3.57 (lower curve).

The comparison of the simulated and measured fractions of the individual organs on total dry matter shows for the parameterisation and the validation experiments that over all organs the model predicted the dry matter fractions quite well (Fig. 2-6). It must be noticed, however, that much of the variation in the dry matter fractions is between rather than within the different organ groups. The correlation between simulated and measured dry matter fractions calculated separately for the different organs, was poor especially for the stem fraction (Table 2-6). This may be due to only little variation of the stem fraction during the growing period. For the curd fraction, which shows a much higher variation, a much closer relationship could be found. The prediction of the model with respect to the dry matter fractions is of similar quality for the validation experiments as for the parameterisation experiments.
The measured length of the growing period ranged from 66 to 112 day from transplanting to maturity. About 69% percent of this variation could be described with the model (Fig. 2-7).

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

The measured length of the growing period ranged from 66 to 112 day from transplanting to maturity. About 69% percent of this variation could be described with the model (Fig. 2-7).
Fig. 2-3: Fraction of the curd growth on total growth of cauliflower as a function of the temperature sum since end of the vernalisation process and the results of the fit of a logistic growth equation to the data.

2.5. Discussion

The purpose of this paper is to present a model for development and vernalisation of cauliflower. Therefore, the dry matter production part of the model is at this stage purely descriptive and used simply as an interpolation tool. However, the parameters were chosen such that they were biologically meaningful. The values for SLA found by the fitting procedure are indeed with some exceptions in the range of measured values for cauliflower ranging from 300 cm\(^2\)g\(^{-1}\) to 40 cm\(^2\)g\(^{-1}\) in the report of Olesen and Grevsen (1997) and of 240 cm\(^2\)g\(^{-1}\) in Aikman and Scaife (1993). This is also true for the LUE where values of 2.8, 3.2, 4.1 and 4.4 (g/MJ) where reported for cauliflower by Wheeler et al. (1995), Olesen and Grevsen (1997), Aikman and Scaife (1993) and Olesen and Grevsen (1995), respectively. However, due to the strong correlation between both parameters and their high standard errors (Tables 2-2 and 2-3), the estimated values of LUE and SLA have to be interpreted very carefully.
Fig. 2-4: Simulated vs. measured parameters for an arbitrarily chosen cauliflower experiment from the validation group (year 1996, experiment 2). Light use efficiency and specific leaf area were fitted, all other parameter values are from independent estimations from the parameterisation data.

a) Simulated vs. measured number of leaves, b) simulated vs. measured total dry matter of plants and dry matter of leaves, stems and flowers, c) simulated vs. measured fraction of single organs on total dry matter.
Chapter 2

Fig. 2-5: Simulated vs. measured leaf numbers for the cauliflower crops (cv. ‘Fremont’) from the independent validation experiments.

Greven and Olesen (1994a) used an exponential model for leaf development, and found a value of about 0.003 (leaf/leaf$^1$.°C$^{-1}$.d$^{-1}$) for the specific leaf initiation rate. This results in a leaf initiation rate of about 0.06 (leaf°C$^{-1}$.d$^{-1}$) for leaf number 20 which is in good agreement with the value found for $k_2$ from Eqn. 2-3 (Table 2-5). A recalculation of data from Booij (1990b) resulted in values of $k_2$ of 0.084 (°C.d$^{-1}$) for his 22°C treatment and 0.0225 for his 14°C treatment, respectively.

With the data available from this study the accuracy of the vernalisation part of the model can be evaluated only indirectly. The indicator parameters we measured were the leaf number and the length of the growing period. The poor prediction of leaf number (Fig. 2-5) may be the result of insufficient prediction of the vernalisation rate. However, due to the high variability of the vernalisation rate of cauliflower (Booij, 1990b) in conjunction with the limited number of plants analysed, it is likely to have results of a high experimental error.
**Fig. 2-6:** Simulated versus measured dry matter fraction (organ mass / total plant mass) for the cauliflower crops cv. ‘Fremont’ and ‘Linday’ from the parameterisation experiments (left graph) and for cauliflower crops cv. Fremont from the validation experiments (right graph).

**Table 2-6:** Intercept (a) slope (b) and correlation coefficient ($r^2$) of the linear regression equation between simulated and measured dry matter fractions of different cauliflower organs in the parameterisation and the validation group of experiments.

<table>
<thead>
<tr>
<th>Experiment group</th>
<th>Organ</th>
<th>a</th>
<th>b</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameterisation</td>
<td>Leaves</td>
<td>-0.7579</td>
<td>2.0129</td>
<td>0.4984</td>
</tr>
<tr>
<td>Parameterisation</td>
<td>Stem</td>
<td>0.0394</td>
<td>0.7614</td>
<td>0.109</td>
</tr>
<tr>
<td>Parameterisation</td>
<td>Curd</td>
<td>-0.0022</td>
<td>1.6629</td>
<td>0.8774</td>
</tr>
<tr>
<td>Validation</td>
<td>Leaves</td>
<td>0.1206</td>
<td>0.9356</td>
<td>0.5448</td>
</tr>
<tr>
<td>Validation</td>
<td>Stem</td>
<td>0.0334</td>
<td>0.3942</td>
<td>0.0823</td>
</tr>
<tr>
<td>Validation</td>
<td>Curd</td>
<td>0.0044</td>
<td>0.8707</td>
<td>0.7668</td>
</tr>
</tbody>
</table>
The simple allometric approach of leaf/stem partitioning in combination with an empirical temperature sum based approach for relative curd growth was able to describe the data from the parameterisation experiments (Table 2-6 and Fig. 2-2) and to predict the dry matter partitioning pattern of cauliflower under optimal nutrient and water supply adequately (Fig 2-6). The poor prediction of stem fraction (Table 2-7), is not critical, since there is only a small variation in the stem fraction during the growth period of cauliflower and the absolute value of this fraction is small.

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

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

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

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

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

The model presented was able to predict leaf number, the fraction of the dry matter of single organs to total dry matter and the length of the growing season of independent experiments sufficiently well when dry matter production was calculated based on LUE and SLA values fitted for each experiment. The functional relationships for the reaction of these parameters on changing environmental conditions have to be evaluated.
Chapter 3

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

I. Photosynthetic parameters of cauliflower leaves and their implications for calculations of dry matter production

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Abstract

Measurements of CO$_2$-exchange of cauliflower leaves were carried out in a field experiment which included two nitrogen fertilisation rates. Irradiance and CO$_2$ concentration were varied at the leaf level within a leaf cuvette and additionally a temperature treatment was applied to field grown plants moved into climate chambers. These measurements were used to estimate parameter values of a rectangular hyperbola describing cauliflower leaf CO$_2$ exchange as a function irradiance and CO$_2$ concentration. The obtained parameter estimates were used to derive empirical regression equations with temperature and nitrogen content of the leaves as independent variables. The resulting relationships were applied within a simple photosynthesis-respiration based dry matter production model in order to derive functional relationships between light use efficiency and irradiance, leaf area index and temperature.

The rectangular hyperbola was able to describe the gas exchange data as varied by irradiance and CO$_2$ concentration on the single leaf level with sufficient accuracy, but estimates of initial light use efficiency (about 25 µg J$^{-1}$) were too high because of the bias emanating from the limited flexibility of this model. Light saturated photosynthesis rate ($P_{max}$) showed an optimum response to temperature and an increase with increasing nitrogen content of leaves. The initial slope $\alpha$ of the rectangular hyperbola showed no consistent responses to ambient temperature and nitrogen content of leaves. The respiration per unit leaf area $\beta$ increased exponential with increasing temperature, resulting in a $Q_{10}$ value of 1.86. Because only a limited number of plants evaluated in this study, additionally work is needed to further substantiate the results of the gas exchange measurements.

The model analysis demonstrated that LUE is only independent on the light integral over a range of 5 to 10 MJ · m$^{-2}$ · d$^{-1}$ photosynthetically active radiation if one assumes an adaptation of $P_{max}$ within the canopy and over time according to the incident irradiance. Acclimatisation within the canopy and higher leaf area indices, LAI, reduce the decrease of LUE with irradiance but a substantial decline remains even for LAI values of 4.
3.1. Introduction

Two main approaches to calculate dry matter production are used in crop growth models: one describes photosynthesis and respiration either scaling up from the single leaf level to the canopy level (Spitters et al., 1989) or using the big leaf approach (de Pury, 1997). The other more empirically founded approach calculates dry matter production simply as the product of intercepted radiation and empirically derived values of light use efficiency, LUE (Monteith, 1977, Gallagher and Biscoe, 1978, Jones and Kiniry, 1986, Williams et al., 1989). Whereas the first approach is regarded to be more physiologically founded, parameterisation from field experiments is difficult, since key parameters like the light saturated photosynthesis rate of single leaves, $P_{\text{max}}$, underlie complex environmental influences (Berry and Björkman, 1980). The second approach is more easily parameterised, but environmental conditions may modify light use efficiency values, limiting its usefulness (see Spitters, 1990, Boote et al., 1996 and Marcelis, 1998 for further discussion). Variations of LUE may occur even for the same crop species grown at the same location if weather conditions vary substantially between the cropping periods. This is especially likely for crops with a relatively short growing period, like cauliflower, which may be cultivated within one year during quite contrasting radiation and temperature regimes. Estimates for LUE may therefore vary for cauliflower crops grown under different radiation regimes (chapter 2).

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

The aim of this study is to examine the influence of the factors irradiance, CO$_2$, temperature and nitrogen on the efficiency of light utilisation of cauliflower crops. This
paper therefore presents parameter estimations describing cauliflower leaf CO$_2$
exchange as influenced by these environmental parameters. A simple photosynthesis-
respiration based canopy dry matter production model is used to derive the functional
dependencies of LUE on temperature, irradiance and LAI.

In a forthcoming study (chapter 4) both model approaches will be tested against data
from field experiments using a previously published model module (Chapter 2)
describing development and dry matter partitioning in cauliflower.

3.2. Material and Methods

3.2.1. Field experiment

Cauliflower plants on which the photosynthesis measurements were taken originated
from a field experiment carried out in 1995 on a humic loamy sand in Hannover,
Germany. The experiment had two nitrogen treatments, i.e. 100 and 50% of
recommended fertilisation level. Nitrogen was given as ammonium nitrate according to
the $N_{\text{min}}$-fertilisation schedule (Scharpf and Wehrmann, 1975). For cauliflower this
defines a target supply level of 270 kg N/ha (135 kg N/ha for the 50% treatment) 6
weeks after planting including soil nitrate from 0 to 60 cm depth. At planting $N_{\text{min}}$ was
adjusted to 130 kg NO$_3$-N/ha from 0-30 cm (65 kg N/ha for the 50% treatment). It was
laid out as a randomised block design with 4 replications. The plot size was 86 m.
Seeds of cauliflower cv. Fremont were germinated in planting plates filled with peat and
transplanted by hand into peat cubes with 4 cm edge length after about 3-5 days. When
the plants had about 2 to 4 visible leaves they were transplanted in the field. The
planting density was 4 plants/m$^2$. Before planting in the field prophylactic applications of
chlorfenvinphos (Birlane™) against cabbage fly, and of molybdenum sulphate were
applied to the peat cubes. Within each plot of this experiment 6 perforated buckets of 10
l volume containing field soil were buried. In each of these buckets one cauliflower plant
was planted. The buckets containing the plants were taken out of the soil into growth
chambers for temperature treatments. On June 2, 8 weeks after planting, the potted
plants of the fully fertilised treatment received an additional amount of 4 g N per plant
because they showed slight symptoms of N deficiency, probably because of their limited
root volume. The temperature and daily radiation integral during the experiment are
shown in Fig. 3-1.
3.2.2. CO₂ exchange measurements

The CO₂ exchange measurements were carried out using a CIRAS-1 combined infrared gas analysis system combined with a Parkinson leaf cuvette (PP-Systems, Hitchin Herts, UK) measuring the gas exchange of 2.5 cm² leaf area. The cuvette was supplied with an artificial illumination unit using a halogen lamp as a light source, providing a maximum irradiance of about 420 W PAR m⁻². The irradiance levels were adjusted using light diffusers and wire meshes of different transmission in the steps 0.0, 39.6, 52.7, 68.1, 107.7, 164.8, 228.6 and 417.6 W PAR m⁻². CO₂ concentrations were varied from 145 to 706 mg m⁻³. All photosynthetic measurements were carried out within the uppermost third on the youngest fully expanded leaf. The incubation time for one measurement was around 1-3 minutes. Irradiance and CO₂ concentration were varied from low to high values. Measurements in the field (May 18, June 2) were performed between 11am to 2pm. The more time consuming measurements on June 19 and June
Chapter 3

20 started at 9 am and were finished at 3 pm. A summary of the measurement dates is presented in Table 3-1.

Table 3-1. Measurement dates, parameter variation and location of measurement of gas exchange measurements on cauliflower plants.

<table>
<thead>
<tr>
<th>Date</th>
<th>No. of plants</th>
<th>Parameter variation</th>
<th>Location of measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 18</td>
<td>1</td>
<td>Light, CO₂</td>
<td>Field</td>
</tr>
<tr>
<td>June 2</td>
<td>1</td>
<td>Light, CO₂</td>
<td>Field</td>
</tr>
<tr>
<td>June 19</td>
<td>1</td>
<td>Light, CO₂, temperature</td>
<td>Growth chamber</td>
</tr>
<tr>
<td>June 20</td>
<td>6</td>
<td>Nitrogen content of leaves, light, temperature</td>
<td>Growth chamber</td>
</tr>
</tbody>
</table>

On June 19, 4 plants from the ‘low’ and another 4 from the ‘high’ fertilisation plots, were taken out of the field into the climate chamber. Before the measurements of CO₂ exchange the plants were treated with temperatures of 8, 12, 16, 20, 26 and 30 °C. The time for acclimatisation to the new temperatures levels was at least 20 minutes. Afterwards 2 plants from the ‘high’ fertilisation plots showed obviously a reduced turgor. These plants were discarded from the measurements. The CO₂ concentration during all this evaluations was 350 (±10) mg m⁻³. The nitrogen content of the leaves from the low N treatment were 1.21, 1.52, 1.72 and 2.1, from the high N treatment 3.83 and 4.79 % N in DM, respectively.

3.2.3. Model calculations

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

$$P_n = \frac{\alpha I \tau C}{\alpha I + \tau C} - \beta$$  (3-1)
Implications of photosynthesis parameters

with the parameters initial light use efficiency $\alpha$ ($\mu$gJ$^{-1}$), leaf conductance to CO$_2$ transfer $\tau$ (m$^2$s$^{-1}$) and leaf dark respiration rate $\beta$ ($\mu$g CO$_2$ m$^{-2}$ s$^{-1}$). For a constant CO$_2$ concentration it is convenient to define the lumped parameter $P_{\text{max}}$ ($\mu$g CO$_2$ m$^{-2}$ s$^{-1}$), which is the product of $\tau$ and C.

One of the nice characteristics of Eqn. 3-1 is that it is possible to integrate it analytically over the whole canopy if one assumes an exponential decline of irradiance and a constant value of $\tau$ within the canopy. Aggregating the effects of radiation reflection and transmission within the canopy into the light extinction coefficient $k$ and using $P_{\text{max}}$ for the product of $\tau$ and C the equation for the whole canopy net photosynthesis, $P_c$ ($\mu$g m$^{-2}$s$^{-1}$), becomes (Thornley and Johnson, 1990):

$$P_c = \frac{P_{\text{max}}}{k} \ln \left( \frac{\alpha k I_0 + P_{\text{max}}}{\alpha k e^{-kLAI} + P_{\text{max}}} \right) - \beta LAI$$  \hspace{1cm} (3-2)

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

Since irradiance usually declines within the canopy and because the photosynthetic capacity adapts to the light environment the assumption of a constant $P_{\text{max}}$ is probably not correct for higher values of LAI (Hirose and Werger, 1987). A computational simple method to investigate possible effects of a declining $P_{\text{max}}$ on the productivity of the canopy is available if one assumes a decline of $P_{\text{max}}$ proportionally to the decline in $I$ within the canopy:

$$P_{\text{max}} = P_{\text{max0}} e^{-kLAI}$$  \hspace{1cm} (3-3)
The solution for whole canopy net photosynthesis then becomes (Charles-Edwards, 1982):

\[
P_c = \frac{\alpha l_0 P_{\text{max}}}{\alpha k l_0 + P_{\text{max}}} \left( 1 - e^{-k \text{LAI}} \right) - \beta \text{LAI}
\]  

(3-4)

In order to calculate daily canopy assimilation from equations 2 or 4 they have to be integrated over the day accounting for the changing light environment. This can efficiently be done using the 3 point Gauss integration method (Goudriaan, 1986) thereby assuming a sinusoidal function of irradiance during the daytime.

Calculation of CO\textsubscript{2} losses through respiration is still one of the weak points of crop simulation models. The most widely used set of assumptions are implemented in the SUCROS model (Spitters et al., 1989) based on the work of McCree (1970) and Penning de Vries (1975). This concept distinguishes between maintenance and growth respiration, the former being proportional to the mass of the crop organs and the latter being a function of the growth rate of the organs. Because the term \( \beta \text{LAI} \) of equations 3 and 4 does not take into account these facts, we didn’t use this approach for the respiration calculations in our model analysis. Instead, maintenance respiration, \( R_{\text{m}} \), of an organ \( i \) was calculated as the daylength \( D_L \) corrected values of night and day respiration from the organ mass \( W_i \) and the maintenance coefficient \( MC_i \):

\[
R_{\text{m}} = MC_i W_i \left( \text{Teff}_{\text{day}} \frac{D_L}{24} + \text{Teff}_{\text{night}} \left( 1 - \frac{D_L}{24} \right) \right)
\]  

(3-5)

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

\[
\text{Teff} = Q_{10} \cdot \frac{T - T_{\text{ref}}}{10}
\]  

(3-6)

The weight of the leaves may be calculated for a given leaf area index \( \text{LAI} \) from the specific leaf area, \( \text{SLA} \) (\( \text{cm}^2 \cdot \text{g}^{-1} \)). For cauliflower a constant value for \( \text{SLA} \) of 120 (\( \text{cm}^2 \cdot \text{g}^{-1} \) DM) was used as an approximation.
Stem weight was derived from the leaf mass using the allometric relationship between stem and leaf mass (chapter 2). Root mass was assumed to be 10% of the sum of leaf and stem mass (chapter 7). For growth respiration the crude assumption of a conversion efficiency of 0.7 from assimilates to dry matter was used (Goudriaan and van Laar, 1994). The dry matter produced per day of the crop is calculated from the numerical integral of gross photosynthesis as calculated from Eqn. 3-2 or 4 without dark respiration term minus the sum of the maintenance respiration of the different plant organs. From this amount of available net assimilates dry matter production is calculated using the conversion efficiency. Canopy light use efficiency, LUE, (g DMMJ PAR\(^{-1}\)) may then be calculated as the ratio of net dry matter produced per day \(\frac{dW_t}{dt}\) (g DM m\(^{-2}\) d\(^{-1}\)) and the amount of intercepted PAR (MJ PAR m\(^{-2}\) d\(^{-1}\)):

\[
LUE = \frac{\frac{dW_t}{dt}}{I(1 - e^{-kLAI})}
\]  

3.2.4. Statistical analysis

Statistical analysis of the data was performed using the procedures REG and NLIN of the SAS software package (SAS Institute, 1988). For a multiple regression analysis of the influence of temperature, T, and nitrogen content, NC on \(P_{max}\) and \(\alpha\) the following equation was suggested: 

\[
P_{max}, \alpha = a + b\cdot NC + c\cdot T + d\cdot T^2 + e\cdot NC^2 + f\cdot NC\cdot T.
\]

Non significant regressors were eliminated using the backward option of ‘PROC REG’ with a critical significance level of 0.10.

3.3. Results

The rectangular hyperbola accurately describes the CO\(_2\) exchange of single cauliflower leaves if fitted separately to the data from the first two different sampling dates (Table 3-2 and Fig. 3-2). The parameter estimates for \(\alpha\), \(\tau\) and \(\beta\), however, differ between both dates, being generally higher for June 2 (Table 3-2). The parameter values estimated on the third measurement date are comparable to the first measurement date regarding the parameter \(\alpha\) but are higher for \(\tau\) and \(\beta\). The level of \(\alpha\) and \(\tau\) was on this third measurement date lower than on the second, even if compared at the 17.2 °C temperature level. A regression analysis using the parameter estimates from the third measurement date showed only significant effects of temperature on parameter values.
using an exponential equation ($\beta=109.95\cdot\text{exp}(0.043\cdot T)$, $p=0.0006$) fitted on the values of parameter $\beta$. Fits of quadratic equations ($\alpha$, $\tau=a+b\cdot T+c\cdot T^2$) to $\alpha$ and $\tau$ were not significant ($p=0.1324$ and $0.0759$). There is an indication ($p=0.06$) for a positive relationship between the estimates of $\alpha$ and $\tau$ for all measurement dates (Table 3-2, Table 3-3).

Using the parameter estimates obtained for $\alpha$, $\beta$ and $P_{\text{max}}$ for the plants transferred into the climate chambers on June 20 resulted in significant regressors for a multiple linear regression on temperature, square of temperature and nitrogen content (Table 3-4) in the case of the parameter $P_{\text{max}}$. For the parameter $\alpha$, however, no significant relationship could be found (data not shown). The parameter $\beta$ was fitted to an equation assuming exponential impact of temperature and a linear impact of nitrogen content on leaf respiration rates (Table 3-4). The value of 0.62 for the exponential temperature coefficient represents a $Q_{10}$ value of 1.86.

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

The response function of LUE to daily radiation sum has for both canopy production models the shape of an asymmetric optimum function, becoming positive at around 1 MJ·m⁻²·d⁻¹ (Fig 3a). Values of LUE are generally higher for the model assuming a constant \( P_{\text{max}} \) than for the light adapting \( P_{\text{max}} \). After reaching the maximum of LUE at around 2-3 MJ·m⁻²·d⁻¹, the decrease of LUE with increasing daily radiation sum is in absolute figures more severe for the model assuming a constant \( P_{\text{max}} \) within the canopy but relative changes of LUE are higher for the light adapting \( P_{\text{max}} \) model. Higher LAI values (Fig. 3-3b) retarded the decline of LUE with increasing daily radiation sum for the model assuming a constant \( P_{\text{max}} \) (Fig. 3-3b).
Table 3-3. Effect of ambient air temperature on parameters of the rectangular hyperbola describing CO$_2$ exchange rates of cauliflower leaves. The values were determined on the June 19 on a single leaf from a cauliflower plant grown in a buried pot within a field plot which was moved for the measurements into a climate chamber. The parameter $P_{\text{max}}$ was calculated from $\tau$ assuming a CO$_2$ concentration of 350 mg m$^{-3}$.

<table>
<thead>
<tr>
<th>Ambient Temperature ($^\circ$C)</th>
<th>$\alpha$ (µg J$^{-1}$)</th>
<th>$\tau$ ($10^3$ m s$^{-1}$)</th>
<th>$\beta$ (µg m$^{-2}$ s$^{-1}$)</th>
<th>$P_{\text{max}}$ (µg m$^{-2}$ s$^{-1}$)</th>
<th>$r^2$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.41</td>
<td>15.6 (±1.5)</td>
<td>2.71 (±0.13)</td>
<td>168.5 (±16.5)</td>
<td>949</td>
<td>0.988*</td>
<td>27</td>
</tr>
<tr>
<td>12.5</td>
<td>24.0 (±1.2)</td>
<td>3.42 (±0.07)</td>
<td>244.5 (±10.8)</td>
<td>1198</td>
<td>0.997*</td>
<td>27</td>
</tr>
<tr>
<td>17.2</td>
<td>27.0 (±1.6)</td>
<td>3.83 (±0.10)</td>
<td>276.3 (±14.4)</td>
<td>1342</td>
<td>0.996*</td>
<td>27</td>
</tr>
<tr>
<td>22.8</td>
<td>22.1 (±1.2)</td>
<td>3.76 (±0.10)</td>
<td>375.5 (±12.5)</td>
<td>1317</td>
<td>0.996*</td>
<td>27</td>
</tr>
<tr>
<td>27.9</td>
<td>20.8 (±1.2)</td>
<td>2.60 (±0.06)</td>
<td>443.1 (±9.3)</td>
<td>909</td>
<td>0.995*</td>
<td>27</td>
</tr>
</tbody>
</table>

The assumption of a constant $P_{\text{max}}$ over such a wide range of daily radiation sum's is at least over longer time periods not realistic (Björkman, 1981, Pons and Pearcy, 1994). If we assume, that the $P_{\text{max}}$ and $P_{\text{max}0}$ values increases linearly with the daily radiation sum, the resulting LUE- daily radiation sum functions now nearly became saturating functions with only minor response of LUE to daily radiation sum above 2 MJ m$^{-2}$ d$^{-1}$ for both photosynthesis models (Fig. 3-3c). However, the overall level of LUE was lower assuming a $P_{\text{max}}$ varying with the daily radiation sum.
Table 3-4. Results from a multiple linear regression of the parameter $P_{\text{max}}$ ($\mu g \, m^{-2} \, s^{-1}$) and $\alpha$ ($\mu g \, J^{-1}$) from the rectangular hyperbola describing the CO$_2$ exchange rate of cauliflower leaves as a function of the ambient air temperature, $T$, ($^\circ$C) and the leaf nitrogen content, NC, (% DM) and results from a non-linear regression relating leaf respiration rates, $\beta$, of cauliflower with temperature and nitrogen content, NC. Regression equations: $P_{\text{max}} = a + b \text{NC} + cT + dT^2$, $\beta = a \cdot \exp(b \cdot T_{\text{dif}}) + c \text{NC}$, $T_{\text{dif}} = (T-T_{\text{ref}})/10$, $T_{\text{ref}} = 20^\circ$C.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>a</th>
<th>b</th>
<th>c</th>
<th>d</th>
<th>$r^2$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_{\text{max}}$</td>
<td>-935.7 (±249.9)</td>
<td>152.8 (±25.1)</td>
<td>140.3 (±27.9)</td>
<td>-3.6 (±0.7)</td>
<td>0.769*</td>
<td>22</td>
</tr>
<tr>
<td>$\beta$</td>
<td>202.7 (±18.2)</td>
<td>0.62 (±0.07)</td>
<td>4.02 (±5.69)</td>
<td></td>
<td>0.883*</td>
<td>22</td>
</tr>
</tbody>
</table>

The leaf area index influences the calculated light use efficiency of both models in different ways. If $P_{\text{max}}$ is assumed to be constant within the canopy, the LUE increases with increasing leaf area index. This is due to higher portions of the canopy operating at lower irradiance where the slope of the photosynthesis/light curve is higher (Fig. 3-4). Assuming a $P_{\text{max}}$ declining proportionally with irradiance within the canopy, however, the LUE of the canopy decreases with increasing LAI. This is because the average $P_{\text{max}}$ value of the canopy also decreases with increasing LAI. At low values of LAI both models predict the same LUE. Using the estimated temperature response of $P_{\text{max}}$ and $\beta$ it can be deduced that LUE has an optimum response to temperature (Fig. 3-5), being between 15 and 25°C always higher than 95% of it’s maximum value, which is reached at around 18°C.
Fig. 3-3. Light use efficiency as a function of daily radiation sum calculated from a simple photosynthesis / respiration model. Assumed conditions: Latitude 52° N, day of year 240, 4.5 (% DM) nitrogen content, day temp. 22°C, night temp. 14°C, \( P_{\text{max}} = 1096 \, \mu g \, m^{-2} \, s \), leaf area index 2.5, initial slope \( \alpha \) 25 \( \mu g \, J \, PAR^{1} \).

a) Effect of constant \( P_{\text{max}} \) over the entire canopy (Eqn. 3-2) or a \( P_{\text{max}} \) varying within the canopy proportional to irradiance (Eqn. 3-4). b) Effect of the leaf area index, assuming \( P_{\text{max}} = \text{const} \). c) \( P_{\text{max}} \) and \( P_{\text{max0}} \) assumed to be a function of irradiance (\( P_{\text{max0}} = 400 + 50 \, PAR \)).
Implications of photosynthesis parameters

Fig. 3-4. Light use efficiency as a function of leaf area index (LAI) calculated with two different photosynthesis models assuming either a $P_{\text{max}}$ constant within the canopy or decreasing proportionally with irradiance within the canopy. Assumed conditions: Latitude 52° N, day 240 of year, day temp. 22°C, night temp. 14°C, ($P_{\text{max}} = 1096 \, \mu g \, m^{-2} \, s$), initial slope $a = 25 \, \mu g \, J \, PAR^{-1}$, daily radiation 8.45 MJ PAR m$^{-2}$.

3.4. Discussion

The aim of this study was to examine the influence of the factors daily radiation sum, CO$_2$, temperature and nitrogen on the efficiency of light utilisation by cauliflower crops. Since the temperature during the growing period does not usually deviate substantially from the optimum for net photosynthesis, field grown cauliflower plants were transferred into climate chambers with controlled temperature in order to get higher variation for the photosynthesis parameters. One of the shortcomings of this method was the disturbance of the root system which resulted in the exclusion of 2 out of 8 transferred plants.
Chapter 3

Fig. 3-5: Relative light use efficiency, LUE, as a function of daily mean temperature (°C) for two values of the leaf area index calculated using a model assuming a constant $P_{\text{max}}$ within the canopy. Regression equations are $y = -0.1630 + 0.1303x - 0.0036x^2$ for LAI = 1 and $y = -0.0512 + 0.1237x - 0.0036x^2$ for LAI = 5.

The parameters of the photosynthesis functions of cauliflower leaves were generally similarly to those of other C$_3$ species (Berry and Björkman, 1980, Kirschbaum and Farquhar, 1984, Jensen et al., 1996). Values for $\tau$ or $P_{\text{max}}$ found here are in the upper range of the values reported in literature for C$_3$ species (Acock et al., 1978, Evans, 1989, Pachepsky and Acock, 1996). Also, the values for the initial light use efficiency, $\alpha$, we obtained are quite high. It has, however, to be considered, that the parameter values of $\alpha$ obtained by fitting the rectangular hyperbola are generally higher than estimates for the non-rectangular hyperbola (Pachepsky and Acock, 1996). A comparison of both models for an example data set of single leaf assimilation (data not shown) gave values for $\alpha$ of 31.27 (±8.65) using the rectangular hyperbola ($r^2$=0.98) but 14.21 (±2.38), $r^2$ = 0.99 using the non-rectangular hyperbola. For the latter model the curvature factor $\theta$ (Thornley and Johnson, 1990) was estimated to be 0.92 (±0.07). The high values and the scatter we found for the parameter $\alpha$ was therefore probably caused by the limited
Implications of photosynthesis parameters

flexibility of the rectangular hyperbola rather than from a true variation of initial slope of the light response curve, which is generally assumed to be a quite conservative characteristic within the C3 group of plants (Ehleringer and Björkman, 1977, Long et al., 1993). Because of this shortcoming the non rectangular hyperbola is now often used to describe single leaf CO$_2$ exchange (Boote and Loomis, 1991, Cannell and Thornley, 1998). However, despite the biased estimates of the parameter $\alpha$ the descriptive power of the rectangular hyperbola was still sufficient for fitting the data from CO$_2$ exchange measurements (Fig. 3-2). This is in accordance with results of Pachepsky et al. (1996), who also concluded in a systematic comparison of photosynthetic models that this quite simple equation is adequate for predictive calculations of dry matter production.

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

The assumption of randomly distributed canopy elements which is underlying our approach for light interception (Eqn. 3-2) is clearly an oversimplification during the early growth stage of cauliflower crops with planting densities of about 4 plants m$^{-2}$ (Röhrig et. al. 2000). We also did not include in our model the effect upon assimilation of variable fractions of direct and diffuse radiation, which can influence LUE values (Bange et al., 1997; Hammer and Wright, 1994; Healey et al., 1998; Sinclair and Shiraiwa, 1993; Sinclair et al., 1992). Also, the assumptions about the distributions of $P_{\text{max}}$ within the canopy we used are extreme, but they may mark the maximum possible impacts of adaptation of $P_{\text{max}}$ within the canopy. Furthermore, different $P_{\text{max}}$ distributions within the canopy may influence the maintenance respiration rate of the canopy if also the total amount of photosynthetic nitrogen is altered. The decline of nitrogen content within the canopy is usually less than of irradiance (Hirose and Werger, 1987), which is in contrast to the assumption of Eqn. 3-4. Sometimes a linear instead of an exponential decline of nitrogen content within the canopy is found (Shiraiwa and Sinclair, 1993).

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

The adaptation of $P_{\text{max}}$ within the canopy alone is not likely to result in a constant value of LUE over a wider range of daily radiation sum (Fig. 3-3a). But in combination with an adaptation of $P_{\text{max}}$ to changing average irradiance over time a conservative behaviour of
LUE seems to be possible. The function we used to mimic this adaptation is somewhat speculative, but it seems to be in good accordance with the outcome of model based studies which optimised \( P_{\text{max0}} \) values (Johnson et al., 1995). The conclusions we derived from this calculation are in accordance with the model based studies of Dewar (1996), Dewar et al. (1998) and Haxeltine and Prentice (1996) which derived constant LUE - daily radiation sum relationships from an optimisation of nitrogen content of leaf layers within the canopy and within time.

The absolute LUE estimates obtained within the range of 5 to 10 MJ \( \text{PARm}^{-2}\text{d}^{-1} \) are somewhat higher than values reported in the literature (Wheeler et al., 1995, Olesen and Grevsen, 1997, chapter 3) for the model assuming a constant \( P_{\text{max}} \) but lower for the model assuming an exponential decline of \( P_{\text{max}} \) within the canopy. This may also be regarded as an indication that the truth may lie in between our extreme assumptions about the behaviour of \( P_{\text{max}} \) within the canopy.

The different influence of LAI on LUE predicted by both models (Fig. 3-5) should have significant influence on the calculated net dry matter production rate over time. This may be used to evaluate the validity of both assumptions by analysing predicted vs. measured time series of dry matter production.

### 3.5 Conclusions

The model analysis of this study is simplifying and also the number of plants investigated is limited, but despite these shortcomings the presented result gives some insight about the consequences of parameter values on the level of single leaf photosynthesis and respiration, measured or assumed, on the aggregated level of crop dry matter production rate.

Regarding the key question of this paper, the relationship between dry matter production and the amount of intercepted radiation, one has to notice that the conclusions from this study remains ambiguous. Depending on the assumptions one makes about the acclimatisation of the photosynthetic parameters (\( P_{\text{max}} \)) a severe decline of LUE with increasing daily radiation sum or a quite stable value of LUE within the range of PAR values usually found under growing period conditions of mid latitudes is found. A linear relationship between dry matter production rate and intercepted PAR, as assumed in many crop growth models, however, seems to be possible only for
Implications of photosynthesis parameters

canopies with an adaptation of the maximum photosynthetic capacity $P_{\text{max}}$ to a changing radiation environment over time. If this adaptation is missing or incomplete, a substantial decline of LUE with increasing daily radiation sum should be expected.
4. Predicting dry matter production of cauliflower (*Brassica oleracea* L. *botrytis*) under unstressed conditions
   II. Comparison of light use efficiency and photosynthesis-respiration based modules

Abstract 60

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Abstract

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

The results indicate that an estimated constant LUE (3.15 (±0.04) gMJ$^{-1}$) is only poorly able to predict total dry matter production for cauliflower (modelling efficiency EF = 0.69) of an independent data set. Using a linear decline of LUE with I (LUE = 6.66 (±0.80) - 0.36 (±0.08) I) drastically increased the predictive value (EF = 0.88) of the LUE approach. The descriptive and predictive value of the photosynthesis based modules was higher when assuming that $P_{\text{max}}$ declines within the canopy. Then the predictive value of the photosynthesis-respiration based approach was better than the simple LUE approach but not generally better than the LUE approach assuming a linear decrease of LUE with increasing daily radiation sum.
4.1. Introduction

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

If such detailed knowledge is not available, one can make assumptions about the behaviour of $P_{\text{max}}$ within the canopy, adjust the model to data measured at the crop level, i.e. total plant dry matter, and compare the consequences of the different hypotheses on the descriptive and predictive ability of the resulting models. Since the calculation of radiation interception is a prerequisite for calculations of total dry matter production, either photosynthesis-respiration or LUE based, the question of the needed level of detail for sufficient predictions of dry matter production is therefore closely coupled with the required level of detail of the light interception module within a crop growth model. The most simple but still often used approach for closed crop canopies is the one proposed by Monsi and Saeki (1953). However, more detailed approaches
have been developed since then (de Wit, 1965; Goudriaan, 1977; Spitters, 1986; Spitters et al., 1986), separating diffuse and direct radiation components and considering the effects of latitude and season on the radiation geometry. We therefore included also modules calculating radiation interception of crop canopies at a different level of detail within our analysis.

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

4.2. Material and methods

4.2.1. Field experiments

The field experiments used in this study are mainly the same as previously described by (chapter 2). Therefore, only a brief description will be given here. In addition to the data set described in chapter 2 data from two nitrogen fertilisation trials from 1996 and 1997 on the same experimental fields are included. From this experiments only the optimum and super optimum nitrogen supply rates 300 and 450 kg N/ha were used.

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

Temperature and radiation data were taken from measurements of an automated weather station (Campbell Sci. Ltd., UK) located on the experimental station. Measured values of global radiation were converted to photosynthetic active radiation, I, using a
factor of 0.5 (Szeicz, 1974). Weekly average values of I and air temperature at 2 m height for the four experimental years are shown in Fig. 4-1.

4.2.2. Modules

The modules used in this study for calculating development and partitioning are essentially the same as those described in chapter 2. The development module distinguishes a juvenile, a vernalization and a generative phase in the development of
cauliflower (Wiebe, 1972a; Wiebe, 1972b; Wiebe, 1972c). The dry matter partitioning part includes an allometric approach to dry matter partitioning between leaf and stem and an empirical logistic function describing the fraction of dry matter allocated to the curd depending on the temperature sum after the end of the vernalisation process. However, a slight re-parametrisation of the partitioning module was carried out in order to obtain the best possible description of development and partitioning. For this purpose the group of experiments was used from which also the parameters of the dry matter production modules were estimated.

For dry matter production six different modules were calibrated and evaluated against the data set. We used two modules based on the light use efficiency approach and four based on a photosynthesis-respiration approach (Table 4-1).

The amount of absorbed photosynthetically active radiation (PAR), \( Q \), \((\text{MJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1})\) is calculated from the daily sum of photosynthetically active radiation recorded above the canopy, \( I \), \((\text{MJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1})\) and the leaf area index LAI (Monsi and Saeki, 1953):

\[
Q = I \cdot (1 - e^{-kLAI})
\]  

(4-1)

were \( k \) is the extinction coefficient for \( I \) (-), taken as 0.65. The growth rate of shoot dry matter of the crop \((g \text{ DM} \cdot \text{m}^{-2} \cdot \text{d}^{-1})\) may be calculated as the product of \( Q \), LUE and a temperature correction factor \( f_{\text{Temp}} \) (-):

\[
\frac{dW}{dt} = Q \cdot \text{LUE} \cdot f_{\text{Temp}}
\]  

(4-2)

The value of \( f_{\text{Temp}} \) is one within a range from 10 to 25 °C average daily air temperature and is linearly decreasing to 0 from 10 down to 0 °C and from 25 to 35 °C. The model module LUE I assumes LUE to be constant, therefore being a parameter within the model.

In this study we examined, however, also the hypothesis that LUE is a function of \( I \). This function may be approximated as being linear for a particular range of \( I \):

\[
\text{LUE} = \text{LUE}_0 - a_{\text{LUE}} \cdot I
\]  

(4-3)
LUE then is a variable dependent on the two parameters \( \text{LUE}_0 \, (\text{gMJ}^{-1}) \), \( a_{\text{LUE}} \, (\text{gDMMJ}^{-2}\text{m}^{-2}\text{d}) \) and the level of \( I \).

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

\[
\text{SLA} = 590 \cdot I_{av}^{-0.851} \tag{4-4}
\]

The leaf area index, \( \text{LAI} \), of the crop then is calculated from:

\[
\frac{d\text{LAI}}{dt} = \frac{dW}{dt} \cdot \text{SLA} \tag{4-5}
\]

Table 4-1. Abbreviations and short description of the modules for total dry matter production used in this study.

<table>
<thead>
<tr>
<th>Module name</th>
<th>Short description</th>
</tr>
</thead>
<tbody>
<tr>
<td>LUE I</td>
<td>Constant LUE, radiation absorption according to Monsi &amp; Saeki</td>
</tr>
<tr>
<td>LUE II</td>
<td>As LUE I, but LUE assumed to be a linear function of average daily radiation sum</td>
</tr>
<tr>
<td>ACOCK I</td>
<td>Analytical integration of the rectangular hyperbola for single leaf photosynthesis over the canopy, numerical 3-point gauss integration over time, Respiration according to SUCROS assumptions</td>
</tr>
<tr>
<td>ACOCK II</td>
<td>As ACOCK I, but assumption of a decline of ( P_{\text{max}} ) within the canopy proportional to irradiance</td>
</tr>
<tr>
<td>SUCROS I</td>
<td>Original algorithms from SUCROS, separating direct and diffuse radiation, but negative exponential function for single leaf photosynthesis replaced by rectangular hyperbola</td>
</tr>
<tr>
<td>SUCROS II</td>
<td>As SUCROS I, but assumption of a decline of ( P_{\text{max}} ) within the canopy proportional to diffuse radiation</td>
</tr>
</tbody>
</table>
The SLA of the analysed cauliflower crops at transplanting was not always measured but with an average value of about 200 cm\(^2\)g\(^{-1}\) was consistently higher than predicted from Eqn. 4-4 which was derived from measurements at later growth stages. LAI was therefore initialised using measured leaf dry matter at transplanting and a value for SLA of 200.

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

The two photosynthesis based modules, ACOCK I and ACOCK II, have been described in chapter 3. Also the respiration part of these modules, which is essentially based on the assumptions used in the SUCROS model (Goudriaan and Van Laar, 1994) is described there.

In order to evaluate the effect of differentiation between shaded and unshaded leaf classes within the canopy and of a more detailed approach of radiation interception on the descriptive and predictive capability, we included also the algorithms from the procedures ASTRO, ASSIM and TOTASS of the SUCROS model (Goudriaan and Van Laar, 1994) to calculate total daily assimilate production in our evaluation. In order to make this module comparable with our ACOCK based sub modules we replaced the negative exponential function used in ASSIM to calculate photosynthesis rate per unit leaf area with the rectangular hyperbola. This module is further referred as SUCROS I (Table 4-1). The parameter initial light use efficiency \(\alpha\) of the rectangular hyperbola was set to a value of 25 \(\mu\text{g}\,\text{J}^{-1}\) as indicated by measurements presented in chapter 3.

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

\[
P_{\text{max}} = P_{\text{max0}} \cdot e^{-k_{\text{dif}}/\text{LAI}}
\]

(4-6)

were \(P_{\text{max0}}\) is the light saturated photosynthesis rate of unshaded leaves at the top of the canopy and \(k_{\text{dif}}\) is the extinction coefficient for diffuse radiation which is calculated according to Spitters et al. (1989). This version of the SUCROS based module is further called SUCROS II (Table 4-1).
Radiation absorption $R_{abs}$ within the canopy is calculated according to the fraction of sunlit leaf area, FSSLA, from the weighted sums of absorbed radiation per unit shaded, VISSHD, and un-shaded, VISSUN, leaf area. Integrated over the day and over the canopy according to the Gauss 5 point integration scheme where $D_L$ is the day length, $W_{DL}$ and $w\_{LAI}$ are weighting coefficients:

$$R_{\text{abs}} = \sum_{i=1}^{5} D_L \cdot w_{DLi} \sum_{j=1}^{5} \left( FSSLA_{ij} \cdot VISSUN_{ij} + (1 - FSSLA_{ij}) \cdot VISSHD_{ij} \cdot LAI \cdot w_{LAIj} \right)$$

(4-7)

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

4.2.3. Parameter estimation and statistics

The whole model is implemented within the HUME modelling environment (Kage and Stützel, 1999a). This modelling environment supports parameter estimation based on the Marquardt algorithm (Marquardt, 1963) and allows easily sub-model exchange because of it’s modular object oriented structure. We used the unweighted square sum of differences between simulated and measured total dry matter as the objective function for estimating $LUE$, $LUE_0$, $a_{LUE}$, $P_{\text{max}}$ and $P_{\text{max}0}$. For a re-parametrisation of some of the parameters of the development and dry matter partitioning modules un-weighted square sums of the differences between simulated and measured model variables were used. For the parameters $k_1$, $k_2$, leaf numbers for $g$, $h$ stem dry matter and for $r$ curd dry matter was used as the objective variable. The whole parameter estimation procedure including the estimation of the parameters of the dry matter production modules was repeated 3 to 4 times until no further significant change in any parameter value could be detected. The new parameter values are shown in the appendix (Table 4-A1).
Chapter 4

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

\[
EF = 1 - \frac{\sum (y_i - \bar{y}_i)^2}{\sum (y_i - \bar{y})^2}
\]

Comparing models having different numbers of parameters solely by their EF value, however, is not appropriate since no correction for parameter number is included within these measure. An approach to overcome this problem is the Akaike information criterion AIC (Akaike, 1969).

\[
AIC = n \cdot \ln \left( \frac{\sum (y_i - \bar{y}_i)^2}{n} \right) + 2 \cdot p
\]

where \( n \) is the number of observations and \( p \) is the number of parameters. The descriptive and predictive power of models is higher the lower the value of the AIC.

Another statistical parameter used in this study is the root mean square error RMSE:

\[
RMSE = \sqrt{\frac{\sum (y_i - \bar{y}_i)^2}{n}}
\]

giving the average model prediction error.

4.3. Results

The two sets of field experiments used in this study differed with respect to the variability of mean daily radiation sum during the growing period of each crop (Table 4-2). Whereas in the first set that was mainly used for calibration, only a small variation, ranging from 8.35 to 9.29 MJ m\(^{-2}\)d\(^{-1}\) could be observed, in the second set of experiments, that was mainly used for evaluation, a considerable range of \( I \) values from 5.45 to 8.13 MJ m\(^{-2}\)d\(^{-1}\) was measured. The reason for this higher variability is the late planting date of some crops of this group (Fig. 4-1). The variability in mean air temperature is generally smaller than the variability in daily radiation sum, since temperature declines not as much in autumn as daily radiation sum does (Fig. 4-1).
Table 4-2. Year, data group (C=calibration, E=evaluation), planting and harvest dates, average daily sum of photosynthetically active radiation and average temperature during the growth period of the cauliflower experiments used in this study.

<table>
<thead>
<tr>
<th>Year</th>
<th>Group</th>
<th>Cultivar</th>
<th>Planting Date</th>
<th>Harvest Date</th>
<th>Avg. I (MJ m(^{-2}) d(^{-1}))</th>
<th>Avg. Temp. (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>C</td>
<td>Fremont</td>
<td>124</td>
<td>194</td>
<td>8.72</td>
<td>15.12</td>
</tr>
<tr>
<td>1994</td>
<td>C</td>
<td>Fremont</td>
<td>152</td>
<td>236</td>
<td>9.24</td>
<td>18.31</td>
</tr>
<tr>
<td>1994</td>
<td>C</td>
<td>Linday</td>
<td>124</td>
<td>194</td>
<td>8.72</td>
<td>15.12</td>
</tr>
<tr>
<td>1994</td>
<td>C</td>
<td>Linday</td>
<td>152</td>
<td>247</td>
<td>8.80</td>
<td>18.03</td>
</tr>
<tr>
<td>1995</td>
<td>C</td>
<td>Fremont</td>
<td>122</td>
<td>200</td>
<td>8.35</td>
<td>14.76</td>
</tr>
<tr>
<td>1995</td>
<td>C</td>
<td>Fremont</td>
<td>137</td>
<td>207</td>
<td>8.48</td>
<td>16.00</td>
</tr>
<tr>
<td>1995</td>
<td>C</td>
<td>Fremont</td>
<td>164</td>
<td>234</td>
<td>9.29</td>
<td>18.79</td>
</tr>
<tr>
<td>1995</td>
<td>C</td>
<td>Linday</td>
<td>122</td>
<td>204</td>
<td>8.41</td>
<td>15.13</td>
</tr>
<tr>
<td>1995</td>
<td>C</td>
<td>Linday</td>
<td>164</td>
<td>253</td>
<td>8.41</td>
<td>18.02</td>
</tr>
<tr>
<td>1994</td>
<td>E</td>
<td>Fremont</td>
<td>97</td>
<td>185</td>
<td>8.13</td>
<td>13.12</td>
</tr>
<tr>
<td>1994</td>
<td>E</td>
<td>Fremont</td>
<td>207</td>
<td>293</td>
<td>5.45</td>
<td>14.52</td>
</tr>
<tr>
<td>1995</td>
<td>E</td>
<td>Fremont</td>
<td>94</td>
<td>187</td>
<td>7.59</td>
<td>12.13</td>
</tr>
<tr>
<td>1995</td>
<td>E</td>
<td>Fremont</td>
<td>200</td>
<td>291</td>
<td>6.10</td>
<td>16.49</td>
</tr>
<tr>
<td>1995</td>
<td>E</td>
<td>Fremont</td>
<td>207</td>
<td>298</td>
<td>5.56</td>
<td>15.69</td>
</tr>
<tr>
<td>1996</td>
<td>E</td>
<td>Fremont</td>
<td>100</td>
<td>189</td>
<td>7.41</td>
<td>12.59</td>
</tr>
<tr>
<td>1996</td>
<td>E</td>
<td>Fremont</td>
<td>200</td>
<td>284</td>
<td>6.18</td>
<td>14.34</td>
</tr>
<tr>
<td>1996</td>
<td>E</td>
<td>Fremont</td>
<td>206</td>
<td>305</td>
<td>5.11</td>
<td>13.45</td>
</tr>
<tr>
<td>1996*</td>
<td>E</td>
<td>Fremont</td>
<td>170</td>
<td>240</td>
<td>7.78</td>
<td>16.08</td>
</tr>
<tr>
<td>1997*</td>
<td>E</td>
<td>Fremont</td>
<td>190</td>
<td>258</td>
<td>7.23</td>
<td>18.56</td>
</tr>
</tbody>
</table>

*) Two N treatments were included in analysis
As a first step in our analysis we estimated the parameters LUE of module LUE I as well as the $P_{\text{max}}$ and $P_{\text{max}0}$ values of the modules ACOCK I and II and their asymptotic standard errors, respectively, for every experiment separately and plotted them against the mean daily radiation sum during the crop’s growth period (Fig. 4-2) Fitting the two parameter module LUE II was avoided during this step because of the limited number of observations in every experiment.

Linear regression analysis showed no significant correlation between LUE and mean photosynthetic active daily radiation sum for the calibration data set, nor for the evaluation data set alone. However, using the parameter estimates from both sets of experiments a significant correlation could be found (Fig. 4-2a). No correlation exists for the parameters $P_{\text{max}}$ and $P_{\text{max}0}$ and mean daily radiation sum during the growing periods of the different crops (Fig. 4-2b).

In the second step of our analysis we used all crops of the calibration set as a whole database for estimating the parameters of our six different dry matter production modules. Calibrating the module LUE I with the data of the calibration set gave a mean value for LUE of 3.15 (g DM MJ$^{-1}$) (Table 4-3). The parameter estimation for module LUE II, however, indicates a significant influence of the mean daily daily radiation sum on LUE, since we found a parameter value for $a_{\text{LUE}}$ significant different from zero (Table 4-3). The values for $a_{\text{LUE}}$ and $\text{LUE}_0$ we obtained are higher than slope and intercept of the linear regression between mean daily radiation sum during the growing period and LUE values estimated for a particular crop (Fig. 4-2b).

Estimating the values of $P_{\text{max}}$ and $P_{\text{max}0}$ for the calibration data set gave significantly different values for both parameters either using the ACOCK or the SUCROS approach (Table 4-3). This is no unusual result since an assumed decline of $P_{\text{max}}$ within the canopy as in Acock II and SUCROS II has to be compensated by a higher $P_{\text{max}}$ at the top of the canopy in order to predict the same dry matter production rate.
LUE (g DM MJ PAR\(^{-1}\))

\[\text{LUE} = 5.64 (\pm 0.51) - 0.29 (\pm 0.06) \cdot \text{PAR}\]

\(r^2 = 0.56^*\)

Fig. 4-2. Parameters average light use efficiency (a), \(P_{\text{max}}\) and \(P_{\text{max0}}\) (b) estimated for different cauliflower crops as a function of the average daily radiation sum during the growing period of the crops. Open and closed circles in the upper graph correspond different groups of experiments.

We also used the second data set which will later be used to evaluate the predictive value of our model for proving the constancy of parameter values. The values obtained
Table 4-3. Parameter estimations for four dry matter production modules assuming either a constant LUE or a LUE being a linear function of daily average radiation sum, \( I \) (MJ m\(^{-2}\) d\(^{-1}\)) \( (LUE = LUE_0 - a_{LUE} I) \) for two different photosynthesis-respiration based modules for two groups of experiments.

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Module</th>
<th>Parameter</th>
<th>Value</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calibration</td>
<td>LUE I</td>
<td>LUE</td>
<td>3.15</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>LUE II</td>
<td>LUE(_0)</td>
<td>6.66</td>
<td>0.80</td>
</tr>
<tr>
<td></td>
<td></td>
<td>a(_{LUE})</td>
<td>0.36</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>ACOCK I</td>
<td>(P_{\text{max}})</td>
<td>1013</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>ACOCK II</td>
<td>(P_{\text{max0}})</td>
<td>1438</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>SUCROS I</td>
<td>(P_{\text{max}})</td>
<td>1349</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>SUCROS II</td>
<td>(P_{\text{max0}})</td>
<td>1928</td>
<td>64</td>
</tr>
<tr>
<td>Evaluation</td>
<td>LUE I</td>
<td>LUE</td>
<td>3.49</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>LUE II</td>
<td>LUE(_0)</td>
<td>6.74</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td></td>
<td>a(_{LUE})</td>
<td>0.38</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>ACOCK I</td>
<td>(P_{\text{max}})</td>
<td>922</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>ACOCK II</td>
<td>(P_{\text{max0}})</td>
<td>1306</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>SUCROS I</td>
<td>(P_{\text{max}})</td>
<td>1269</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>SUCROS II</td>
<td>(P_{\text{max0}})</td>
<td>1789</td>
<td>71</td>
</tr>
</tbody>
</table>

SE = Asymptotic standard error, \(n=60\) for calibration, \(n=43\) for evaluation

from this data base are slightly but not significant different from the formerly estimated values for the module LUE II. For all photosynthesis based modules somewhat lower values for \(P_{\text{max}}\) were estimated for the evaluation data set. For the LUE I module a significant higher value of LUE was obtained (Table 4-3).

The descriptive and predictive value of the modules was evaluated by comparison of simulated with measured total dry matter production data from the parameterisation and evaluation data sets using for both data sets the parameter values obtained from the
calibration data set. Both versions of the LUE based dry matter production module seem to have similar descriptive power for the calibration data set (Table 4-4 and Fig. 4-3a). The linear regressions between simulated and measured total dry matter values have in both cases a slope and an intercept not significantly different from one and zero, respectively, and comparable modelling efficiencies 0.92 for the LUE I and of 0.94 for the LUE II module. The situation is, however, somewhat different for the application of the LUE based modules on the evaluation group of experiments. (Table 4-4 and Fig. 4-3). The LUE II module was able to give also for the evaluation data an acceptable prediction (EF = 0.88), compared to the LUE I module (EF = 0.69).

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

The data points of the photosynthesis-respiration modules tend to lie above the 1/1 line if one assumes a constant $P_{\text{max}}$ and they lie mostly below the 1/1 line for the assumption of a decreasing $P_{\text{max}}$ within the canopy (Fig. 4-3). This is due to the fact that the predicted time course of dry matter production differs in the way that, in general, the modules which assume a constant $P_{\text{max}}$ within the canopy estimate a lower production during the early crop growth phase which is over-compensated during the later growing phase (Fig. 4-4). The LUE modules predict an almost constant dry matter increase under conditions of quite stable values of daily radiation sum. For a late planted crop, however, which is growing under a decreasing daily radiation sum, the LUE II module is clearly superior to all other modules, as it compensates lower radiation intensities by an increasing LUE.
Fig. 4-3. Simulated and measured shoot dry matter of several cauliflower crops from calibration and independent evaluation experiments using 6 different modules for calculating dry matter production (For explanation of modules see Table 4-1).
Table 4-4. Number of fitted parameters $p$, coefficient of determination for the model prediction $r^2$, Akaike information criterion and parameters of the linear regression between simulated and measured total above ground dry matter of cauliflower crops from calibration (Cal.) and evaluation (Eval.) groups of experiments using 4 different dry matter production modules (for explanation see Table 4-1). Modules are grouped by Dataset and AIC (Akaike information criterion).

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Module</th>
<th>$p$</th>
<th>EF</th>
<th>RMSE</th>
<th>AIC</th>
<th>Slope</th>
<th>Intercept</th>
<th>$r^2$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cal.</td>
<td>LUE II</td>
<td>2</td>
<td>0.941</td>
<td>98.706</td>
<td>555.1</td>
<td>0.98 (±0.03)</td>
<td>27.99 (±17.20)</td>
<td>0.94</td>
<td>60</td>
</tr>
<tr>
<td>Cal.</td>
<td>ACOCK II</td>
<td>1</td>
<td>0.916</td>
<td>118.185</td>
<td>574.7</td>
<td>1.04 (±0.04)</td>
<td>-35.78 (±22.56)</td>
<td>0.92</td>
<td>60</td>
</tr>
<tr>
<td>Cal.</td>
<td>LUE I</td>
<td>1</td>
<td>0.916</td>
<td>114.381</td>
<td>574.7</td>
<td>0.95 (±0.04)</td>
<td>23.22 (±20.26)</td>
<td>0.92</td>
<td>60</td>
</tr>
<tr>
<td>Cal.</td>
<td>SUCROS I</td>
<td>1</td>
<td>0.901</td>
<td>127.918</td>
<td>584.2</td>
<td>0.98 (±0.04)</td>
<td>1.83 (±23.81)</td>
<td>0.90</td>
<td>60</td>
</tr>
<tr>
<td>Cal.</td>
<td>ACOCK I</td>
<td>1</td>
<td>0.886</td>
<td>137.684</td>
<td>593.0</td>
<td>0.89 (±0.04)</td>
<td>47.80 (±22.81)</td>
<td>0.90</td>
<td>60</td>
</tr>
<tr>
<td>Cal.</td>
<td>SUCROS II</td>
<td>1</td>
<td>0.882</td>
<td>139.944</td>
<td>594.9</td>
<td>1.10 (±0.05)</td>
<td>-59.63 (±27.26)</td>
<td>0.89</td>
<td>60</td>
</tr>
<tr>
<td>Eval.</td>
<td>LUE II</td>
<td>2</td>
<td>0.879</td>
<td>113.914</td>
<td>411.2</td>
<td>0.88 (±0.05)</td>
<td>39.39 (±25.16)</td>
<td>0.90</td>
<td>43</td>
</tr>
<tr>
<td>Eval.</td>
<td>ACOCK II</td>
<td>1</td>
<td>0.833</td>
<td>134.040</td>
<td>423.2</td>
<td>0.86 (±0.05)</td>
<td>11.56 (±28.78)</td>
<td>0.88</td>
<td>43</td>
</tr>
<tr>
<td>Eval.</td>
<td>SUCROS II</td>
<td>1</td>
<td>0.820</td>
<td>139.003</td>
<td>426.4</td>
<td>0.93 (±0.07)</td>
<td>5.19 (±35.08)</td>
<td>0.83</td>
<td>43</td>
</tr>
<tr>
<td>Eval.</td>
<td>SUCROS I</td>
<td>1</td>
<td>0.780</td>
<td>153.566</td>
<td>434.9</td>
<td>0.82 (±0.06)</td>
<td>70.87 (±32.42)</td>
<td>0.82</td>
<td>43</td>
</tr>
<tr>
<td>Eval.</td>
<td>LUE I</td>
<td>1</td>
<td>0.690</td>
<td>182.547</td>
<td>449.8</td>
<td>1.07 (±0.11)</td>
<td>108.79 (±42.15)</td>
<td>0.78</td>
<td>43</td>
</tr>
<tr>
<td>Eval.</td>
<td>ACOCK I</td>
<td>1</td>
<td>0.682</td>
<td>184.784</td>
<td>450.9</td>
<td>0.70 (±0.05)</td>
<td>93.54 (±28.53)</td>
<td>0.85</td>
<td>43</td>
</tr>
</tbody>
</table>
Fig. 4-4. Measured and simulated shoot dry matter of cauliflower crops c.v. ‘Fremont’ planted early (a) (DOY 122) and late (b) (DOY 164) in 1995 vs. time using six different modules for calculating dry matter production (For explanation of modules see Table 4-1).

Plotting the calculated daily light use efficiencies of the ACOCK I and II modules for an early and a late planted cauliflower versus the daily radiation sum values, a
considerable scatter of calculated LUE on a daily basis becomes obvious. This is because variations in temperature and crop dry weight at similar levels of daily radiation sum affect respiration losses and thereby net assimilation values. However, also a clear decrease of LUE with increasing daily radiation sum values (Fig. 4-5). This trend corresponds well with the functional relationship between LUE and I estimated for the LUE II module (Fig. 4-5).

4.4 Discussion

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

Our analysis shows that LUE for unstressed cauliflower crops is not constant, but decreases with increasing daily radiation sum (Fig. 4-2, Table 4-3). The observed decrease of LUE with I agrees with measurements of Olesen and Grevsen (1997) and calculations of Medlyn (1998). From data of the first mentioned authors we estimated a linear decrease of LUE to I of LUE = 6.3 - 0.34 \cdot I whereas for Medlyn's (1998) data we estimated a decrease of 0.33 g DMMJ\(^{-2}\) \(m^2\) \(d^{-1}\). From theoretical considerations (Kage et al., 2000), however, it seems to be likely that LUE is a non-linear function of I and that the slope of the LUE - I function is also less negative for higher LAI values. A linear approximation, like the one we present, may therefore be valid only for a limited range of daily radiation sum and may be further refined by including an influence of LAI.

The estimated values of \(P_{\text{max}}\) and \(P_{\text{max}0}\) for our photosynthesis based modules (Table 4-3) are within the range of the measured values presented in chapter 3, maybe despite the value for the SUCROS II module. But the assumption that \(P_{\text{max}}\) values decline directly proportional to the irradiance level within the canopy probably overestimates the degree of light adaptation within the canopy (chapter 3). Too high estimates for \(P_{\text{max}0}\) values are therefore needed to compensate this error.

In chapter 3 it was shown that either if one assumes a decline of \(P_{\text{max}}\) within the canopy or not, LUE seems to be a negative function of PAR. Therefore, the different predictive value of the ACOCK I and II and the SUCROS I and II modules for dry matter production (Table 4-4) cannot mainly be explained by a different change of LUE under varying daily radiation sum values. The difference in the predictive value of the modules seems to be mainly caused by the fact that for a constant \(P_{\text{max}}\) within the canopy (ACOCK I, SUCROS I) LUE increases with increasing LAI whereas it decreases for a \(P_{\text{max}}\) decreasing proportionally to irradiance level within the canopy (ACOCK II, SUCROS II). Consequently, different time courses of dry matter production are predicted (Fig. 4-5). This increase of LUE with increasing LAI, which is largest for the ACOCK I module, probably is the reason for its inferior descriptive and predictive power (Table 4-4). This may also hold as an argument that the assumption of the ACOCK II and SUCROS II modules, a decline of \(P_{\text{max}}\) within the canopy, is somewhat more realistic than a constant \(P_{\text{max}}\). The failure of the constant LUE hypothesis on the other
hand may be regarded as an indication that the adaptation of $P_{\text{max}}$ to a changing radiation environment over time is limited, since the analysis presented in chapter 3 shows that this process seems to be a prerequisite for a constant LUE.

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

One reason for the popularity of the constant LUE concept seems to be the possibility to derive this parameter directly from measurements in field experiments by plotting total dry matter data of a crop vs. values of cumulative intercepted radiation and to interpret the slope of the linear regression as LUE. This method has the shortcoming that one usually has to assume a constant LUE throughout the growing season or at least over a longer time period in order to get a sufficient amount of data pairs. Variations of LUE due to rapidly changing environmental conditions like radiation and temperature can therefore not easily be detected. Even if one is able to identify such a relationship (Fig. 4-2) this is only valid at the time scale at which it was evaluated. This becomes clear from the distinct effects of daily radiation sum on LUE at the time scale of a cropping period and on a daily basis (cv. Fig. 4-2 and Table 4-3).
Parameters from photosynthesis based models on the other hand are more difficult to obtain. Furthermore, these parameters are not constant over time (chapter 3) and within the canopy and are always only interpretable on the crop scale after up-scaling using mathematical models. Some of this methodological drawbacks, however, may decrease because of the increasing computational power and the availability of commercial software like ‘Modelmaker™’ (Cherwell Scientific Inc., 1999) or by modelling environments (Kage and Stützel, 1999a) which allow parameter estimation within dynamic models. But also LUE based approaches may be further refined by parameter estimation techniques and an appropriate data base. The approach we used for calibration of our LUE II module, for instance, resulted in a simple structured module with good descriptive and predictive value. Adjusting parameters of dynamic crop growth models like LUE or $P_{\text{max}}$ by minimising the prediction error for an aggregated variable like total above ground dry matter on the other hand implies the risk, that structural errors of a model are masked and the estimated parameter values are biased. This cannot totally be ruled out for our analysis, but since the obtained parameter values are well within a physiological meaningful range, we don’t expect that these effects are serious.

Recognising that $P_{\text{max}}$ seems to be a more conservative parameter than LUE (Fig. 4-2) one may conclude that even if based on several assumptions, the parameterisation of a photosynthesis-respiration based approach usually gives more generally applicable predictions than a LUE based approach. However, the usefulness of the constant LUE concept for calculating dry matter production in crop growth models cannot be judged ultimately from the presented analysis. At least for annual crops which have a limited time span for sowing or planting each year, it seems likely that year to year variation in average daily radiation sum during cropping time at one location is small (see analysis of Medlyn, 1998)). For a particular crop grown under these conditions constant LUE values may allow sufficient exact predictions of crop productivity.

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

4.5. Conclusions

The constant LUE hypothesis is a too crude simplification for calculation of dry matter production of the short season crop cauliflower. Acceptable predictions seem to be possible by assuming a linear decrease of LUE with increasing levels of daily radiation sum, at least for the range of 5 to 10 MJ m\(^{-2}\) d\(^{-1}\) PAR we analysed. Parameter estimation techniques may help to calibrate photosynthesis based dry matter production modules directly from field measurements, however, one should be aware of the possible influence of structural model errors. This type of model inherently implies a decline of LUE with increasing daily radiation sum and is therefore of superior descriptive and predictive value compared to simple LUE models. Our results indicate that assumptions about the behaviour of \(P_{\text{max}}\) within the canopy seem to be of higher importance for correct predictions than detailed calculations of light interception.
4.6. Appendix

Table 4-A1: Name, units and values of parameters from the development and partitioning model (Chapter 2) as well as the equation nr. from the original publication. Parameters signed with an * are changed in this study.

<table>
<thead>
<tr>
<th>Name</th>
<th>Units</th>
<th>Value</th>
<th>Equation Nr.</th>
</tr>
</thead>
<tbody>
<tr>
<td>$k_1^*$</td>
<td>(leaf leaf$^{-1}$ °C$^{-1}$ d$^{-1}$)</td>
<td>0.00392</td>
<td>(2-1)</td>
</tr>
<tr>
<td>$k_2^*$</td>
<td>(leaf °C$^{-1}$ d$^{-1}$)</td>
<td>0.0424</td>
<td>(2-3)</td>
</tr>
<tr>
<td>$g^*$</td>
<td>(-)</td>
<td>1.617</td>
<td>(2-18)</td>
</tr>
<tr>
<td>$h^*$</td>
<td>(-)</td>
<td>-4.958</td>
<td>(2-18)</td>
</tr>
<tr>
<td>$f_0$</td>
<td>(-)</td>
<td>0.000215</td>
<td>(2-21)</td>
</tr>
<tr>
<td>$r_i^*$</td>
<td>($°$C$^{-1}$ d$^{-1}$)</td>
<td>0.0133</td>
<td>(2-21)</td>
</tr>
<tr>
<td>$f_f$</td>
<td>(-)</td>
<td>0.815</td>
<td>(2-21)</td>
</tr>
</tbody>
</table>
5. Predicting dry matter partitioning between individual cauliflower leaves using a source limitation / sink hierarchy model

- Abstract

5.1. Introduction

5.2. Material and Methods

5.3. Model

5.4. Parameter estimation and regression analysis

5.5. Results

5.6. Discussion

5.7. Conclusions
Abstract

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 3 and 5 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.
5.1. Introduction

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 to describe the growth and senescence of the leaf fraction more mechanistically, since the 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; chapter 6) 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 rather descriptive than explanatory, since final leaf sizes are input values (Porter, 1984), are 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.
5.2. Material 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 two field experiments carried out in 1996 and 1997 on a experimental farm located about 20 km south of Hannover.

5.2.1. Container experiment

The container experiment was carried from May 2 to July 7 (Table 5-1) using the cauliflower cultivar ‘Fremont’ with two different irrigation levels. Seeds were sown in seed plates and transplanted after germination into peat cubes of 4 cm edge length until about 6 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 up 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 height was placed upon the loess layer to minimise soil evaporation. Nutrients were given once a week to ensure an optimal supply. The containers were placed in distances of 0.4 m up to the last week. During the last week the distances were 0.7 m. There were two irrigation treatments, seven harvest with 3 plants each, resulting in 42 containers. 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

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

*Final harvest of N-fertilised treatments of un-shaded light environment.
supply treatment was irrigated in the same way as the optimal supply treatment until 20
days 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 3000
\(\text{cm}^3\) of water per container during the first 20 days. From day 21 to the end of the
experiment the W1 treatment received 93000 \(\text{cm}^3\) and the W2 treatment 45000 \(\text{cm}^3\)
(Fig. 5-1). Amounts of irrigation water were calculated from daily determined containers
weights. From 31 dap on 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.

5.2.2. Field experiment

The field experiments used in this study were already described in Alt (1999) and Alt et
al. (2000c), therefore only a brief description will be given here.

Two independent field experiments with cauliflower (\textit{Brassica oleracea} L. convar.
\textit{botrytis} var. \textit{botrytis} L. cv. Fremont) were conducted on the institute’s experimental farm
located 15 km south of Hanover, 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 5-1). 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 different light environments, i.e.
shaded and unshaded, as main plots and four different nitrogen-fertiliser levels as sub-
plots. In the analysis presented here, only the two highest N fertilisation treatments are
considered. Shaded main plots were covered in one meter height with a net absorbing
40% of the photosynthetically active radiation (PAR) either immediately after
transplanting (1996) or two weeks after transplanting (1997). Nitrogen fertilisation was
given as ammonium nitrate at the time of 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.
5.2.3. 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 inflorescence. 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 the leaf area showed a senescent colour, they were classified as ‘senescent’. Leaf area of every leaf

---

**Fig. 5-1:** Average daily air temperature (°C), photosynthetic active radiation (PAR) (MJ PAR m⁻² d⁻¹) and daily water use of cauliflower plants (kg pl⁻¹) grown in containers with either high (W1) or low (W2) water supply.
group was measured with a LICOR 3100 leaf area meter (LICOR Inc., Lincoln, NE, USA). The samples of all plant compartments were oven dried and weighed.

5.3. Model

5.3.1. Dry matter partitioning between 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, the final leaf area or leaf mass is determined by the product of leaf growth duration and the leaf growth rate (Fig. 5-2a). 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 (Fig. 5-2b).

Such a behaviour may be explained by an early exponential growth during which potential growth rates are limiting (sink limited growth) followed by 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 dissimillatory processes then commence the senescence phase.

These assumptions are the base of our combined hierarchic/sink limitation approach for calculation of individual leaf growth. Potential growth rate is calculated from the product of a relative growth rate parameter, \( rgr_{SL} \), \( (d^{-1}) \), temperature, \( T \), \( (^\circ C) \) and the actual dry matter of the individual leaf \( W_{SL_i} \). \( (g \text{ DM} \text{ pl}^{-1}) \). The availability of assimilates for the growth of a particular leaf, i, is calculated from the amount of assimilates for total leaf growth \( dW_L/dt \) \( (g \text{ DM} \text{ pl}^{-1} \cdot d^{-1}) \) left over by younger leaves (central bracket of Eqn. 5-1), 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 older leaves are assumed to have still a comparable high sink strength. Additionally a translocation term, \( dT_{wsl}/dt \) \( (g \text{ pl}^{-1} \cdot d^{-1}) \), is introduced which accounts for the loss of dry matter from an individual leaf during senescence.
The growth rate of an individual leaf then is calculated from:

\[
\frac{dW_{SL_i}}{dt} = \min \left( r_{gr_{SL}} \cdot T \cdot W_{SL_i}, f_{av} \left( \frac{dW_L}{dt} - \sum_{i=1}^{n_L} \frac{dW_{SL_i}}{dt} \right) - \frac{dT_{WSL}}{dt} \right) \tag{5-1}
\]

Here, \( n_L \) denotes the youngest visible leaf with the highest index.

The potential attraction of assimilates by a particular organ, i.e. the sink strength, is not only a property of the organ itself 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 (chapter 2). As an additional hypothesis it was therefore postulated that the relative growth rate parameter \( r_{gr_{SL}} \) is decreasing linearly with temperature sum after the end of vernalisation and the initiation of the generative organ:

\[
r_{gr_{SL}} = r_{gr_0} - r_{gr_{dec}} \cdot TS_3
\tag{5-2}
\]

Here \( r_{gr_0} \) is the \((d^{-1})\) is the relative growth rate until vernalisation, \( r_{gr_{dec}} (°C^{-1}d^{-2}) \) is the decrease of \( r_{gr_{SL}} \) with increase of temperature sum since end of vernalisation, \( TS_3 (°C\cdot d) \). For \( TS_3 \) a base temperature of 0°C is assumed.

### 5.3.2. Leaf senescence

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

\[
\frac{dn_{LS}}{dt} = \begin{cases} 
0 & TS < TS_{sen} \\
 s_r \cdot T & TS \geq TS_{sen} 
\end{cases}
\tag{5-3}
\]

Here, \( dn_{LS}/dt \) is the increase in senescent leaves per time \((n_L\cdot d^{-1})\), \( TS (°C\cdot d) \) is the temperature sum since transplanting, \( s_r (leaf°C^{-1}d^{-1}) \) is a senescence parameter and \( TS_{sen} (°C\cdot d) \) is a lag phase without senescence.
Fig. 5-2: 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 α). 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.
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 a N fraction of 6.25% for proteins is postulated. 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 translocable dry matter, TLW (g DM·pt⁻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 overweight dissimilatory processes and senescence starts in the opposite case.

As our analysis relies on data of 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 days falls below a value of 0.1% of the initial growth rate rgrSL or as an alternative condition 250°C·d before the leaf is expected to be senescent as calculated from Eqn. 5-3.

The translocation rate $dT_{SLW}/dt$ (g DM·pt⁻¹) then is given by:

$$\frac{dT_{SLW}}{dt} = \max \left(0, \frac{TLW_i}{TS_{sen} + \frac{i}{S_{r}} - TS}\right)$$

(5-4)

Where $dT_{SLW}/dt$ (g DM·pt⁻¹·d⁻¹) is the translocation rate from an individual leaf and i is the leaf number.

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

The dry matter of newly formed leaves are initialised with 1/50 gpt⁻¹, expressing the assumption that leaves become visible with a leaf area of 1 cm² and that newly formed leaves have a specific leaf area (SLA) of 50 cm²·g⁻¹.
5.3.3. Leaf area growth

The specific leaf area of cauliflower, SLA (cm$^2\cdot$g$^{-1}$), depends on a several plant internal and external factors like temperature (Olesen and Grevsen, 1997) and the intensity of incident radiation (Alt, 1999). Because during the container experiment neither temperature nor radiation intensity was changing systematically (Fig. 5-1) it was assumed that for the data analysed here this factors did not affect SLA seriously. It is therefore postulated that SLA depends linearly on the leaf number, $i$, and on the actual size of the leaf, expressed as leaf weight $WSL_i$:

$$SLA_i = SLA_0 + a_{SLA} \cdot i + b_{SLA} \cdot WSL_i$$  \hspace{1cm} (5-5)

Where $a_{SLA}$ (cm$^2\cdot$g$^{-1}$) and $b_{SLA}$ (cm$^2\cdot$g$^{-2}$pl) are parameters.

In the field experiment, the net shading introduced a severe change of the radiation environment. We therefore expanded Eqn. 5-5 and introduced according to Alt (1999) an average value of the radiation intensity during the last 10 days, $\overline{I}$ (MJ$\cdot$m$^{-2}\cdot$d$^{-1}$) as an influence factor for SLA:

$$SLA_i = SLA_0 + a_{SLA} \cdot i + b_{SLA} \cdot WSL_i + c_{SLA} \cdot \overline{I}$$  \hspace{1cm} (5-6)

With $c_{SLA}$ (cm$^2\cdot$g$^{-1}$MJ$^{-1}$m$^{-2}$d) as an additional parameter.

Because SLA is dependent on the leaf weight the expansion of leaf area, the increase in leaf area of an individual leaf $dASL_i/dt$ (cm$^2\cdot$d$^{-1}$) has to be calculated from the increase of leaf dry weight, the specific leaf area $SLA_i$ and the change of the SLA with leaf weight, $dSLA_i/dWSL_i$ (cm$^2\cdot$g$^{-2}$pl):

$$\frac{dASL_i}{dt} = \frac{dWSL_i}{dt} \left( SLA_i + SWL_i \cdot \frac{dSLA_i}{dWSL_i} \right)$$  \hspace{1cm} (5-7)

5.3.4. Estimation of total leaf dry matter production

The total leaf dry matter production was estimated for the container and the field experiments with simple empirical models, however, in a different way. This was mainly done because simple radiation interception models (Monsi and Saeki, 1953) assume randomly distribution and horizontal homogeneity of leaf area, a condition which clearly
not holds for the isolated grown plants of the container experiment. A light use efficiency approach was therefore not applicable here. Alternatively we calculated the growth rate of shoot dry matter, \( \frac{dW_{sh}}{dt} \), \((\text{g} \text{pl}^{-1} \text{d}^{-1})\) of the plants from the container experiment simply from the amount of transpired water, \( T_{act} \), \((\text{kg} \text{pl}^{-1} \text{d}^{-1})\) and the transpiration use efficiency i.e. the dry matter production per unit of transpired water, TUE \((\text{g DMkg}^{-1})\):

\[
\frac{dW_{sh}}{dt} = T_{act} \cdot \text{TUE} \tag{5-8}
\]

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

For the field experiment a light use efficiency approach was used similar as already described in chapter 4. In the calculations performed for this study, however, the extinction coefficient, \( k \), was now taken as 0.75 and a correction for uneven leaf area distribution during growth phases with incomplete ground cover was introduced according to Röhrig and Stützel (2000). Therefore, the equation for calculating the amount of intercepted radiation \( Q \) \((\text{MJ PARm}^{-2} \text{d}^{-1})\) now reads:

\[
Q = Clf \cdot I \cdot \left(1 - e^{-kLAI}\right) \tag{5-9}
\]

The correction factor, \( Clf \) (-) was calculated according to Röhrig and Stützel (2000) from the relative ground cover, \( rgc \) (-):

\[
Clf = 0.77 + 0.28 \cdot \left(1 - e^{-1.65 rgc}\right) \tag{5-10}
\]

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

\[
rgc = \min\left(D^2 \frac{\pi}{4}, 1.0\right) \tag{5-11}
\]
Plant diameter is derived from the vegetative dry matter of cauliflower plants, $W_v$, (g m$^{-2}$) using the empirical equation of Röhrig and Stützel (2000):

$$D = \frac{0.656 \cdot W_v}{46.31 + W_v}$$  \hspace{1cm} (5-12)

Two different approaches for partitioning of dry matter between the vegetative plant parts of cauliflower i.e. leaves and stem have been developed (chapter 2; Alt, 1999), where the first approach was validated for conditions without water and nitrogen stress 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 originally was derived. A slight re-parameterisation of the first approach was necessary to minimise effects of erratic estimations of total leaf growth rate. The values of the changed parameters are summarised in Table 5-2. 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 chapter 2, Eqn. 2-21 was used. However, also in this case the growth rate parameter $\tau$ of the logistic equation was estimated separately for all treatments of the field experiment in order to minimise the effect of biased curd dry matter predictions.

### 5.4. Parameter estimation and regression analysis

The parameters of equations 3 and 5 were estimated from the experimental data using the PROC REG of the SAS statistical package (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. 5-8) and those determining partitioning (Eqn. 5-1, 5-2 and 5-4) were estimated separately and in an iterative way until no significant change in parameter values could be detected. The parameters $\text{SLA}_0$ and $c_{\text{SLA}}$ of Eqn. 5-6 were estimated also within the HUME environment from the total leaf area data of the 1996 field experiment.
5.5. 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 (Fig. 5-3). Total dry matter production and partitioning between leaves, stem and curd was described with high accuracy (Fig. 5-3) using the TUE and LUE approach with the adjusted parameter values shown in Table 5-2 and Table 5-3. 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. 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 $r_f$ was lower for the shaded treatments (Table 5-3).

The number of visible leaves increased expo-linearly (chapter 2, Fig. 5-4a), however, leaf formation especially during the second linear phase was faster in the container experiment. The estimated parameter value for the parameter $k_2$ was therefore considerably higher (Table 5-2) 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 (Fig. 5-4b), 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 senescent rate significantly (Fig. 5-4b), however, there was a tendency of an increased number of senescent leaves for the shaded treatment of the field experiment.
Fig. 5-3: 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 and with (+net) or without net shading (-net).
Table 5-2: Values and standard error (SE) of parameters which were adjusted to the data of the container experiment

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Value</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>TUE</td>
<td>(g·l⁻¹)</td>
<td>4.45 (W1)</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.22 (W2)</td>
<td>0.10</td>
</tr>
<tr>
<td>r_f</td>
<td>(°C·d⁻¹)</td>
<td>0.0161</td>
<td>0.00025</td>
</tr>
<tr>
<td>g</td>
<td>(-)</td>
<td>0.900</td>
<td>0.16</td>
</tr>
<tr>
<td>h</td>
<td>(-)</td>
<td>-2.121</td>
<td>0.83</td>
</tr>
<tr>
<td>k1</td>
<td></td>
<td>0.00253</td>
<td>7.96E-5</td>
</tr>
<tr>
<td>k2</td>
<td></td>
<td>0.0508</td>
<td>0.005</td>
</tr>
</tbody>
</table>

Table 5-3: Estimated values and standard errors (SE) of light use efficiency and growth rate parameter r of Eqn. 2-21 from chapter 2.

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>net shading</th>
<th>LUE (g·MJ⁻¹)</th>
<th>r_f (°C⁻¹·d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>96</td>
<td>2</td>
<td>no</td>
<td>2.75 (±0.02)</td>
<td>0.026 (±0.0014)</td>
</tr>
<tr>
<td>96</td>
<td>3</td>
<td>no</td>
<td>2.96 (±0.09)</td>
<td>0.027 (±0.0053)</td>
</tr>
<tr>
<td>96</td>
<td>2</td>
<td>yes</td>
<td>3.50 (±0.04)</td>
<td>0.019 (±0.0012)</td>
</tr>
<tr>
<td>96</td>
<td>3</td>
<td>yes</td>
<td>3.42 (±0.06)</td>
<td>0.018 (±0.0018)</td>
</tr>
<tr>
<td>97</td>
<td>2</td>
<td>no</td>
<td>3.09 (±0.07)</td>
<td>0.030 (±0.0075)</td>
</tr>
<tr>
<td>97</td>
<td>3</td>
<td>no</td>
<td>3.13 (±0.05)</td>
<td>0.022 (±0.0023)</td>
</tr>
<tr>
<td>97</td>
<td>2</td>
<td>yes</td>
<td>3.18 (±0.02)</td>
<td>0.016 (±0.0007)</td>
</tr>
<tr>
<td>97</td>
<td>3</td>
<td>yes</td>
<td>3.17 (±0.02)</td>
<td>0.018 (±0.0009)</td>
</tr>
</tbody>
</table>
Fig. 5-4: 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 expolinear equation (for parameters see text). The regression line for senescent leaves for both water supply levels of the container experiment is \( y = -2.74 (\pm 0.42) + 0.0067 (\pm 0.0005) TS \), \( r^2 = 0.95 \), \( n=12 \). The regression line for the field experiment is \( y = -2.916 (0.313) + 0.00901 (0.000296) TS \), \( r^2 = 0.97 \), \( n=29 \).
The time course of dry weight for the leaf groups showed in both irrigation treatments a similar behaviour, however, at a lower level for the W2 treatment (Fig. 5-5). Maximum leaf weights were found for the 10-12 and 13-15 groups, earlier and later formed groups are approaching lower maximum values. Even at the aggregated level of groups consisting of 3 leaves, the s-shaped growth dynamics postulated in Eqn. 5-1 becomes obvious. The model outlined in Eqn. 5-1 and 5-2 successful described the leaf mass of leaf groups consisting of 3 individual leaves from both irrigation treatments of the container experiment (Fig. 5-5). The estimated parameter value for $f_{av}$ (Table 5-4) indicates that during the source limited growth phase one leaf is able to attract about one third of the 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 g DM$\cdot$pl$^{-1}\cdot$d$^{-1}$ after about 260 °C$\cdot$d$^{-1}$ since initiation and of 1.5 g DM$\cdot$pl$^{-1}\cdot$d$^{-1}$ after about 315 °C$\cdot$d$^{-1}$ 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 5-4) is significant 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 (Fig. 5-6) 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 analysis of soil water potential influences on SLA will be shown in a forthcoming study (Kochler et al., 2000).

The observed dynamics of leaf area in the W1 treatment (Fig. 5-7) was quite similar to the dynamics of leaf dry matter (Fig. 5-5). 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 (Fig. 5-7). 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 too high SLA values (Fig. 5-5).
Fig. 5-5: Comparison of simulated and measured leaf dry weight of leaf groups consisting of 3 consecutive leaves from container grown cauliflower plants under two water supply regimes. For estimated parameter values see Table 5-4. The modelling efficiency for both treatments is 0.97 and the linear regression equation between simulated and measured values is 

$$y = -0.08 \pm 0.45 + 0.994 \pm 0.0182 \cdot x, \ r^2 = 0.97, \ n = 80.$$
The evaluation of the model using the data from the field experiment indicates in a good predictive quality of the model regarding the simulated dry matter for groups of 5 leaves in both evaluated years (Fig. 5-8a, c). The values of parameters SLA$_0$ and $c_{SLA}$ were estimated to be 242.18 (±6.29) (cm$^2$.g$^{-1}$) and -12.61 (±0.916) (cm$^2$.g$^{-1}$.MJ$^{-1}$.d), respectively. With these parameter values the descriptive value for leaf area was quite good (Fig. 5-8b), the predictive value, however, is only of moderate quality (Fig. 5-8d), 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 1996: $y=-0.099$ (±0.198) 1.032 (±0.070)$x$, $r^2=0.956$, n=12, 1997: $y=-0.279$ (±0.278) 1.215 (±0.096)$x$, $r^2=0.931$, n=14.

Table 5-4: Estimated values and standard errors (SE) of the parameters of Eqn. 5-1, describing the growth of individual leaves of cauliflower obtained from adjustment to the leaf weight data of the container experiment.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>$f_{av}$</td>
<td>0.366</td>
<td>0.027</td>
</tr>
<tr>
<td>$rgr_0$</td>
<td>0.0211</td>
<td>0.00027</td>
</tr>
<tr>
<td>$rgr_{dec}$</td>
<td>2.59E-5</td>
<td>1.02E-6</td>
</tr>
</tbody>
</table>
Fig. 5-6: 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: 
\[ SLA = 125.47 (±2.32) -2.59 (±0.125)nL^{-1.705} (±0.1185)WSL, r^2=0.78, n=141. \]

5.6. Discussion

The aim of the presented work was to derive a model from data of container and field experiments 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 5-3) further substantiate the results of (Chapter 4) 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 5-2) are a consequence of increasing stomata resistances which affect transpiration more than photosynthesis (Jones, 1992).

There were marked differences between the container and the field experiments regarding leaf development and senescence (Fig. 5-4). The reason for the more rapid increase of visible leaf number in the container experiment compared to the field experiment (Fig. 5-4a) 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 which also affects the growth rate did not influence leaf appearance (Fig. 5-4a), this argument remains weak. Regarding the differences in the relationship between the temperature sum since transplanting and the number of senescent leaves between the field and the container experiment (Fig. 5-4b), the most promising explanation may be the higher assimilate supply of the container grown plants, again as a consequence of the missing light competition. The delayed curd growth of the shaded plants (Fig. 5-3, Table 5-2) may thereby explain the missing influence of shading on the number of senescent leaves.

One may try to describe the senescence process which is determining the number of senescent leaves more mechanistically by 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 depending on the source-sink relationships within the whole plant may be taken into account. However, leaf age seems to be of comparable importance than 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.
Growth of individual leaves

Fig. 5-7: Measured and simulated leaf area of leaf groups consisting of 3 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 $y = 38.68 \pm 0.96 \pm 0.031$, $r^2=0.96$, $n=40$. 
Fig. 5-8: Simulated vs. measured dry weight (a and c) and area (b and d) of leaf groups consisting of 5 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: \( y = -1.2296 \pm 1.0021 + 1.0831 \pm 0.0527 x, \ r^2 = 0.87, \ n = 63 \) (leaf DM)

\[ y = -467.8 \pm 239.3 + 1.463 \pm 0.111 x, \ r^2 = 0.77, \ n = 55 \] (leaf area)

Bell shaped curves for maximum leaf area and leaf mass as we found for cauliflower (Fig. 5-5, Fig. 5-7) were reported by Wolfe et al., (1988) and Carberry et al., (1993). Such growth patterns are well described by our model, because maximum leaf area and mass is according to our assumptions closely coupled to the total assimilate flow in the
Growth of individual leaves

‘total leaf fraction’. This flow also follows a bell shaped pattern, since an early increase of assimilates available for leaf production is counteracted after curd initiation by increasing amounts of assimilates allocated to the curd. As the level of assimilate supply neither alters the phyllochrone (Fig. 5-4) nor seems to influence the leaf growth duration seriously (Fig. 5-5), 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 (Fig. 5-3), 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 (Fig. 5-3) is equivalent to an relative error of about 5-10% but may cause errors of more than 30% on the single leaf level. Considering this fact, the descriptive and predictive value of our model seems to be satisfying. On the other hand it may concluded that 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 \( \sum S \) and assumed to be directly proportional to the fraction of assimilates allocated to a particular organ, \( f_i \):

\[
  f_i = \frac{S_i}{\sum S}
\]  

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 subject of debate if sink size is better characterised by cell number or by organ size (see Marcelis, 1996 for
A sink strength calculated from the product of organ size and relative growth rate is, however, in contradiction 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). 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 5-2, Fig. 5-5, Fig. 5-8).

Therefore, both of the above outlined approaches for defining sink strength may give a satisfying description and prediction of our data after a considerable refinement. The approach presented here describes sink hierarchy more algorithmic rather than based on equations which are established in growth kinetic studies. However, the main assumptions that assimilates allocated to the leaf pool are portioned successively top down from the youngest to older leaves and that 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).

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 (cm$^2$g$^{-1}$) or the inverse leaf mass per area LMA (gc$m^{-2}$) 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 increases 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 load 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 more physiologically founded as an process which is, within certain limits, independent from 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).

5.7. 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 sound 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.

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 calculating leaf area expansion as an independent process.
6. *Nitrogen content of cauliflower organs as determined by organ size, N supply and radiation environment*

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<td>6.4. Discussion</td>
<td>126</td>
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<td>6.5. Conclusions</td>
<td>137</td>
</tr>
</tbody>
</table>
Abstract

Data from field experiments carried out in 3 consecutive years under contrasting N supply and radiation environment were used analyse the decline of nitrogen contents in cauliflower at different levels of morphological aggregation. Radiation environment was varied in two of three years using a net shading, reducing radiation intensity by 40%. The decline of average shoot nitrogen contents, Nc, (%N DM) with shoot dry matter, $W_{sh}$ (t ha$^{-1}$) for cauliflower ($N_c = 4.84 (0.071) \cdot W_{sh}^{-0.089(0.011)}$, $r^2=0.67$) is much less than as described for some arable crops. Radiation environment had no significant influence on total nitrogen concentrations of leaves and only a small influence on protein nitrogen contents in lower layers of the canopy. Total nitrogen content of leaf groups consisting of 5 leaves, N$_{Lc}$, under optimal N supply could be described using a multiple linear regression on leaf weight of the leaf group, W5L, (g dm 5 leaves$^{-1}$) and the average leaf number of the leaf group, n$_L$, (-) $N_{Lc} = 7.58 - 0.82 W5L - 0.074 n_L + 0.024 W5L n_L$, $r^2=0.76$, n=76. Fractions of leaf nitrate nitrogen to total nitrogen, f$_{Nitr}$, (-) could linearly related to the average irradiance incident on different leaf layers, $I_{av}$ (W PAR m$^{-2}$) ($f_{Nitr} = 0.2456 (±0.0188) - 0.0023(±0.0004) I_{av}$, $r^2 = 0.67$.

Reference N concentrations were obtained from the N dilution curves and used to identify critical soil nitrate values, N$_{min critically}$, where nitrogen content of cauliflower organs begin to decline because of a limited N supply. Linear response plateau functions were fitted using log transformed values of soil nitrate values from 0-60 cm as independent variables. N$_{min critically}$ values for total nitrogen were estimated at 85, 93 and 28 kg N ha$^{-1}$ for leaves, stem and curd, respectively. Within the canopy, N$_{min critically}$ values for total N of leaves increased from the top to the bottom from 44 to 188 kg N ha$^{-1}$. N$_{min critically}$ values for protein N in leaves from different layers of the canopy were much lower at around 30 kg N ha$^{-1}$, without a large gradient within the canopy.
6.1. Introduction

Nitrogen contents of plant organs usually decline during growth even under sufficient N supply because an increasing portion of assimilated carbon is allocated to structural organs or to structural parts of organs with a low N content (Caloin and Yu, 1984). This has motivated the derivation of ‘critical nitrogen dilution curves’ which relate average shoot nitrogen content and shoot dry matter under conditions of optimal N nutrition (Colnenne et al., 1988; Greenwood et al., 1991; Greenwood et al., 1990; Justes et al., 1994; Sheehy et al., 1998). Such dilution curves may be used to identify N deficiency of crops by comparison with measurements of actual nitrogen content. This may facilitate the analysis of experimental data and the derivation of fertilisation recommendations (Lemaire and Gastal, 1997). Functional relationships between dry weight and nitrogen content, but mostly at the organ level, are also used for the calculation of N demand in crop growth models (Stockle and Debaeke, 1997). Dynamic crop growth models may then again help to apply N dilution curves by updating the plant size dependent reference N values (Jeuffroy and Recous, 1999).

It is, however, well known that plants are able to adapt their nitrogen content to the level of radiation intensity (Björkman, 1981; Drouet and Bonhomme, 1999; Rousseaux et al., 1999) probably in order to enhance net carbon assimilation (Hirose and Werger, 1987). It may therefore be questioned if unique relationships between organ size or plant size and nitrogen content exists for crops grown under variable light regimes. Also of concern is the level of morphological aggregation where useful weight / nitrogen content relationships should be obtained, since the determination of N content with modern rapid field methods usually are performed at the single leaf level and not at the shoot level.

There is evidence that many C3 species reduce leaf area under nitrogen shortage rather than the nitrogen content of the leaves (van Keulen and Stol, 1991; Vos and van der Putten, 1998). If either reference nitrogen contents or reference values of leaf area index are more useful measures of nitrogen deficit therefore has therefore to be proven for a particular species. In order to optimise N use efficiency it may be further necessary to divide the total nitrogen content of the plant and their organs into productive protein and less productive nitrate nitrogen.
Vegetable crops like cauliflower often have high nitrogen uptake rates because of high nitrogen contents of their organs and high growth rates. High specific nutrient influx rates have therefore to be maintained throughout the crop’s growing period in order to ensure maximum growth and critical soil nitrate levels may be high. Such empirical critical N\textsubscript{min} values are already used in the calculation of fertiliser demand (Lorenz \textit{et al.}, 1989), but are rather empirical guesses than based on a sound analysis. Plant or organ size dependent dilution curves may help to identify critical levels of soil nitrate nitrogen which sustain sufficient N uptake rates of a crop under changing environmental conditions.

The aim of the presented paper therefore is to derive nitrogen dilution curves for cauliflower at different levels of morphological aggregation, ranging from the whole shoot to certain leaf groups within the canopy. These dilution curves are then used to identify critical soil nitrate levels, which may cause a decline of nitrogen contents of cauliflower below the reference values from the dilutions curves. For this purpose data from field experiments with cauliflower from 3 years were used covering a wide range of N supply and a variation of the light environment due to net shading in two of tree years.

### 6.2. Material and Methods

Two of the field experiments used in this study were already described in (Alt, 1999) and the third experiment conducted in 1998 had a similar layout, therefore only a brief description will be given here.

The field experiments with cauliflower (\textit{Brassica oleracea} L. \textit{convar. botrytis} var. \textit{botrytis} L. cv. Fremont) were conducted on the institute’s experimental farm located 15 km south of Hanover, Germany, on a typical loess derived hapludalf soil. Transplanting dates, harvest dates, initial leaf number and initial plant dry weight are summarised in Table 6-1. The high initial leaf number and dry weight in 1998 was due to a need for replanting of the experiment caused by severe bird attacks. The too big transplants caused some problems in crop establishment and therefore the first intermediate harvest in 1998 was omitted from the analysis. The average plant density in all experiments was 3.5 plants m\textsuperscript{-2}. Irrigation was given whenever needed to ensure optimal growth.
The experiments were laid out as split plots with two different light environments, i.e. shaded and unshaded, as main plots in 1996 and 1997 and irrigated and non-irrigated plots in 1998 and four different nitrogen-fertiliser levels as sub-plots. In the analysis presented here, only the irrigated treatments from the 1998 experiment are used. Shaded main plots were covered in one meter height with a net absorbing 40% of the photosynthetically active radiation (PAR) either immediately after transplanting (1996) or two weeks after transplanting (1997). Nitrogen fertilisation was given as ammonium nitrate at the time of transplanting. Soil nitrate content of 10-15 kg N ha$^{-1}$ in 1996, 1997 and 1998 in 0-60 cm were subtracted from 150 (N1), 300 (N2) and 450 kg ha$^{-1}$ (N3) target values. Furthermore a N0 treatment was included, which received no nitrate nitrogen.

On several intermediate harvests (Table 6-1) six plants per plot were collected and separated into stem, leaf including petioles, and inflorescence. Leaves were considered and counted down to a size of approximately 1 cm$^2$. Stems were cut 1 cm below field level and at the onset of inflorescence. Leaf area was measured with a LICOR 3100 leaf area meter (LI-COR Inc., Lincoln, NE, USA). The samples of all plant compartments were oven dried and weighed. Total nitrogen and nitrate nitrogen was determined by the micro-Kjeldahl method and a nitrate sensitive electrode, respectively.

Weather data were recorded using an automated weather station (Campbell Sci. Ltd., UK) located on the experimental station less than 500 m from the experimental plots apart. For relating nitrate concentrations in different leaf groups of cauliflower average values of radiation intensity for the last 10 day before each intermediate harvest were calculated taking account of the transmissivity of the net of the shaded plots. Radiation

<table>
<thead>
<tr>
<th>Year</th>
<th>Sowing date</th>
<th>Transplanting date</th>
<th>Harvests (days after transplanting)</th>
<th>n$_{L0}$</th>
<th>d. w. (g plant$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td>23 May</td>
<td>18 June</td>
<td>28, 49, 69</td>
<td>3.25</td>
<td>0.34</td>
</tr>
<tr>
<td>1997</td>
<td>3 June</td>
<td>9 July</td>
<td>26, 47, 68*, 82</td>
<td>3.5</td>
<td>0.39</td>
</tr>
<tr>
<td>1998</td>
<td>18 May</td>
<td>18 June</td>
<td>21, 33, 48, 71</td>
<td>5.2</td>
<td>0.63</td>
</tr>
</tbody>
</table>

*Final harvest of N-fertilised treatments of non-shaded light environment.*
intensity incident in different leaf groups was calculated from the a negative exponential extinction equation (bracket in Eqn. 2-10) using and extinction coefficient of 0.75 (chapter 5).

6.2.1. Regression analysis

It was hypothesised that 100 kg soil nitrate N from 0-60 cm are sufficient for optimal N supply on a loess loam soil under irrigation. Therefore, a sub-set was extracted from the experimental data of the N2 and N3 treatments for regression analysis of organ size influence on organ nitrogen contents where as additionally condition the soil nitrate content from 0-60 cm soil depth is higher than 100 kg N ha\(^{-1}\). Furthermore leaf nitrogen content data for the leaf group 6-10 were included only for the first two harvests because leaf senescence may have influenced nitrogen contents at later stages of plant development. Also the first harvest from the 1998 experiment was excluded because plant establishment problems caused exceptional low nitrogen contents. These data were used to derive organ size dependent reference nitrogen content under optimal nitrogen supply. For leaves, the organ size was expressed alternatively as leaf dry matter or leaf area.

From this reference nitrogen content a difference (Ndif) to the actual measured nitrogen content is calculated. To these values a linear response-plateau model was fitted using log transformed soil nitrate contents from 0-60 cm as independent variable:

\[
Ndif = \begin{cases} 
0 & N_{\text{min}} > N_{\text{min crit}} \\
\text{slope} \cdot (\ln(N_{\text{min crit}}) - \ln(N_{\text{min}})) & N_{\text{min}} \leq N_{\text{min crit}}
\end{cases} \quad (6-1)
\]

A similar model was used to relate relative LAI values to soil nitrate nitrogen.

This model was fitted to the data using the procedure NLIN from the SAS statistical package (SAS Institute, 1988)

6.3. Results

The average nitrogen content of cauliflower shoots clearly shows a decrease with increasing shoot dry matter (Fig. 6-1). This decrease, however, is substantially lower than as found for winter rape by Colnenne et al. (1988) and was derived for C3 plants in general by Greenwood et al. (1990).
The average leaf nitrogen content of the leaf compartment of cauliflower plants under optimal nitrogen supply is decreasing with increasing organ size, expressed either as dry weight or as leaf area (Fig. 6-2, Table 6-2). The only significant difference between the parameter values found for the different data groups was the lower absolute value of the slope of the regressions for the year 1997 compared to both other years using either dry matter or leaf area index as independent variables. There was no significant effect of net shading on the regression parameters. The predictive quality of LAI for leaf total nitrogen content was somewhat higher than for leaf dry matter if compared at the level of single data groups, but not for the whole data set (Table 6-2).

Fig. 6-1: Relationship between shoot N concentration ($N_c$) and shoot dry matter ($W_{sh}$) of cauliflower plants grown under optimal N supply in three different years (1996, 1997, 1998) either with (+net) or without net shading (-net). The lines shown are: —— fit to the data $N_c = 4.84 \ (\pm 0.071) \ W_{sh}^{-0.089 \ (\pm 0.011)}$, $r^2=0.67$, $n=32$, · · · · · · $N_c = 4.48 \ W_{sh}^{-0.25}$ after Colenne et al. (1988) and - - - - - - $N_c=5.7 \ W_{sh}^{-0.5}$ after Greenwood et al. (1990).
Fig. 6-2: Average leaf nitrogen content (% DM) of cauliflower plants under optimal nitrogen supply as a function of the leaf dry matter (g pl⁻¹) (a) and of the leaf area index (b). Hatched line is indicating the confidence interval of the regression equation (p=0.05).
Nitrogen content of cauliflower organs

Curd nitrogen content is also strongly decreasing with curd size (Fig. 6-3), without any significant differences between shading and years. Likewise the nitrogen content of stem and tap roots of cauliflower are decreasing with increasing organ size (Fig. 6-4).

The deviations of the total nitrogen contents leaves, stem and curd from the values of well supplied cauliflower plants could successfully be described using the approach outlined in Eqn. 6-1 (Fig. 6-5). This implies the validity of our hypothesis that there is no significant response of total plant nitrogen content to soil nitrate above levels of 100 kg N ha\(^{-1}\). The estimated parameter values (Table 6-3) indicate that the vegetative organs leaves and stem show decreasing nitrogen contents at higher levels of soil nitrate than

### Table 6-2: Parameters intercept (% N DM), slope (% N DM g\(^{-1}\) pl) (±SE), number of observations (n) and the \(r^2\) of linear regressions between average leaf nitrogen content of cauliflower plants under optimal nitrogen supply with either the leaf dry matter per plant (DM) or the leaf area index (LAI) as independent variables. The data were grouped into different experimental years and net shaded and unshaded treatments.

<table>
<thead>
<tr>
<th>Independent Variable</th>
<th>Year</th>
<th>Net shading</th>
<th>Intercept</th>
<th>Slope</th>
<th>(r^2)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM</td>
<td>1996</td>
<td>all</td>
<td>5.85 (±0.11)</td>
<td>-0.0168 (±0.0017)</td>
<td>0.91</td>
<td>13</td>
</tr>
<tr>
<td>DM</td>
<td>1997</td>
<td>all</td>
<td>5.54 (±0.13)</td>
<td>-0.0072 (±0.0019)</td>
<td>0.56</td>
<td>11</td>
</tr>
<tr>
<td>DM</td>
<td>1998</td>
<td>no</td>
<td>5.69 (±0.11)</td>
<td>-0.0209 (±0.0023)</td>
<td>0.96</td>
<td>5</td>
</tr>
<tr>
<td>DM</td>
<td>all</td>
<td>no</td>
<td>5.53 (±0.17)</td>
<td>-0.0102 (±0.0023)</td>
<td>0.60</td>
<td>15</td>
</tr>
<tr>
<td>DM</td>
<td>all</td>
<td>yes</td>
<td>5.86 (±0.15)</td>
<td>-0.0164 (±0.0027)</td>
<td>0.75</td>
<td>14</td>
</tr>
<tr>
<td>DM</td>
<td>all</td>
<td>all</td>
<td>5.63 (±0.11)</td>
<td>-0.0118 (±0.0017)</td>
<td>0.63</td>
<td>29</td>
</tr>
<tr>
<td>LAI</td>
<td>1996</td>
<td>all</td>
<td>5.90 (±0.10)</td>
<td>-0.426 (±0.037)</td>
<td>0.93</td>
<td>13</td>
</tr>
<tr>
<td>LAI</td>
<td>1997</td>
<td>all</td>
<td>5.62 (±0.13)</td>
<td>-0.178 (±0.040)</td>
<td>0.64</td>
<td>11</td>
</tr>
<tr>
<td>LAI</td>
<td>1998</td>
<td>no</td>
<td>5.58 (±0.04)</td>
<td>-0.404 (±0.018)</td>
<td>0.99</td>
<td>5</td>
</tr>
<tr>
<td>LAI</td>
<td>all</td>
<td>no</td>
<td>5.53 (±0.16)</td>
<td>-0.262 (±0.055)</td>
<td>0.63</td>
<td>15</td>
</tr>
<tr>
<td>LAI</td>
<td>all</td>
<td>yes</td>
<td>5.85 (±0.16)</td>
<td>-0.303 (±0.056)</td>
<td>0.71</td>
<td>14</td>
</tr>
<tr>
<td>LAI</td>
<td>all</td>
<td>all</td>
<td>5.66 (±0.12)</td>
<td>-0.271 (±0.040)</td>
<td>0.63</td>
<td>29</td>
</tr>
</tbody>
</table>
the curd. The response of leaves, stem and curd to nitrogen shortage is similar for the different experimental years and the shading treatments. However, the deviations from nitrogen concentrations of the shaded treatments lie somewhat below the values of the unshaded treatments (Fig. 6-5).

Fig. 6-3: Nitrogen content of cauliflower curds from plants under optimal nitrogen supply as a function of their dry weight (g pl⁻¹). The regression line shown is \( y = 6.70 (\pm 0.147) \exp(-0.0106(\pm 0.001) x) \), \( r^2 = 0.89, n = 19 \).
Nitrogen content of stem and tap root of cauliflower plants under optimal nitrogen supply as a function of organ weight (g.pl⁻¹). The regression lines shown are $y=3.45(\pm0.063) - 0.366(\pm0.029) \ln(x)$, $r^2=0.93$ for stem (——, 96 and 98 data only) $y=3.47(\pm0.088) - 0.0137(\pm0.0058)x$, $r^2=0.33$ (- - -, 97 data) and $y=2.65 - 0.0381x$, $r^2=0.68$ for tap root.

Table 6-3: Critical soil nitrogen content (kg N ha⁻¹ 0-60 cm) (Nmin$_{crit}$) and slope of a linear response-plateau model describing the dependency of deviations from reference nitrogen content.

<table>
<thead>
<tr>
<th>Organ</th>
<th>Nmin$_{crit}$ (kg N ha⁻¹)</th>
<th>Slope (%N kgN⁻¹ ha⁻¹)</th>
<th>$r^2$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf</td>
<td>85.93$^a$ (±16.37)</td>
<td>-1.24 (±0.17)</td>
<td>0.77</td>
<td>53</td>
</tr>
<tr>
<td>Stem</td>
<td>93.04$^{ab}$ (±22.41)</td>
<td>-0.64 (±0.10)</td>
<td>0.74</td>
<td>48</td>
</tr>
<tr>
<td>Curd</td>
<td>28.74$^b$ (±5.05)</td>
<td>-2.13 (±0.52)</td>
<td>0.57</td>
<td>37</td>
</tr>
</tbody>
</table>
Fig. 6-5: Deviations from a reference nitrogen content as a function of the soil mineral nitrate content (0-60cm) for leaves, stem and curd of cauliflower plants. For parameters of the regression lines see Table 6-3.
Nitrogen content of cauliflower organs

Table 6-4: Parameters (±SE) slope, intercept, $r^2$ and number of observations (n) of linear regressions between the logarithms of leaf dry matter (g pl$^{-1}$) or leaf area (cm$^2$ pl) of different leaf number groups consisting of 5 leaves each and leaf nitrogen content (%N DM)

<table>
<thead>
<tr>
<th>Independent Variable</th>
<th>Leaf group</th>
<th>Intercept (±SE)</th>
<th>Slope (±SE)</th>
<th>$r^2$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>ln(DM) 6-10</td>
<td></td>
<td>6.92(±0.19)</td>
<td>-0.65(±0.07)</td>
<td>0.84</td>
<td>18</td>
</tr>
<tr>
<td>ln(DM) 11-15</td>
<td></td>
<td>6.70(±0.18)</td>
<td>-0.52(±0.06)</td>
<td>0.77</td>
<td>24</td>
</tr>
<tr>
<td>ln(DM) 16-20</td>
<td></td>
<td>6.27(±0.11)</td>
<td>-0.42(±0.04)</td>
<td>0.83</td>
<td>20</td>
</tr>
<tr>
<td>ln(DM) 21-25</td>
<td></td>
<td>5.84(±0.13)</td>
<td>-0.39(±0.08)</td>
<td>0.66</td>
<td>14</td>
</tr>
<tr>
<td>ln(LA) 6-10</td>
<td></td>
<td>9.95(±0.53)</td>
<td>-0.63(±0.07)</td>
<td>0.83</td>
<td>18</td>
</tr>
<tr>
<td>ln(LA) 11-15</td>
<td></td>
<td>9.04(±0.98)</td>
<td>-0.50(±0.12)</td>
<td>0.47</td>
<td>20</td>
</tr>
<tr>
<td>ln(LA) 16-20</td>
<td></td>
<td>8.19(±0.29)</td>
<td>-0.39(±0.04)</td>
<td>0.87</td>
<td>16</td>
</tr>
<tr>
<td>ln(LA) 21-25</td>
<td></td>
<td>7.58(±0.25)</td>
<td>-0.35(±0.04)</td>
<td>0.86</td>
<td>12</td>
</tr>
</tbody>
</table>

Likewise, at the level of single leaf groups there is a clear trend of decreasing total nitrogen contents with increasing organ size either expressed as leaf area or leaf dry matter (Table 6-4, Fig. 6-6). The values of the intercepts and the absolute values of the slopes of the regression equations between total nitrogen contents and leaf dry weight or leaf area are almost linearly decreasing with increasing leaf number (Table 6-4). It was therefore possible to construct multiple linear regression models which explains nitrogen concentrations of the single leaf groups as a function of the organs size expressed either as leaf dry matter or leaf area, the average leaf number of the group and the interaction between leaf size and average leaf number (Table 6-5). The estimated parameter values are not significantly different for the shaded and unshaded treatments. There is a slightly advantage for leaf dry matter compared to leaf area as explaining variable for total leaf nitrogen content.
Again, the deviations of the total nitrogen contents of the leaf groups from the level of well supplied cauliflower plants could successfully described using Eqn. 6-1 (Table 6-6, Fig. 6-2). The critical soil nitrate amount is decreasing with increasing leaf number from a value above 100 kg N ha\(^{-1}\) for the group of leaf 6-10 down to a value of about 45 kg N ha\(^{-1}\) for the youngest leaf group under consideration (Table 6-6). There are no obvious differences in the response of total leaf nitrogen contents to limiting amounts of soil nitrate nitrogen between years and shaded and un-shaded treatments (Fig. 6-7).

The leaf protein contents of the leaf groups are also declining with increasing leaf size (Fig. 6-8, Table 6-7), however, for the leaf groups 6-10 and especially for the group 11-15 there is an indication that the decline of leaf protein content with leaf size is higher for the shaded plants. Therefore distinct equations for shaded and unshaded treatments for these two leaf groups were used to the compute reference nitrogen contents. The differences from this reference nitrogen content plotted against the soil nitrate content from 0-60 cm again could be described using the linear response - plateau model of Eqn. 6-1 with the exception of the leaf group 6-10 (Fig. 6-9, Table 6-8). In contrast to the response of the total leaf nitrogen contents (Table 6-6) protein N declines at very similar levels within the different leaf groups of cauliflower. There is no indication that the response of the protein N concentrations to a limited N supply differs for either the shaded and un-shaded treatments or the different experimental years.

The functional relationship between relative leaf area index soil nitrate nitrogen is not as clear as for the response of leaf nitrogen content (Fig. 6-10). However, there seems to be no severe reduction of leaf area above values which were found to influence leaf nitrogen content (Fig. 6-6). The fractions of leaf nitrate N on total leaf N from the 1996 experiment show a significant negative correlation to the average radiation incident on the different leaf groups of shaded and unshaded plants (Fig. 6-11).
Fig. 6-6: Nitrogen content (% DM) of cauliflower leaf groups under optimal nitrogen supply as dependent on the leaf area. For parameters of linear regressions see Table 6-5.
Table 6-5: Parameters (±SE), $r^2$ and number of observations of multiple regressions explaining total leaf nitrogen content of cauliflower plants (%N DM) using the leaf size expressed as leaf dry matter (DM) (g 5 leaves$^{-1}$) or leaf area (cm$^2$ 5 leaves$^{-1}$), the leaf number and the product of leaf size and leaf number as independent variables.

<table>
<thead>
<tr>
<th>Ind. Var.</th>
<th>Net</th>
<th>Intercept</th>
<th>Organ size</th>
<th>Leaf number</th>
<th>Number* Size</th>
<th>$r^2$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM</td>
<td>Yes</td>
<td>7.56</td>
<td>-0.85</td>
<td>-0.079</td>
<td>0.028</td>
<td>0.81</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(±0.32)</td>
<td>(±0.13)</td>
<td>(±0.02)</td>
<td>(±0.008)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DM</td>
<td>No</td>
<td>7.57</td>
<td>-0.76</td>
<td>-0.070</td>
<td>0.016</td>
<td>0.78</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(±0.44)</td>
<td>(±0.18)</td>
<td>(±0.02)</td>
<td>(±0.011)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DM</td>
<td>All</td>
<td>7.58</td>
<td>-0.81</td>
<td>-0.074</td>
<td>0.021</td>
<td>0.78</td>
<td>76</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(±0.28)</td>
<td>(±0.11)</td>
<td>(±0.02)</td>
<td>(±0.007)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area</td>
<td>Yes</td>
<td>11.33</td>
<td>-0.78</td>
<td>-0.188</td>
<td>0.024</td>
<td>0.71</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(±1.24)</td>
<td>(±0.16)</td>
<td>(±0.06)</td>
<td>(±0.008)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area</td>
<td>No</td>
<td>10.90</td>
<td>-0.75</td>
<td>-0.143</td>
<td>0.018</td>
<td>0.76</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(±1.43)</td>
<td>(±0.20)</td>
<td>(±0.08)</td>
<td>(±0.012)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area</td>
<td>All</td>
<td>11.03</td>
<td>-0.76</td>
<td>-0.158</td>
<td>0.020</td>
<td>0.75</td>
<td>66</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(±0.95)</td>
<td>(±0.13)</td>
<td>(±0.05)</td>
<td>(±0.007)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

6.4. Discussion

The aim of this study was to establish functional relationships between plant/organ size and nitrogen contents under optimal nitrogen supply for cauliflower. These functions were used to identify nitrogen shortage and corresponding critical soil nitrate levels.

There was no significant influence of net shading on the relationships between leaf size expressed either as leaf area or leaf dry weight and total nitrogen content (Fig. 6-6, Table 6-5). Only protein N in the oldest leaf groups showed a differentiation between shaded and unshaded plants (Fig. 6-8). Such a limited impact of irradiance levels on leaf nitrogen content was also reported by Hikosaka et al. (1994). They found that leaf age was of similar importance for leaf nitrogen content of vine (Ipomoea tricolor Cav.) than irradiance. A limited light adaptation of leaf N content was also found for rice (Makino et al., 1997).
High growth rates within the *Brassica* genus and further selection of fast growing cultivars may coincidence with only limited adaptation of nitrogen contents to a changing light environment. But there is also the possibility that net shading is not an appropriate method to initiate such adaptations, since there seems to be a closer relationship between the red/far red ratio which single leaves perceive than to the absolute level of radiation intensity (Rousseaux *et al.*, 1999).

The impeded decline of total leaf nitrogen content (Table 6-2, Fig. 6-2) and stem nitrogen content (Fig. 6-4) in 1997 may be caused by a somewhat delayed vernalisation (Final number of leaves: 32) which also delayed curd growth and therefore the onset of intensive plant internal competition for nitrogen.
Table 6-7: Parameters slope, intercept, $r^2$ and number of observations (n) of linear regressions between the logarithms of leaf dry matter (g pt$^{-1}$) or leaf area (cm$^2$ pt$^{-1}$) of different leaf number groups and leaf protein N content (%N DM).

<table>
<thead>
<tr>
<th>Ind. Var.</th>
<th>Leaf group</th>
<th>Shading</th>
<th>Intercept</th>
<th>Slope</th>
<th>$r^2$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM</td>
<td>6-10</td>
<td>all</td>
<td>6.34 (±0.45)</td>
<td>-0.81 (±0.17)</td>
<td>0.62</td>
<td>16</td>
</tr>
<tr>
<td>DM</td>
<td>6-10</td>
<td>no</td>
<td>6.85 (±0.63)</td>
<td>-0.89 (±0.22)</td>
<td>0.73</td>
<td>8</td>
</tr>
<tr>
<td>DM</td>
<td>6-10</td>
<td>yes</td>
<td>6.05 (±0.61)</td>
<td>-0.80 (±0.24)</td>
<td>0.65</td>
<td>8</td>
</tr>
<tr>
<td>DM</td>
<td>11-15</td>
<td>all</td>
<td>6.09 (±0.21)</td>
<td>-0.63 (±0.07)</td>
<td>0.84</td>
<td>19</td>
</tr>
<tr>
<td>DM</td>
<td>11-15</td>
<td>no</td>
<td>6.37 (±0.22)</td>
<td>-0.58 (±0.06)</td>
<td>0.93</td>
<td>8</td>
</tr>
<tr>
<td>DM</td>
<td>11-15</td>
<td>yes</td>
<td>5.94 (±0.28)</td>
<td>-0.69 (±0.09)</td>
<td>0.87</td>
<td>11</td>
</tr>
<tr>
<td>DM</td>
<td>16-20</td>
<td>all</td>
<td>5.67 (±0.16)</td>
<td>-0.48 (±0.07)</td>
<td>0.79</td>
<td>15</td>
</tr>
<tr>
<td>DM</td>
<td>21-25</td>
<td>all</td>
<td>5.27 (±0.14)</td>
<td>-0.39 (±0.08)</td>
<td>0.72</td>
<td>11</td>
</tr>
<tr>
<td>LA</td>
<td>6-10</td>
<td>all</td>
<td>10.97 (±1.01)</td>
<td>-0.90 (±0.14)</td>
<td>0.76</td>
<td>16</td>
</tr>
<tr>
<td>LA</td>
<td>6-10</td>
<td>no</td>
<td>11.22 (±1.55)</td>
<td>-0.92 (±0.21)</td>
<td>0.76</td>
<td>8</td>
</tr>
<tr>
<td>LA</td>
<td>6-10</td>
<td>yes</td>
<td>10.65 (±1.41)</td>
<td>-0.88 (±0.19)</td>
<td>0.78</td>
<td>8</td>
</tr>
<tr>
<td>LA</td>
<td>11-15</td>
<td>all</td>
<td>12.98 (±3.52)</td>
<td>-1.09 (±0.42)</td>
<td>0.34</td>
<td>15</td>
</tr>
<tr>
<td>LA</td>
<td>11-15</td>
<td>no</td>
<td>12.43 (±4.32)</td>
<td>-0.98 (±0.51)</td>
<td>0.48</td>
<td>6</td>
</tr>
<tr>
<td>LA</td>
<td>11-15</td>
<td>yes</td>
<td>15.57 (±4.52)</td>
<td>-1.43 (±0.54)</td>
<td>0.50</td>
<td>9</td>
</tr>
<tr>
<td>LA</td>
<td>16-20</td>
<td>all</td>
<td>8.66 (±0.92)</td>
<td>-0.57 (±0.12)</td>
<td>0.71</td>
<td>11</td>
</tr>
<tr>
<td>LA</td>
<td>21-25</td>
<td>all</td>
<td>7.16 (±0.11)</td>
<td>-0.38 (±0.02)</td>
<td>0.98</td>
<td>9</td>
</tr>
</tbody>
</table>
Nitrogen content of cauliflower organs

Table 6-8: Critical soil nitrogen content (kg N ha\(^{-1}\) 0-60 cm) (N\(_{\text{min, crit}}\)) and slope of a linear response-plateau model describing the dependency of deviations from reference protein content (%N DM) for different leaf groups each consisting of 5 leaves of field grown cauliflower.

<table>
<thead>
<tr>
<th>Group</th>
<th>N(_{\text{min, crit}}) (±sd)</th>
<th>Slope (±sd)</th>
<th>(r^2)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>L 11-15</td>
<td>32.65 (±5.07)</td>
<td>-1.86 (±0.34)</td>
<td>0.75</td>
<td>30</td>
</tr>
<tr>
<td>L 16-20</td>
<td>25.56 (±2.53)</td>
<td>-1.95 (±0.27)</td>
<td>0.86</td>
<td>26</td>
</tr>
<tr>
<td>L 21-25</td>
<td>22.63 (±2.51)</td>
<td>-1.88 (±0.32)</td>
<td>0.85</td>
<td>22</td>
</tr>
</tbody>
</table>
Fig. 6-7: Deviation from reference nitrogen content as a function of the soil mineral nitrate content (0-60 cm) for different leaf groups of cauliflower plants. For parameters of the regression lines see Table 6-6.
Fig. 6-8  Protein N content (% DM) of cauliflower leaf groups under optimal nitrogen supply as dependent on the leaf area. For parameters of linear regressions see Table 6-7.
Fig. 6-9: Deviation from reference protein N content as a function of the soil mineral nitrate content (0-60cm) for different leaf groups of cauliflower plants. For parameters of the regression lines see Table 6-8.
From the results presented in Fig. 6-5 and Table 6-3 one may conclude that there exists a general sink priority for nitrogen of the generative organs. However, the situation is somewhat more complex as the results in Table 6-6, Fig. 6-7, Table 6-8 and Fig. 6-9 clearly show. The older leaves, situated deeper in the canopy clearly reduce their total nitrogen content already at much higher levels than the younger leaf groups, which seem to lower their nitrogen contents at a soil nitrogen level comparable to the curd. Looking at the response of the leaf protein N contents, however, it becomes clear that much of this differentiation between older and younger leaf groups and between leaves and the curd is only due to differences in nitrate nitrogen.
Chapter 6

Daily average incident irradiance (W PAR m$^{-2}$)

Nitrate nitrogen fraction (-)

0 20 40 60 80 100

0.0 0.1 0.2 0.3 0.4 0.5

6-10 -net
6-10 +net
11-15 -net
11-15 +net
16-20 -net
16-20 +net

Fig. 6-11: Nitrate nitrogen fraction of total nitrogen of cauliflower leaves as a function of daily average irradiance for different leaf groups as well as shaded and unshaded plants. Data are from the 1996 field experiment and were selected for soil nitrate nitrogen 0-60 cm $>$ 100 kg N ha$^{-1}$. The regression line shown is:

$$y = 0.2456 \pm 0.0188 - 0.0023(\pm 0.0004)x, \quad r^2 = 0.67, \quad n=23.$$ 

One may speculate that the differentiation of nitrate and protein nitrogen in their response to the soil nitrate level may be caused by the well documented fact of two nitrogen uptake systems with differentiated nitrate affinity (Peuke and Kaiser, 1996). However, within the interpretation of static statistical dependencies between soil nitrate levels and plant nitrogen contents one has to bear in mind the fact that they are caused by dynamic processes and disregarding the time scale may introduce severe errors. Therefore, this difference may also be explained by a more rapid translocation of the nitrate N pool rather than by two different critical Nmin levels for nitrate and protein nitrogen due to two distinct uptake systems.

A substantial decline of protein N and therefore of the net assimilation rate occurs at quite low levels of soil nitrate (Fig. 6-8). This is in accordance with model calculations.
which predict very low critical soil nitrogen levels for most arable and vegetable crops because of the high mobility of the nitrate ion in the soil solution (De Willigen and Van Noordwijk, 1987a; Kage, 1997). However, often the results from simulation studies concerning nitrate availability contradict with empirical results (Wiesler and Horst, 1994a). The results presented here therefore may help to calibrate process oriented nitrogen uptake models. After such a calibration such models may be able to predict critical soil nitrogen levels from their functional dependence on rooting pattern, soil moisture and the needed nitrogen uptake rate of a crop.

The decline of average shoot nitrogen contents with increasing shoot dry matter for cauliflower is much less than as described for some arable crops (Greenwood et al., 1990; Sheehy et al., 1998). Possible reasons may be the short growing period which limits the amount of N that can be translocated from older leaves situated deeper in the canopy to the generative organs. This may also explain the almost missing adaptation of the N content of cauliflower leaves to a changing radiation environment. However, adaptations of leaf nitrogen contents to changing radiation environments in other species seem to be possible with time spans of about one week (Evans, 1993).

However, also the absence of a significant booting in cauliflower until commercial maturity and the therefore lower portion of stem dry matter may explain the marked difference to other crops. Leaf/Stem dry matter ratios of cauliflower are usually well above 4 (Fig. 2-4) and therefore much higher than values of less than 1 reported for oilseed rape and winter wheat (Colnenne et al. 1998). Also Booij et al. (1996) found for brussels sprouts and leeks a smaller decline of shoot nitrogen contents with increasing shoot dry matter than for arable crops, however, interpreted this differences by a higher N availability for vegetable crops up to the end of the growing season.

6.5. Conclusions

The derived functional relationships between organ size and nitrogen contents may be used to derive values for estimating crop’s nitrogen demand within a the crop simulation model. They also clearly demonstrate the need for a differentiation between nitrate and protein N in any model of the N dynamics of the cauliflower crop, since the nitrate pool consists of significant fractions of total plant nitrogen, is influenced by the radiation environment and the N supply in a different way than the protein fraction.
7. Root growth of cauliflower (*Brassica oleracea* L. *botrytis*) under unstressed conditions: measurement and modelling

Abstract

7.1. Introduction

7.2. Material and Methods

7.3. Model

7.4. Parameter estimation and statistics

7.5. Results

7.6. Discussion

7.7. Conclusions

7.8. Appendix
Abstract

Root observations were carried out on cauliflower using the minirhizotron and the soil core method in two years on two locations with different soil types, a loess loam and a humic loamy sand. Total root length (RL) (cm$^2$ cm$^{-2}$) of cauliflower was correlated to total shoot dry weight ($W_{sh}$) (g m$^{-2}$) $RL = 0.0124(±0.005)W_{sh}$, $r^2 = 0.76$. There was an acceptable correlation ($r^2 = 0.88$) between the minirhizotron and the soil core methods for the sub-soil data, whereas the minirhizotron method underestimated rooting intensity for the top soil. Changes in rooting depth over time could be described for both soil types using a segmented function of temperature sum, consisting of an early exponential and a later linear phase. The increase of rooting depth during the linear phase was $0.107(±0.01)$ cm °C$^{-1}$.d$^{-1}$.

A simple descriptive root growth model based on the assumptions of a negative exponential decline of root length density (RLD) with soil depth, of a fixed ratio of RLD at the top of the soil profile and at rooting depth ($R_{RLD}$) and of a fixed fraction of dry matter increase allocated to fine-roots ($f_{fr}$) was formulated and used to describe the temporal and spatial variation of RLD found in the field. Slightly different estimates of $f_{fr}$ and of $R_{RLD}$ could be found for the different soil types, indicating a higher fraction of fine-root dry matter for the loess loam soil and a somewhat deeper root system for the humic loamy sand soil. A cross validation using the parameter values obtained from adjusting to the rooting data of one soil type for predicting RLD values of the other soil type, however, indicated that still quite satisfactory estimates ($r^2 = 0.91$ and 0.95) of RLD could be obtained.
7.1. Introduction

Fertilisation and irrigation supply regimes aiming to optimise resource use efficiency have to take into account the temporal and spatial rooting pattern of a crop (Schenk et al., 1991). The development of such strategies may strongly be facilitated by the use of well calibrated crop growth models which include modules that are able to predict these patterns with sufficient accuracy (Benjamin et al., 1996).

In intensively managed vegetable cropping systems the relevance of appropriate root growth models is high, because under these conditions often considerable amounts of nitrate are leached into the subsoil (Hähndel, 1993 De Neve and Hofman, 1998) where nitrate availability may become low because of low root length density (Kuhlmann et al., 1989; van Noordwijk, 1993; Wiesler, 1994; Kage, 1997). The amount and the time when these nitrogen amounts become available can only be predicted with detailed knowledge of the root growth patterns of a particular crop in combination with appropriate models for nutrient transport to the root system (Baldwin, 1973; de Willigen, 1987; Van Noordwijk, 1996; Kage, 1997). Because of the higher mobility of water compared with nitrate, critical values of root length density for water uptake very low (Kage and Ehlers, 1996) and models which predict rooting depth (Chapman et al., 1993; Groot, 1987) may be sufficient for many practical purposes like irrigation scheduling despite the fact that absolute rooting density and spatial arrangement of the roots influences water availability (Droogers et al., 1997; Tardieu et al., 1992).

The availability of rooting data for vegetable crops is still limited, but older studies (Fröhlich, 1956; Greenwood et al., 1982) are now supplemented by more recent work (Jackson and Bloom, 1990; Jackson and Stivers, 1993; Smit et al., 1996; Thorup-Kristensen, 1998; Thorup-Kristensen and Van den Boogaard, 1998) often using the minirhizotron technique (Taylor, 1987). This method has several advantages like moderate time consumption, non destructivity and the possibility to study root turn-over (Cheng et al., 1991; Van Noordwijk et al., 1994). However, it needs to be calibrated using core sampling methods (Box and Ramseur, 1993; Majdi et al., 1992; Upchurch, 1987) if absolute values of RLD are desired.

According to Van Noordwijk (1996) approaches for root growth models within crop growth models may be categorised in a) simple descriptive functions of the temporal
and spatial root distribution without any feedback between shoot growth and root growth and distribution (Gerwitz and Page, 1974), b) models including the interaction of root and shoot growth based on their functional equilibrium (Brouwer and Wit, 1969; Savin et al., 1994) but describing spatial root distribution still with empirical functions and c) models which also take into account responses of root expansion to local growing conditions. e.g. nutrient or water supply (Asseng et al., 1997; Grant, 1993; Jones et al., 1991; Manschadi et al., 1998; Pages and Jordan, 1991). Van Noordwijk and Van de Geijn (1996) state that for most applications quantifying the root effects on above ground processes, models of type ‘b’ may be more appropriate because they are more robust and more easily parameterised than models at a higher level of complexity.

The aim of the presented study is to quantify root growth and distribution of field grown cauliflower on different soil types in relation to above ground dry matter production. Thereby the minirhizotron and soil core method were used. The obtained data were used to elaborate and parameterise a root growth model for cauliflower. This was done within the context of an existing crop growth model for cauliflower (chapter 2). Such a calibrated root growth model may contribute to model based optimisations of fertilisation strategies.

### 7.2. Material and Methods

The field experiments were carried out on two different locations. One location (Hannover) was on the campus of the department of horticulture in Hannover, Germany. There, the soil type is a loamy humic sand with 1.5% C, 78% sand, 10% silt and 6% clay in the plough layer, 0-30 cm depth. The second location (Ruthe), on an experimental station situated about 15 km south of Hannover, has a loess loam with 1% C, 10% sand, 80% silt and 10% clay in the plough layer of 30 cm depth.

The experimental layout at Hannover in 1994 was a two factorial split plot design with two nitrogen fertilisation (normal/reduced) as sub-units, two irrigation levels (irrigated/not irrigated) as main units and four replications as randomised blocks. Rooting data were collected only from the irrigated treatment. In this experiment birds attacked the plants shortly before the last harvest, which resulted in some underestimation of crop productivity during the last part of the growth period. In 1996 the experiment was a completely randomised block design with 3 irrigation treatments.
and 4 replications from which only data of the optimally irrigated treatment are presented. The experiment at ‘Ruthe’ is a long-term rotational experiment consisting of two crop rotations, two tillage regimes, and two nitrogen fertilisation levels with three replications. In this experiment root data were collected only from the mouldboard tillage plots. Nitrogen was given in all experiments as ammonium nitrate according to the N_{min} fertilisation schedule (Scharpf and Wehrmann, 1975). For cauliflower this defines a target supply level of 300 kg N/ha including the soil nitrate from 0 to 60 cm depth. Reduced fertilised plots received 70% of this supply. The planting density was 4 plants m^{-2} in a 0.5·0.5 m pattern for all experiments except for the experiment in 1996 at Hannover where the planting density was 3.3 plants m^{-2} (0.5·0.6m). The cultivar “Fremont” was used in all experiments. Planting dates are summarised in Table 1. General crop husbandry was as described in (chapter 2).

Soil cores were extracted on one or two sampling dates per experiment (Table 1) with a special root auger of 8 cm diameter (Eijkelkamp Agriresearch Equipment, Giesbeek, NL) down to a depth of 90 cm. Cores were divided into 10 cm depth increments except for the loess loam experiment in 1996, where 15 cm increments were used. Samples were taken at two positions within a field plot, one beneath a cauliflower plant and one in a mid-row position. Soil cores were stored at 4°C until roots were washed out over a 1.25 mm sieve and root length was determined after removing organic debris from the sample using the method of Newman (1966).

Two minirhizotron tubes made of polyacryl with an outer diameter of 4.6 cm and a total length of 120 cm were installed per plot at an angle deviating 30° from the vertical to avoid preferential root growth along the tubes (Bragg et al., 1983). The upper parts of the tubes were painted black and closed with a rubber stopper to avoid light penetration (Levan et al., 1987). Holes for the tubes were drilled by hand-driven soil augers in a two step procedure. First, an auger of a diameter of 4 cm was used for a pilot hole, followed by a second spiral auger of 4.5 cm diameter. The minirhizotron tubes usually could be installed manually into the resulting hole with slight pressure indicating a close fit of the tube to the soil without severe soil compaction in the vicinity of the tube.
Table 7-1: Planting dates, dates of root observations in the field experiments used in this study.

<table>
<thead>
<tr>
<th>Year</th>
<th>Activity</th>
<th>Loamy sand</th>
<th>Loess loam</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>Planting</td>
<td>March 31</td>
<td>April 7</td>
</tr>
<tr>
<td></td>
<td>Installation of tubes</td>
<td>April 6</td>
<td>April 8</td>
</tr>
<tr>
<td></td>
<td>Minirhizotron observations</td>
<td>May 26</td>
<td>June 1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 08</td>
<td>June 14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 23</td>
<td>June 29</td>
</tr>
<tr>
<td></td>
<td></td>
<td>July 04</td>
<td>July 12</td>
</tr>
<tr>
<td></td>
<td>Soil core extractions</td>
<td>July 5</td>
<td>June 15</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>July 11</td>
</tr>
<tr>
<td>1996</td>
<td>Planting</td>
<td>June 27</td>
<td>April 9</td>
</tr>
<tr>
<td></td>
<td>Installation of tubes</td>
<td>July 9</td>
<td>April 17</td>
</tr>
<tr>
<td></td>
<td>Minirhizotron observations</td>
<td>August 2</td>
<td>June 1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August 9</td>
<td>June 14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August 15</td>
<td>June 29</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August 22</td>
<td>July 12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August 27</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Soil core extractions</td>
<td>August 29</td>
<td>July 1</td>
</tr>
</tbody>
</table>

For root observations an endoscope equipped with a glass fiber light source (Richard Wolf GmbH, Knittlingen, Germany) of a total length of 180 cm and a diameter of 1.8 cm was used. The view of the endoscope was at the right angle to its main axis and the aperture angle of the endoscope lens was 60°. To ensure a constant distance between the endoscope lens and the tube surface the endoscope was fixed within the tube by means of two PVC rings attached 15 cm from the bottom of the endoscope 10 cm apart. To facilitate an inspection of the minirhizotron tubes in effective soil depth increments of 5 cm at an installation angle of 30°, the endoscope was marked with rings in 5.77 cm spacings. Observations were taken from every tube in two view directions each deviating 45° from of the perpendicular in effective vertical increments of 5 cm. In 1994 all inspections were recorded using a video camera mounted on top of the endoscope, whereby video as well as audio data for location identification were stored using a
battery driven video recorder. Thereafter video tapes were analysed in the laboratory, using the scoring scheme of Maertens, 1987; Fig. 7-1). In 1996 root observations were directly converted into root score values at the field plot. For correlation with soil core measurements the scores were pooled according to the respective spatial aggregation of the soil core data.

Tap root extraction was performed using a spade by excavating a single cauliflower plant to a soil depth of 30 cm. The above-ground plant parts were cut off for further analysis and the remaining tap root was washed thoroughly using an intensive jet of water until all soil was removed. Afterwards the root parts were oven dried at 70° and 105° C and weighed.

### 7.3. Model

The model module outlined in the following section aims to calculate the root growth and distribution of cauliflower based on a given total dry matter production rate, a simple dry matter partitioning scheme and some easily determined relationships describing the increase of rooting depth and the vertical root distribution. Thereby the root system of cauliflower is divided into two parts, a tap-root part mainly fulfilling supporting functions for the stem and a fine-root part responsible for water and nutrient uptake. Fine-root growth is modelled with respect to total length, depth increase and vertical root distribution.
7.3.1. Tap root growth

The whole-plant dry matter growth rate, \(\frac{dW}{dt}\), \((g \cdot m^{-2} \cdot d^{-1})\) is the sum of the growth rate of the shoot, \(\frac{dW_{sh}}{dt}\), the growth rates of the tap root, \(\frac{dW_{tR}}{dt}\), and the fine-roots, \(\frac{dW_{fR}}{dt}\):

\[
\frac{dW}{dt} = \frac{dW_{sh}}{dt} + \frac{dW_{tR}}{dt} + \frac{dW_{fR}}{dt} \tag{7-1}
\]

If allometric growth of the shoot and the tap root is assumed, as was found for the relationship between leaf and stem dry matter in cauliflower (Chapter 2) the relationship between the natural logarithms of shoot and tap root dry matter is linear:

\[
\ln W_{tR} = p_{tR} + o_{tR} \cdot \ln W_{sh} \tag{7-2}
\]

The parameters \(o_{tR}\) and \(p_{tR}\) represent constants, which may be easily derived from linear regression analysis of double logarithmic plots of tap root versus shoot dry matter. Following the analysis of chapter 2 and assuming that a certain fraction of total dry matter growth rate, \(f_{fR}\), is allocated to the fine roots the following equation is obtained (for details of derivation see appendix):

\[
\frac{dW_{sh}}{dt} = \frac{dW}{dt} \left( \frac{1 - f_{fR}}{1 + e^{p_{tR} o_{tR} W_{sh}^{o_{tR} - 1}}} \right) \tag{7-3}
\]

which expresses the shoot dry matter growth rate as a function of the whole-plant growth rate, the standing shoot dry matter, and the fraction of dry matter allocated to the fine roots.

Assuming that a certain fraction of total dry matter growth rate, \(f_{fR}\), is allocated to the fine root fraction the fine root growth rate simply is:

\[
\frac{dW_{fr}}{dt} = f_{fR} \cdot \frac{dW}{dt} \tag{7-4}
\]
Tap root growth then simply is calculated by inserting Eqn. 7-3 and Eqn. 7-4 into Eqn. 7-1, and solving for $dW_t/dt$:

$$\frac{dW_{tR}}{dt} = \frac{dW_t}{dt} - \frac{dW_t}{dt} \left(1 - f_{fR} \cdot \frac{1}{1 + e^{p_{in}o_{fR}W_{sh}^{o_{sh}}}}\right) - \frac{dW_t}{dt} \cdot f_{fR} \cdot f_{fR} \cdot f_{fR}$$

(7-5a)

which may be further simplified to:

$$\frac{dW_{fR}}{dt} = \frac{dW_t}{dt} \left(e^{p_{in}o_{fR}W_{sh}^{o_{sh}}}(1 - f_{fR}) \right)$$

(7-5b)

### 7.3.2. Fine-root growth

If the fraction of dry matter increase attributed to fine-root growth, $f_{fR}$, is known, the increase of total fine-root length $dR_{L}/dt$ (cm m$^{-2}$ d$^{-1}$) may simply be calculated from the total dry weight increase (g m$^{-2}$ d$^{-1}$) and the average specific root length $SRL$ (cm g$^{-1}$).

$$\frac{dRL}{dt} = \frac{dW_t}{dt} \cdot f_{fR} \cdot SRL$$

(7-6)

The value of $SRL$ may be regarded as a parameter or calculated from the average diameter and the average dry matter content of the roots. Here, a constant value of 7000 cm g DM$^{-1}$ was used which was derived from experiments with cauliflower grown in large containers filled with loess loam soil (Kochler, unpublished results).

### 7.3.3. Rooting depth

Rooting depth $z_r$ (cm) is often found to increase linearly with temperature sum within certain development stages, but lag phases in rooting depth increase (Thorup-Kristensen, 1998; Thorup-Kristensen and Van den Boogaard, 1998) as well as diminishing rooting depth increases in later developmental stages (Jaafar et al., 1993; Masse et al., 1991) have been observed. As physiological maturity is not reached in cauliflower crops for commercial vegetable production, we used a combination of an early exponential increase followed by a linear increase in rooting depth for rooting depth description.
During the first phase rooting depth increase, \( \frac{dz_r}{dt} \) \( \text{cm} \cdot \text{d}^{-1} \) therefore is:

\[
\frac{dz_r}{dt} = a_{zr} \cdot (T_a - T_b) \cdot z_r
\]

(7-7)

Where \( T_a \) (°C) is the daily mean of air temperature, \( T_b \) (°C) is the base temperature for root growth and \( a_{zr} \) is a constant (°C\(^{-1}\)d\(^{-1}\)).

This equation can be integrated:

\[
z_r = z_{r0} \cdot e^{a_{zr} \cdot TS}
\]

(7-8)

where \( z_{r0} \) is the rooting depth at the day of transplanting and TS the sum of average daily temperatures above the base temperature, which we assumed to be 0 °C.

During the linear phase rooting depth increase is simply:

\[
\frac{dz_r}{dt} = b_{zr} \cdot (T_a - T_b)
\]

(7-9)

where \( b_{zr} \) (cm °C\(^{-1}\)d\(^{-1}\)) is another constant.

In order to obtain a continuously derivable function the exponential and the linear part of the function have to predict the same rooting depth increase at the switching point from one part to the other. Therefore, by combining the right hand sides of equation (7-7) and (7-9) and solving for \( z_r \) at this switching point, \( z_{rc} \), where maximum rooting depth increase is reached can be calculated:

\[
z_{rc} = \frac{b_{zr}}{a_{zr}}
\]

(7-10)

The temperature sum at which the rooting depth increase switches from the exponential to the linear phase, \( TS_{crit} \), is obtained by substituting \( z_{rc} \) from Eqn. 7-10 for \( z_r \) in Eqn. 7-8. Rearranging gives:

\[
TS_{crit} = \frac{\ln\left(\frac{z_{rc}}{z_{r0}}\right)}{a_{zr}}
\]

(7-11)
The rooting depth at any time after the plants received the critical temperature sum can now be calculated with the following equation:

\[ z_r = z_{rc} + b_z \cdot (TS - TS_{crit}) \]  

(7-12)

### 7.3.4. Vertical root distribution

The root length density, RLD, (cm\( \cdot \)cm\(^{-3} \)) of many annual arable and vegetable crops decreases approximately exponentially with soil depth (Barraclough, 1984; Gerwitz and Page, 1974; Greenwood et al., 1982):

\[ RLD = RLD_0 \cdot e^{-k_r \cdot z} \]  

(7-13)

where the constant \( k_r \) (cm\(^{-1} \)) is the fractional decrease in RLD per unit increase of soil depth and RLD\(_0\) is the root length density at zero soil depth.

Integration of Eqn. 7-13 from \( z=0 \) to a depth \( z=z_r \) were the root length density is very low yields the root length RL (cm\( \cdot \)cm\(^{-2} \)):

\[ RL = \int_{z=0}^{z=z_r} RLD_0 \cdot e^{-k_r \cdot z} \cdot dz = \frac{RLD_0}{k_r} \cdot (1 - e^{-k_r \cdot z_r}) \]  

(7-14)

The second term of Eqn. 7-14 approaches 1 if the product of \( k_r \) and \( z_r \) is high.

To calculate the average rooting density RLD\(_{av}\) (cm\( \cdot \)cm\(^{-3} \)) within a certain soil layer located between two soil depths \( z_1 \) and \( z_2 \) Eqn. 7-14 may be set up for both depths. The difference between RL at \( z_2 \) and \( z_1 \) divided by the distance \( z_2-z_1 \) gives the desired value of RLD\(_{av}\):

\[ RLD_{av} = \frac{RLD_0 \cdot (e^{-k_r \cdot z_1} - e^{-k_r \cdot z_2})}{k_r \cdot (z_2 - z_1)} \]  

(7-15)

At the moment \( k_r \) and RLD\(_0\) remain unknown parameters.
Eqn. 7-14 may then rearranged to calculate RLD₀ from \( z_r \), which is given from Eqn. 7-7 to 7-12) and RL which can be derived from numerical integration of Eqn. 7-6:

\[
RLD₀ = RL \cdot k_r \frac{1}{1 - e^{-k_r z_r}} \tag{7-16}
\]

Using Eqn. 7-13 for the depth \( z = z_r \) and introducing a new parameter, \( r_{RLD} \), describing the ratio of RLD at \( z_r \), RLD₂r, and RLD₀ the following identity can be found for the parameter \( k_r \):

\[
k_r = -\frac{\ln \left( \frac{RLD_{z_r}}{RLD₀} \right)}{z_r} = -\frac{\ln (r_{RLD})}{z_r} \tag{7-17}
\]

Thereby, the introduction of \( r_{RLD} \) avoids the necessity of using an iterative solution of the above set of equations.

### 7.4. Parameter estimation and statistics

The above algorithms were implemented as a submodel for root growth and as a modified partitioning submodel for cauliflower within the HUME modelling environment (Kage and Stützel, 1999a) and combined with other submodels for light use efficiency based calculation of dry matter production and development (Chapter 2). The HUME modelling environment supports parameter estimation based on the Marquardt algorithm (Marquardt, 1963) using an algorithm from Press et al. (1986).

To calculate the increase of total root length (Eqn. 7-6) the fraction of dry matter increase attributed to fine root growth, \( f_R \), the specific root length and the total dry matter growth rate need to be known. An estimate of total dry matter growth rate may be obtained from derivatives of fitted growth curves or from more complex crop growth models. We used the latter approach and adopted for this purpose a light use efficiency (LUE) based dry matter production module (Chapter 2) in combination with model modules for predicting development and dry matter partitioning of cauliflower (Chapter 2).
The dry matter production model module used assumes a linearly decreasing LUE with increasing levels of daily radiation according to the equation:

$$\frac{dW_t}{dt} = Q \cdot (LUE_0 - LUE_{\text{dec}} \cdot \text{PAR})$$

where $Q$ is the amount photosynthetic radiation intercepted by the canopy (MJ·m$^{-2}$·d$^{-1}$). $LUE_0$ (g DM·MJ$^{-1}$) and $LUE_{\text{dec}}$ (g DM·MJ$^{-2}$·m$^{-2}$·d$^{-1}$) are parameters describing a function of a linear decrease of LUE with the daily sum of photosynthetically active radiation, PAR (MJ·m$^{-2}$·d$^{-1}$). The parameter $LUE_0$ had to be re-adjusted to take into account the growth of the tap root and the fine-roots, which the previous version of the module did not consider. As objective function the un-weighted squared sum of measured and simulated shoot dry weight of all normal fertilised treatments was used. The value of $LUE_{\text{dec}}$, however, was left unchanged at 0.36 (g DM·MJ$^{-2}$·m$^{-2}$·d$^{-1}$).

The parameters $f_R$ (Eqn. 7-6) and $r_{RLD}$ (Eqn. 7-17) were estimated by minimising the unweighted square sum of measured and simulated RLD values. Measured values are obtained either directly from soil core measurements or are derived from minirhizotron observation data using an empirical regression equation.

The parameter estimation procedure for the parameter $LUE_0$ from the dry matter production module and the parameters $f_R$ and $r_{RLD}$ from the root growth module were performed separately in an iterative way for the whole data set, until no further change of parameter values occurred. Specific estimates of $f_R$ and $r_{RLD}$ for parts of the data set then were made using the $LUE_0$ value obtained for the whole data set.

All other statistical analyses were performed using the procedures ANOVA, REG and NLIN from the SAS system (SAS Institute, 1988).

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

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

(7-19)
Where $y_i$ is the value of the $i^{th}$ observation, $\hat{y}_i$ is the $i^{th}$ model prediction and $\bar{y}$ is the average of the observations. Modelling efficiency approaches one for complete agreement between simulated and measured values, but may also become negative if the model describes the data less well than the observation mean.

### 7.5. Results

A close linear relationship exists between the natural logarithms of tap root and shoot dry weight (Fig. 7-2), which was not significantly influenced by the level of nitrogen supply in our experiments. From this linear regression the parameters of $p_{R}$ and $o_{R}$ of Eqn. 7-2 are estimated to be $-2.221 \pm 0.0133$ and $0.9501 \pm 0.0246$ (Fig. 7-2).
Likewise, the root length density data from all experiments showed no significant difference between the nitrogen treatments (Fig. 7-3), even for the 1996 experiment on the loess loam location where a slight tendency towards higher RLD values of the normal-fertilised treatment in the subsoil could be found. The 30% reduction of N supply had no significant effect on total plant dry matter production in our experiments (data not shown). The differences between the RLD values for the two sampling positions (near plant, inter row) were not significant (data not shown). The absolute values of RLD at the end of the growing season were in the range of 1-3 cm cm\(^{-3}\) in the upper 10 cm and about 0.1 cm cm\(^{-3}\) in 80-90 cm soil depth. The decrease with depth is in general linear on a logarithmic scale or negative exponential for non-transformed values. Increase of RLD from June 15 to July 11 on the loess loam experiment in 1994 was substantial. In the soil depth of 50-60 cm, for instance, the RLD increased from about 0.1 cm cm\(^{-3}\) to...
nearly 1 cm cm$^{-3}$. Eqn. 7-13 then was used to summarise the soil core observations from different soil depths, giving estimates of RLD$_0$ and $k_r$ for the different sampling dates from which also RL may be estimated (Eqn. 7-14). Thereby the median depth of the soil cores was taken for $z$. Again, there were no significantly different estimates of $k_r$ and RLD$_0$ for the different fertilisation treatments, with the exception of the 1996 loess loam data. Here the significant different estimates of RLD$_0$ and $k_r$ were obtained for the normal and reduced fertilised treatment. There was substantial variation in total root length (Fig. 7-3). This variation is related to differences in shoot dry matter (Fig. 7-5, Fig. 7-4). Because for some soil core measurement data no corresponding measured shoot dry matter were available, we used the model interpolation from measured values of shoot dry matter (Fig. 7-4). There is an indication that the ratio of total root length to shoot dry matter is higher for the reduced fertilisation plots, but this effect was not significant (Fig. 7-5).
Fig. 7-3: Root length density of cauliflower determined by the soil core method from 2 years and two locations in northern Germany. Bars indicate sample standard error.
Fig. 7-4: Measured and simulated shoot dry matter of cauliflower from 2 years and two different soil types. Error bars indicate standard error of the sample. Simulations are performed with a light use efficiency adjusted to the measured data from the normal fertilised plots.
Table 7-2: Parameters $RLD_0$ and $k_r$ ($\pm$SE) together with the coefficient of determination, $r^2$, of the negative exponential function describing the decrease of root length density with soil depth (Eqn. 7-13). Also shown are the corresponding calculated total root length $RL = RLD_0/k_r$ (Eqn. 7-14) and the simulated total above-ground dry matter, $W_{sh}$, of the cauliflower crops. Data from two years at two different soil types (loess loam, loamy sand) with two different N-supply levels (normal/reduced).

<table>
<thead>
<tr>
<th>Date</th>
<th>Soil</th>
<th>Fert.</th>
<th>$RLD_0$ (cm$^3$cm$^{-3}$)</th>
<th>$k_r$ (cm$^{-1}$)</th>
<th>$r^2$</th>
<th>$RL$ (cm$^3$cm$^{-2}$)</th>
<th>$W_{sh}$ (g m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994 June 15</td>
<td>Loess loam</td>
<td>Norm.</td>
<td>3.31 ($\pm$0.32)</td>
<td>0.052 ($\pm$0.007)</td>
<td>0.96</td>
<td>64</td>
<td>539.3</td>
</tr>
<tr>
<td>1994 June 15</td>
<td>Loess loam</td>
<td>Red.</td>
<td>3.78 ($\pm$0.16)</td>
<td>0.056 ($\pm$0.003)</td>
<td>0.99</td>
<td>67</td>
<td>421.9</td>
</tr>
<tr>
<td>1994 July 11</td>
<td>Loess loam</td>
<td>Norm.</td>
<td>4.00 ($\pm$0.37)</td>
<td>0.032 ($\pm$0.004)</td>
<td>0.93</td>
<td>127</td>
<td>1257.4</td>
</tr>
<tr>
<td>1994 July 11</td>
<td>Loess loam</td>
<td>Red.</td>
<td>3.73 ($\pm$0.32)</td>
<td>0.031 ($\pm$0.004)</td>
<td>0.94</td>
<td>122</td>
<td>1045.1</td>
</tr>
<tr>
<td>1994 July 05</td>
<td>Loamy sand</td>
<td>Norm.</td>
<td>2.74 ($\pm$0.18)</td>
<td>0.032 ($\pm$0.003)</td>
<td>0.96</td>
<td>86</td>
<td>948.9</td>
</tr>
<tr>
<td>1994 July 05</td>
<td>Loamy sand</td>
<td>Red.</td>
<td>2.96 ($\pm$0.42)</td>
<td>0.033 ($\pm$0.007)</td>
<td>0.84</td>
<td>89</td>
<td>812.8</td>
</tr>
<tr>
<td>1996 July 01</td>
<td>Loess loam</td>
<td>Norm.</td>
<td>1.60 ($\pm$0.27)</td>
<td>0.025 ($\pm$0.006)</td>
<td>0.86</td>
<td>64</td>
<td>752.7</td>
</tr>
<tr>
<td>1996 July 01</td>
<td>Loess loam</td>
<td>Red.</td>
<td>3.93 ($\pm$0.10)</td>
<td>0.068 ($\pm$0.002)</td>
<td>0.99</td>
<td>58</td>
<td>647.7</td>
</tr>
<tr>
<td>1996 August 29</td>
<td>Loamy sand</td>
<td>Norm.</td>
<td>2.74 ($\pm$0.29)</td>
<td>0.049 ($\pm$0.007)</td>
<td>0.94</td>
<td>55</td>
<td>647.7</td>
</tr>
</tbody>
</table>
Fig. 7-5: Relationship between total root length (RL) obtained from fitting a negative exponential equation to data from soil cores (Table 7-2) and simulated shoot dry matter ($W_{sh}$) of cauliflower for two different nitrogen supply rates. Data are from experiments in two years and on two soil types. Regression equation for all data shown is $RL = 0.1024 \pm 0.0053 \cdot W_{sh}, r^2 = 0.76$.

The data obtained from the minirhizotron observations showed no significant differences between the nitrogen treatments. The differences between the sampling locations (near plant, mid row) were also not significant although there was an indication of fewer roots at the inter row position at early observations dates (data not shown). Therefore, all data for one soil depth class were pooled giving one value for each day and observation date. Except for the early sampling dates, where a steadily decrease of score values with soil depth could be found, root scores increased from 0 to about 40 cm soil depth and decreased from there on (Fig. 7-6). This decrease was strongly dependent on sampling date. The absolute values of the root scores and the observed rooting depth increased substantially with time for the subsoil. The increase of rooting depth could well be described using the approach outlined in Eqns. 6-11, indicating a lag phase of
rooting depth increase followed by a linear increase with temperature sum (Fig. 7-7). There were no significant differences in this relationship between years and soil types. Interrow sampling positions tended towards a slightly, but insignificantly longer lag phase than inrow positions (data not shown).

A highly significant relationship could be found between the minirhizotron root scores below 30 cm soil depth and the corresponding RLD values from the soil cores (Fig. 7-8). The non-linear function used here was motivated by the upper limit of root scores of 5. Again, there were no significant differences between years and soil types. Parameters of linear regressions fitted to different sampling dates on the loess loam soil were quite different (Fig. 7-8).

The non-linear function shown in Fig. 7-8 was used to convert the root scores from soil depths > 30 cm into root length density values for all sampling dates where no core measurements were available. These RLD’s and the available RLD data from soil core measurements were used to estimate the fraction of dry matter increase attributed to the fine-roots \( f_r \) and the ratio of RLD at the rooting depth to the RLD at the soil surface, \( r_{RLD} \), as described above.

The value of LUE\(_0\) obtained by adjustment to the measured shoot dry matter data as 7.36(±0.06) g DM MJ\(^{-1}\) for total plant dry matter instead of 6.66 (Chapter 4) for above ground dry matter production. The resulting prediction of shoot dry matter gives a linear regression with an insignificant intercept of \( Y = 0.96 \pm 0.03 \) \( X \), \( r^2 = 0.96 \), n=16 for the data of the normal fertilised treatments (Fig. 7-4).
Fig. 7-6: Root length density scores for cauliflower observed in minirhizotrones from two years and two locations in northern Germany.
The estimated values of \( f_R \) and \( r_{RLD} \) indicate that the fraction of dry matter increase attributed to fine-root growth was higher in the loess loam soil than in the humic loamy sand and that in the humic loamy sand a greater percentage of roots is in the deeper soil layers. There were also marked differences between the two experimental years with respect to the value of \( r_{RLD} \), \( r_{RLD} \) being higher in 1994 than in 1996 (Table 7-3). The model described the total variation found in the experimental data with parameter values obtained from the same data set (Fig. 7-9a), but again the two soil types behaved differently. The descriptive value of the model was generally better for the medium soil depth than for either the upper soil and deeper soil layers (\( z_r \)). However, the parameter values obtained from an adjustment to either the data from the experiments

\[ z_r = z_{r0} \exp(a_{zr} T_{sum}) \text{ for } T_{sum} < \ln((b_{zr}/a_{zr})/z_{r0})/a_{zr} \text{ and } z_r = b_{zr}/a_{zr} + b_{zr} (T_{sum} - \ln((b_{zr}/a_{zr})/z_{r0})/a_{zr}) \].

Parameter values: \( z_{r0} = 6.04(\pm 1.52) \), \( a_{zr} = 0.00394(\pm 0.000384) \), \( b_{zr} = 0.107(\pm 0.00953) \), \( r^2 = 0.953 \), \( n = 14 \).
on humic loamy sand or to the loess loam also gave an acceptable prediction for the
other data group (Fig. 7-9b and c).

### 7.6. Discussion

The aim of the presented paper was to characterise rooting dynamics of cauliflower in
relation to shoot growth using the soil core and the minirhizotron method. The collected
rooting data were used to develop and parameterise a simple empirical root growth
model module which describes and predicts rooting pattern of cauliflower as determined
by temperature sum and crop growth rate.

<table>
<thead>
<tr>
<th>Data set</th>
<th>$f_{R}$</th>
<th>$r_{RLD}$</th>
<th>C</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loess loam</td>
<td>0.120</td>
<td>0.0180</td>
<td>0.59</td>
<td>0.95</td>
</tr>
<tr>
<td></td>
<td>(±0.00530)</td>
<td>(±0.00395)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Loamy sand</td>
<td>0.0984</td>
<td>0.0286</td>
<td>0.49</td>
<td>0.90</td>
</tr>
<tr>
<td></td>
<td>(±0.00512)</td>
<td>(±0.00706)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1994</td>
<td>0.110</td>
<td>0.0257</td>
<td>0.55</td>
<td>0.91</td>
</tr>
<tr>
<td></td>
<td>(±0.00539)</td>
<td>(±0.00615)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1996</td>
<td>0.114</td>
<td>0.0127</td>
<td>0.58</td>
<td>0.95</td>
</tr>
<tr>
<td></td>
<td>(±0.00577)</td>
<td>(±0.00331)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All Data</td>
<td>0.117</td>
<td>0.0210</td>
<td>0.55</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td>(±0.00441)</td>
<td>(±0.00384)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 7-3:** Estimates for parameters $r_{RLD}$ (±SE) (ratio of root length densities at soil
surface to RLD at rooting depth) and fraction of fine root dry weight, $f_{R}$, (±SE) correlation between the parameters, $C$, and modelling efficiency, $EF$. Data
set from four field experiments: two years and two locations with different soil
types (loess loam, loamy sand).
Table 7-4: Slope and intercept of the linear regression of the calculated vs. observed root length density values of cauliflower plants for the different soil depths from the parameterisation procedure as well as $r^2$ of the linear regression, residual mean square error, RMSE, and modelling efficiency, EF.

<table>
<thead>
<tr>
<th>Soil depth (cm)</th>
<th>slope</th>
<th>intercept</th>
<th>$r^2$</th>
<th>n</th>
<th>RMSE</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-10</td>
<td>0.4383</td>
<td>1.5665</td>
<td>0.4422</td>
<td>5</td>
<td>0.3745</td>
<td>-0.4115</td>
</tr>
<tr>
<td>10-20</td>
<td>0.2148</td>
<td>1.4995</td>
<td>0.1450</td>
<td>5</td>
<td>0.4358</td>
<td>-1.9545</td>
</tr>
<tr>
<td>20-30</td>
<td>1.1773</td>
<td>-0.2201</td>
<td>0.5593</td>
<td>5</td>
<td>0.4155</td>
<td>0.5466</td>
</tr>
<tr>
<td>30-40</td>
<td>0.7681</td>
<td>0.0719</td>
<td>0.7336</td>
<td>15</td>
<td>0.2026</td>
<td>0.6476</td>
</tr>
<tr>
<td>40-50</td>
<td>0.9469</td>
<td>0.0349</td>
<td>0.8022</td>
<td>15</td>
<td>0.1357</td>
<td>0.7966</td>
</tr>
<tr>
<td>50-60</td>
<td>0.9935</td>
<td>0.0365</td>
<td>0.8649</td>
<td>13</td>
<td>0.0881</td>
<td>0.8400</td>
</tr>
<tr>
<td>60-70</td>
<td>1.1574</td>
<td>0.0089</td>
<td>0.7653</td>
<td>12</td>
<td>0.1093</td>
<td>0.7097</td>
</tr>
<tr>
<td>70-80</td>
<td>1.0766</td>
<td>0.0085</td>
<td>0.6112</td>
<td>11</td>
<td>0.0990</td>
<td>0.5890</td>
</tr>
<tr>
<td>80-90</td>
<td>0.7271</td>
<td>0.0113</td>
<td>0.7759</td>
<td>11</td>
<td>0.0473</td>
<td>0.5001</td>
</tr>
</tbody>
</table>
Fig. 7-8: Correlation between root scores (sc) from minirhizotron observations and root length density (RLD) of cauliflower as determined by soil core measurements for two different locations and two years for soil depths > 30 cm. The nonlinear regression line for all data is: $\text{RLD} = \ln(1 - \text{sc}/5)/f$, $f = -2.299 \pm 0.099$, $r^2 = 0.83$, $n=28$. The linear regression for loess loam, July 11 1994 (••••) is $y = 0.2191 (\pm 0.1581) + 0.2510 (\pm 0.0460)x$, $r^2 = 0.88$, $n=6$ and for loess loam, June 15 1994 (- - -) is $y = -0.0021 (\pm 0.0632) + 0.0985 (\pm 0.0326)x$, $r^2 = 0.70$, $n=6$. 
Fig. 7-9: Calculated vs. measured root length density (RLD) of cauliflower a) parameterisation using the whole data set for both soil types, b) Validation of the model using the data from the loamy sand soil and the parameter estimations derived from the loess loam soil experiments c) validation of the model using the data values from the loess loam soil and the parameter estimates derived from the RLD values of the loamy sand soil experiments.
The regression equations shown are a) \( y = 0.0233 \pm 0.0299 + 0.9824 \pm 0.0321x \), \( r^2 = 0.92 \) for parameterisation, all data, \( y = -0.0272 \pm 0.0425 + 1.1031 \pm 0.0403x \), \( r^2 = 0.95 \) parameterisation, data from the loamy sand experiments, \( y = 0.0686 \pm 0.0335 + 0.8274 \pm 0.0411x \), \( r^2 = 0.90 \) parameterisation for the data from the loess loam experiments, b) validation \( y = 0.0710 \pm 0.0279 + 0.7669 \pm 0.0341x \), \( r^2 = 0.91 \) for loamy sand, c) validation for loess loam \( y = -0.0819 \pm 0.0420 + 1.3040 \pm 0.0462x \), \( r^2 = 0.95 \).
The minirhizotron method gave unrealistic estimates of the root distribution in the topsoil (Fig. 7-3 and Fig. 7-6). This drawback of the method has been previously observed (Vos and Groenwold, 1987; Wiesler and Horst, 1994b) and may be caused by several factors e.g. soil compaction due to agitating the tube during the measurement, soil drying in the vicinity of tubes due to gaps between soil and tube or light penetration into the minirhizotron tube. However, the method seemed to give reliable values of the rooting depth (Fig. 7-7) and root scores for the subsoil correlated quite well with the RLD values of the soil coring method (Fig. 7-8). The linear regression between the soil core data and minirhizotron scores obtained for the loess loam in 1994 indicate that the relationship between the data from both methods may vary with time even within one crop (Bragg et al., 1983; Wiesler and Horst, 1994b). This problem may partly be overcome by using a non-linear relationship between root scores and root length density values (Fig. 7-8). The limitations of the minirhizotron method in the top-soil region is not in every case very critical since here root length density is usually high enough to rapidly exhaust mobile resources like water and nitrate. The sub-soil region, where the method gives more reliable results seems more relevant for this resources because here low RLD may be critical for uptake (Kage, 1997; Kuhlmann et al., 1989).

From Eqn. 7-14 follows that \( k_r \) decreases with increasing rooting depth. This is in accordance with the results from June 15 and July 11 in 1994 obtained at the loess loam (Fig. 7-4) and those of Greenwood et al. (1982) who found \( k_r \) for cauliflower and other vegetable crops to decrease with increasing total root length. Also, the absolute \( k_r \) values of Greenwood et al. (1982) ranging from about 0.1 for early sampling dates with low total root length to about 0.05 for later states agree quite well with our data (Fig. 7-4). But their reported values of total root length and the ratio of total root length to shoot dry weight for cauliflower are considerably higher. From their data the relationship \( RL = 0.215 (\pm 0.012) \cdot W_{sh}, r^2=0.97 \) was calculated, which predicts almost twice the amount of root length per unit shoot dry weight than we found (Fig. 7-5). This may partly be explained by the fact that the experiments of Greenwood et al. (1982) were carried out with direct-drilled cauliflower seeds and not with transplants as in our experiments. Root growth may substantially be reduced due to the limited volume of the peat cubes in which the cauliflower plants were cultivated during the plant nursery period.

Linear increases of rooting depth with accumulating thermal time (Fig. 7-7) have been found by several authors (Barraclough and Leigh, 1984; Jaafar et al., 1993; Pellerin and
The finding of (Thorup-Kristensen and Van den Boogaard, 1998) that rooting depth of cauliflower increases after a lag phase with a rate of 0.102 cm day\(^{-1}\) °C\(^{-1}\) agrees strikingly well with our data from two different soil types (Fig. 7-7). This indicates that rooting depth development of cauliflower is not strongly dependent on soil conditions as long as critical parameters like bulk density and soil water content are within a certain range optimal for root growth (Barber et al., 1988; Vepraskas, 1988). The lag phase in rooting depth development of cauliflower may be explained by limited assimilate supply to the root system at early growth stages (Aguirrezabal and Tardieu, 1996, March) or by the transplanting shock and the root system disturbance caused by using transplants instead of direct-drilled plants.

One critical point of our model approach may be fact that root density at rooting depth is, according to Eqs. 7-14 and 7-12, changing with changing values of RLD\(_0\) and therefore with total root length and time, because we assume a constant ratio, \(f_{RLD}\), between rooting density at zero soil depth and rooting depth. Rooting depth, however, as we describe it with Eqn. 7-12 using our minirhizotron data (Fig. 7-7) is operationally defined as the deepest soil depth where roots could be detected. This should imply a more or less constant value of RLD at \(z_r\). But this approach avoids the need for an iterative solution of the equation system describing the root distribution (Hansen et al., 1990) and is obviously still able to describe and predict our data with sufficient accuracy (Fig. 7-9, Table 7-3). Furthermore the ratio of root density at the soil surface and at rooting depth is quite low (Table 7-3) and therefore the absolute calculated values of RLD at rooting depth are also low.

Models of root growth can be motivated by the aim to achieve a fundamental understanding of the complex interactions between soil, plant and climatic factors resulting in the immense complexity and plasticity of a plant root system (Jones, 1991; Grant, 1993; Pages, 1991). More applied approaches like the one presented here aim at acceptable descriptions of rooting patterns in time and space (Barraclough and Leigh, 1984; Greenwood et al., 1982) which may facilitate the prediction of the main functional aspects of root growth, like water and nutrient uptake with mechanistic models (De Willigen and Van Noordwijk, 1987a). The presented model is simple and needs only four parameters, i.e. \(\text{f}_{R}\), the fraction of dry matter increase attributed to fine-roots, \(a_{cr}\) and \(b_{cr}\) describing the increase of rooting depth during the early exponential and the
later linear phase, respectively, and $r_{RLD}$, the ratio of root length density at the top of the soil profile and at rooting depth. Additionally, an average value of the specific root length is needed. Such a simple model may be successfully parameterised even with the limited amount of data which are usually available from rooting studies in field experiments. Our parameterisation approach was successful with one examination of root length distribution with the soil core method at the end of the growing season of the crop accompanied by some minirhizotron observations throughout the growing season. Whereas the more time consuming soil core method gives reliable estimates of total root length and its vertical distribution, the minirhizotron method is able to give additional information needed to identify the parameter values for describing the rooting depth development and the change of the vertical root distribution during time. If this approach is able to describe and predict root distribution pattern under altered nitrogen and water limitations remains to be proven. Problems will arise for soil profiles with compacted layers (Barraclough and Weir, 1988; Tardieu, 1988) or under extreme stress situations (Klepper and Rickman, 1990).

7.7. Conclusions

Fine and tap root growth of cauliflower are closely coupled to shoot growth, as indicated by an allometric relationship of tap root and shoot dry weight and a linear relationship of root length to shoot dry weight. The development of rooting depth could successfully be described using an expo-linear function of temperature sum. The vertical root distribution follows the negative exponential decline which has been observed for many other annual agricultural crops. Using this relationships it was possible to construct a simple empirical root growth model module for cauliflower which may facilitate further analysis of root function as a key characteristic for nutrient and water use efficiency. Further refinements of the model may include a value of $f_R$ and rooting depth development depending on the nutrient and water supply of the crop.
7.8. Appendix

Eqn. 7-2 may be transformed to:

\[ W_{tR} = e^{p_w} W_{sh}^{o_{iR}} \quad (7-A1) \]

Differentiation of Eqn. 7-A1 with respect to \( W_{sh} \) results in:

\[ \frac{dW_{tR}}{dW_{sh}} = e^{p_w} o_{iR} W_{sh}^{o_{iR} - 1} \quad (7-A2) \]

Applying the chain rule to the left hand side of Eqn. 7-A2 and rearranging leads to:

\[ \frac{dW_{tR}}{dt} = \frac{dW_{tR}}{dW_{sh}} \frac{dW_{sh}}{dt} \quad (7-A3) \]

Assuming that a certain fraction of total dry matter growth rate, \( f_{iR} \), is allocated to the fine-root fraction the fine root growth rate simply is:

\[ \frac{dW_{fr}}{dt} = f_{fr} \frac{dW_{t}}{dt} \quad (7-A4) \]

From this Eqn. 7-1 may be rewritten:

\[ \frac{dW_{sh}}{dt} = \frac{dW_{t}}{dt} (1 - f_{fr}) - \frac{dW_{tR}}{dt} \quad (7-A5) \]

Introducing Eqn. 7-A2 into Eqn. 7-A3 and substituting for \( dW_{tR}/dt \) in Eqn. 7-A5 and some rearranging gives:

\[ \frac{dW_{sh}}{dt} = \frac{dW_{t}}{dt} \left( \frac{1 - f_{fr}}{1 + e^{p_w} o_{iR} W_{sh}^{o_{iR} - T}} \right) \quad (7-A6) \]
8. Aspects of nitrogen use efficiency of cauliflower I. A simulation modelling based analysis of nitrogen availability under field conditions

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Abstract

Data from two annual and a long term field experiment summing up to 8 crops grown under a differentiated nitrogen supply on a loess loam soil are used for a simulation modelling based analysis of nitrogen availability of cauliflower. The model was built out of components describing root growth, nitrate transport to the roots and the vertical nitrate transport within the soil. Net nitrogen mineralisation was input to the model and was derived from the initial amounts and change of N in plant and soil. N uptake of the plants was derived from a plant growth model described in second part of this paper.

The root observations obtained in two years indicated an increased fraction of dry matter allocated to the fine roots under N deficiency. An adopted version of the root growth model for cauliflower presented in chapter 7 taking this into account described the rooting data with sufficient accuracy ($r^2=0.75$ and 0.80). Based upon a acceptable description of the soil water budget as indicated by agreement between measured and simulated soil water tensions, vertical nitrate movement during the growth period of cauliflower was correctly described. The magnitude of this movement, however, was limited to soil depths of about 60 cm even after periods of high rainfall, because of a high soil water holding capacity. An analysis of the factors determining nitrate availability indicated that apparent mass flow was only of high importance for overfertilised conditions when high amounts of nitrate nitrogen remain in the soil up to the end of the growing season. Otherwise, the dominating fraction of nitrate has to be transported to the roots by diffusion. The single root model for calculating maximum nitrate transport to roots overestimated N availability as indicated by a too low estimated level of soil nitrate N when transport to roots limited N uptake of the plant. The introduction of an restricted uptake activity period of the roots was used to bridge the gap between theoretical calculations and empirical results. However, a probably too short uptake period was needed to give a good agreement between measurements and simulations. Scenario calculations were carried out to obtain functional relationships between N supply and residual soil nitrate levels. Thereby also hypothetical conditions for a sandy soil and possible benefits of split N applications were investigated.
8.1. Introduction

Crops from intensive vegetable cropping systems like cauliflower often have high nitrogen uptake rates because of high nitrogen contents of their organs and high growth rates (Schenk, 1998; Van den Boogaard and Thorup-Kristensen, 1997). However, often these crops also have comparable low total root lengths (Jackson, 1995), especially when cultivated as transplants (Chapter 7; Thorup-Kristensen, 1993a). This agronomic practice shortens their growth period on the field and thereby the time available for the root system to exploit the soil volume. High specific nutrient influx rates therefore have to be maintained throughout the crop’s growing period in order to ensure maximum growth (Burns, 1980). Under similar conditions this is only possible with higher soil nitrogen contents than for crops with higher total root length. Higher residual soil nitrogen contents, however, may lead to leaching losses and therefore to a decrease of the nitrogen use efficiency of the cropping system and to environmental pollution (De Neve and Hofman, 1998).

Because of the high mobility of the nitrate ion in the soil solution most crops are able to exhaust the soil down to very low nitrate concentrations and thereby sustain nitrate influx rates sufficient for satisfying the nitrogen demand of the crop (De Willigen and Van Noordwijk, 1987a). Critical conditions for nitrate availability therefore be found in the sub soil, were rooting density is low (Wiesler and Horst, 1994a) or for very sparse rooted crops (Kage, 1997).

In Chapter 6 it could be shown that for conditions of a loess loam soil under ample water supply amounts of soil mineral nitrogen of about 40-50 kg N ha\(^{-1}\) in the upper 60 cm of the soil profile have to be maintained to sustain leaf protein contents of cauliflower at an optimal level. Such an empirical analysis hampers from the fact that changing soil conditions, an altered water regime or a different distribution of the mineral nitrogen in the soil profile may change considerably this empirical value for critical soil mineral nitrogen contents.

The aim of the presented paper therefore is to analyse the availability of soil nitrogen for cauliflower using a mechanistically model approach. For this purpose we combine a previously published model for root growth of cauliflower (Chapter 7) with a mechanistically model for soil nitrate availability (Baldwin \textit{et al.}, 1973; Kage, 1997)
which is based on the single root approach (Gardner, 1960). Data from two annual and a long term field experiment summing up to 8 crops grown under a differentiated nitrogen supply are used for our analysis. Furthermore a scenario calculations were carried out to quantify potentially leaching losses during the growing period on an hypothetical sandy soil and to derive functional dependencies between nitrogen supply rate and residual soil nitrate levels.

8.2. Material and methods

8.2.1. Field experiments

The field experiments used in this study belong to two different groups. The first group from two annual nitrogen fertilisation trials from 1996 and 1997 (Alt, 1999). Additionally, data from a long term crop rotation experiment are used for further model evaluation. They represent a sub set of the data previously described in Chapter 2, but for this study also the reduced N supply treatments are included in the analysis.

All field experiments were conducted on the same experimental farm located 15 km south of Hannover, Germany, on a typical loess derived hapludalf soil. Crops were established in the field using transplants grown in peat cubes of 4 cm edge length, the average visible leaf number at planting ranged from 2.9 to 4.03 leaves/plant. Crop husbandry in all experiments was regarded to ensure a crop growth not limited by the availability of water. Pesticides were applied when needed to ensure a healthy growth.

Nitrogen fertilisation was given as ammonium nitrate at the time of transplanting only for the annual experiments. Soil nitrate content of 10-15 kg N ha$^{-1}$ in 1996 and 1997 in 0-60 cm were subtracted from 150 (N1), 300 (N2) and 450 kg ha$^{-1}$ (N3) target values. Furthermore a N0 treatment was included, which received no nitrate nitrogen. For the long term experiment a nitrogen fertilisation schedule according to the KNS system (Lorenz et al., 1989) was applied, defining two target values of 130 kg N ha$^{-1}$ from 0-30 cm soil depth at transplanting and of 270 kg N ha$^{-1}$ from 0-60 cm soil depth about 4 weeks after transplanting. The two N treatments received either 100 % of this recommended N supply level or a reduced N supply of 70% of this level in 1994 and 1995 and of 50% of this level in 1996.
Temperature and radiation data were taken from measurements of an automated weather station (Campbell Sci. Ltd., UK) located on the experimental station. Measured values of global radiation were converted to photosynthetic active radiation, $I$, using a factor of 0.5 (Szeicz, 1974). Average values of $I$ and air temperature at 2 m height for the experimental years are shown in Table 8-1.

Soil cores were extracted at the last harvest of the annual experiments in 1996 in all nitrogen treatments and in 1997 in the N0 and N2 treatment only using a special root auger of 8 cm diameter (Eijkelkamp Agriresearch Equipment, Giesbeek, NL) down to a depth of 90 cm in 15 cm increments. Samples were taken at two positions within a field plot, one beneath a cauliflower plant and one in a mid-row position. Soil cores were stored at 4°C until roots were washed out over a 1.25 mm sieve and root length was determined after removing organic debris from the sample using the method of Newman (1966).

Soil mineral N was determined down to a depth of 120 cm in 4 intervals of 30 cm thickness. From every plot 6 auger samples were collected. Soil nitrate N was

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### Table 8-1: Type of experiment (LT=long term, A=annual) year, planting and harvest dates, average incident photosynthetic active radiation, $I$, and average temperature during the growth period of the cauliflower experiments used in this study.

<table>
<thead>
<tr>
<th>Type</th>
<th>Year</th>
<th>Planting Date</th>
<th>Harvest Date</th>
<th>Avg. I (MJ m$^{-2}$ d$^{-1}$)</th>
<th>Avg. Temp. (°C)</th>
<th>No. of N Treatments</th>
</tr>
</thead>
<tbody>
<tr>
<td>LT</td>
<td>1994</td>
<td>97</td>
<td>185</td>
<td>8.13</td>
<td>13.12</td>
<td>2</td>
</tr>
<tr>
<td>LT</td>
<td>1994</td>
<td>207</td>
<td>293</td>
<td>5.45</td>
<td>14.52</td>
<td>2</td>
</tr>
<tr>
<td>LT</td>
<td>1995</td>
<td>94</td>
<td>187</td>
<td>7.59</td>
<td>12.13</td>
<td>2</td>
</tr>
<tr>
<td>LT</td>
<td>1995</td>
<td>200</td>
<td>291</td>
<td>6.10</td>
<td>16.49</td>
<td>2</td>
</tr>
<tr>
<td>LT</td>
<td>1996</td>
<td>100</td>
<td>189</td>
<td>7.41</td>
<td>12.59</td>
<td>2</td>
</tr>
<tr>
<td>LT</td>
<td>1996</td>
<td>200</td>
<td>284</td>
<td>6.18</td>
<td>14.34</td>
<td>2</td>
</tr>
<tr>
<td>A</td>
<td>1996</td>
<td>170</td>
<td>240</td>
<td>7.78</td>
<td>16.08</td>
<td>4</td>
</tr>
<tr>
<td>A</td>
<td>1997</td>
<td>190</td>
<td>258</td>
<td>7.23</td>
<td>18.56</td>
<td>4</td>
</tr>
</tbody>
</table>

Temperature and radiation data were taken from measurements of an automated weather station (Campbell Sci. Ltd., UK) located on the experimental station. Measured values of global radiation were converted to photosynthetic active radiation, $I$, using a factor of 0.5 (Szeicz, 1974). Average values of $I$ and air temperature at 2 m height for the experimental years are shown in Table 8-1.

Soil cores were extracted at the last harvest of the annual experiments in 1996 in all nitrogen treatments and in 1997 in the N0 and N2 treatment only using a special root auger of 8 cm diameter (Eijkelkamp Agriresearch Equipment, Giesbeek, NL) down to a depth of 90 cm in 15 cm increments. Samples were taken at two positions within a field plot, one beneath a cauliflower plant and one in a mid-row position. Soil cores were stored at 4°C until roots were washed out over a 1.25 mm sieve and root length was determined after removing organic debris from the sample using the method of Newman (1966).

Soil mineral N was determined down to a depth of 120 cm in 4 intervals of 30 cm thickness. From every plot 6 auger samples were collected. Soil nitrate N was
measured photometrically at 210 nm after extraction with 0.025 N CaCl₂ (Navone, 1964). One tensiometer per plot was installed shortly after transplanting in depths of 20, 40, 70 and 90 cm, respectively in the 1997 annual experiment in 1997 and in the crops of the long term experiment.

There was generally an exceptionally high variation in the data of soil water tension and soil nitrate for the late planted crops of the long term experiment (Table 8-1). The reasons are the need for irrigations of these crops, which were carried out using a micro sprinkler technique inducing a substantial local variation of water supply and the incorporation of crop residues from the previous cauliflower crop. From these crops only net mineralisation data are presented here. They are, however, used for analysis of crop productivity in the following chapter 9.

8.2.2. Calculation of net mineralisation

Net mineralisation was calculated for every treatment and for periods between soil and plant analyses separately from the data of soil nitrate nitrogen from 0-120 cm and measurements of shoot dry matter and nitrogen content. An additional amount of 10 and 5 % of measured shoot nitrogen was assumed to be located in the root part of the fertilised and unfertilised plants, respectively, and net mineralisation was corrected for that.

8.3. Model

8.3.1. Root Growth

The root growth module is described in Chapter 7, however, modifications are included to account a) for the effects of root ageing on water and nitrogen uptake and b) for the effects of an altered dry matter partitioning under nitrogen stress.

The nitrate uptake properties of roots clearly change during ageing, thereby a decrease of the maximum nitrate capacity can be observed (Reidenbach and Horst, 1997). The assumption that all roots are fully active in nitrate and water uptake, which is often made within crop growth models (Benjamin et al., 1996), therefore is invalid. However, studies on the temporal change of root activity under field conditions are still lacking. We therefore tried to bridge this knowledge gap in a very simplifying way. Roots are
assumed to be fully active during a certain span from their occurrence, active duration, AD, and are assumed to be fully non active afterwards. Using this simplification it is possible to calculate an effective root length $RL_{eff}$ and rooting density $RLD_{eff}$ for all soil layers, $i$, from the total root length and their distribution in different age classes, $j$:

$$RL_{eff_i} = \sum_{j=1}^{j_{dt<AD}} RL_{mat_i,j}$$  \hspace{1cm} (8-1)

The two dimensional matrix $RL_{mat}$ is updated in daily time steps, thereby all elements of the matrix are shifted one step forward in the time dimension, $j$:

$$RL_{i,j} = RL_{i,j-1}$$  \hspace{1cm} (8-2)

The first grid cell in every layer becomes the actual increase in root length, if positive:

$$RL_{i,1} = \max\left(0, \frac{dRL}{dt}\right)$$  \hspace{1cm} (8-3)

From the effective root length, the effective root length density is calculated:

$$RLD_{eff_i} = \frac{RL_{eff_i}}{AZ}$$  \hspace{1cm} (8-4)

It is well known that the fraction of assimilates allocated to the roots increases under restricted nitrogen (Ericsson, 1995) or water supply (Huck et al., 1986) and this behaviour motivated the postulation of the functional equilibrium law (Brouwer, 1962). We consider this effect also in a simplistic manner, assuming that the fraction of assimilates allocated to the fine roots, $f_{fr}$, is up-regulated to a maximum value $f_{fr_{max}}$ during periods of nitrogen deficiency, i.e. when the N demand, $N_{dem}$ is higher than the N supply, $N_{sup}$, and down regulated to the value of unstressed plants $f_{fr_0}$ if the nitrogen supply is sufficient:

$$\frac{df_{fr}}{dt} = \begin{cases} 
   f_{fr} \cdot r_{fr} \left(1 - \frac{f_{fr}}{f_{fr_{max}}}\right) & \text{if } N_{dem} > N_{sup} \\
   -(f_{fr_{max}} - f_{fr} + f_{fr_0}) \cdot r_{fr} \left(1 - \frac{f_{fr}}{f_{fr_0}}\right) & \text{if } N_{dem} \leq N_{sup}
\end{cases}$$  \hspace{1cm} (8-5)
Thereby the parameter \( r_{fr} \) (d\(^{-1}\)) determines the rapidity of the adaptation process. Here a value of 0.2 was used.

**8.3.2. Water transport**

Vertical water transport in the soil profile is calculated using the water content based formulation of the Richard’s equation:

\[
\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left[ D_w(\theta) \left( \frac{\partial \theta}{\partial z} \right) + k(\theta) \right] - S(\psi)
\]

where \( \theta \) is the volumetric water content of the soil (cm\(^3\) cm\(^{-3}\)), \( t \) is the time (d), \( z \) is the depth (cm), \( D_w(\theta) \) is the diffusivity of water (cm\(^2\) d\(^{-1}\)), \( k(\theta) \) is the unsaturated hydraulic conductivity (cm d\(^{-1}\)) and \( S(\psi) \) is the so called sink term (d\(^{-1}\)) which accounts for the water uptake of the roots.

Equation (8-6) is solved numerically by an implicit finite difference scheme with explicit linearisation (Remson *et al.*, 1971). For this purpose the soil column was divided into 20 intervals of 10 cm thickness down to a depth of 2 m. For the upper boundary condition of equation (8-6) the sum of soil evaporation and precipitation corrected for interception was used. The lower boundary condition was defined through a fixed volumetric water content in 200 cm depth.

The relationships between \( D_w \) and \( \theta \) and \( k \) and \( \theta \) were described using the functions suggested by van Genuchten (1980) in the revised form of Wösthen and Genuchten (1988). The necessary parameters for this relationships were estimated with the program RETC (van Genuchten *et al.*, 1991) using data from Künkele (1996) and Bohne (1999) for the loess loam soil of the experimental site. Additionally parameters for a sandy soil were derived for a scenario calculation using data taken from Wösthen *et al.* (1986) (Table 8-2, Fig. 8-1).
Table 8-2: Parameters of the Van Genuchten-Mualem equations found by fitting to data on soil water tension vs. soil water content.

<table>
<thead>
<tr>
<th>Soil</th>
<th>Depth (cm)</th>
<th>$\theta_r$ (cm$^3$.cm$^{-3}$)</th>
<th>$\theta_s$ (cm$^3$.cm$^{-3}$)</th>
<th>$\alpha$ (cm$^{-1}$)</th>
<th>n</th>
<th>$h^*$</th>
<th>$K_s^*$ (cm.d$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loess loam</td>
<td>0-30</td>
<td>0.0</td>
<td>0.4295</td>
<td>0.01479</td>
<td>1.276</td>
<td>0.5</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>30-80</td>
<td>0.0347</td>
<td>0.4367</td>
<td>0.00903</td>
<td>1.448</td>
<td>0.5</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>80-200</td>
<td>0.0</td>
<td>0.4485</td>
<td>0.00675</td>
<td>1.238</td>
<td>0.5</td>
<td>7</td>
</tr>
<tr>
<td>Sand (Scenario)</td>
<td>0-30</td>
<td>0.0</td>
<td>0.4429</td>
<td>0.0332</td>
<td>1.336</td>
<td>0.5</td>
<td>40.19</td>
</tr>
<tr>
<td></td>
<td>30-200</td>
<td>0.0</td>
<td>0.3800</td>
<td>0.01997</td>
<td>1.627</td>
<td>0.5</td>
<td>50</td>
</tr>
</tbody>
</table>

*) estimated value

Fig. 8-1: Volumetric soil water content vs. soil water potential for three different depths of the experimental field (loess loam) and functions for a sandy soil used for a scenario calculation.
The sink term $S(\psi)_i$ in the layer $i$ of the finite difference scheme is calculated from a hypothetical maximum sink term $S_{\text{max}}(\psi)_i$ that is defined by the following equation:

$$S_{\text{max}}(\psi)_i = T_p \frac{RLD_i^{cf}}{\sum RLD_i^{cf}}$$

(8-7)

where $T_p$ is the potential transpiration rate, $RLD_i$ is the rooting density in the layer $i$, $n_r$ is the number of the rooted compartments computed from the the maximum rooting depth $z_r$ is and the thickness of the layers, $\Delta z$. The parameter $cf$ is an empirical factor that accounts for root competition. This factor is set to a value of 0.5 according to the results of Ehlers et al. (1991) and Kage and Ehlers (1996).

The maximum sink term $S_{\text{max}}(\psi)_i$ is converted to the actual sink term $S(\psi)_i$ by multiplication with an empirical reduction factor $\alpha(\psi)$ as described by (Feddes et al., 1978). This factor was assumed to decline from a value of one at matrix potentials $\geq -1000$ hPa down to zero at $-20000$ hPa.

### 8.3.3. Evapotranspiration

Evaporation of a plant canopy depends like dry matter production on the amount of intercepted radiant energy but also on the vapour pressure deficit of the ambient air. One of the most fundamental methods to calculate the evaporation rate of a closed plant canopy is the Penman-Monteith equation (Monteith, 1973):

$$\lambda E = \frac{sR_n + \rho_a c_p e_a - e_a}{s + \gamma \left(1 + \frac{r_c}{r_a}\right)}$$

(8-8)

with evaporation $E$ (kg m$^{-2}$ s$^{-1}$), latent heat of vaporisation of water $\lambda$ (J kg$^{-1}$), net radiation $R_n$ (W m$^{-2}$), total resistance of the pathway between the evaporating sites and the bulk air $r_a$ (s m$^{-1}$), the canopy resistance $r_c$ (s m$^{-1}$), the vapour pressure deficit between the evaporating sites and the bulk air $e_a - e_a$ (hPa), the slope of the vapour saturation curve $s$ (hPa K$^{-1}$), the volumetric heat capacity of dry air $c_p$ (J kg$^{-1}$), the density of dry air $\rho_a$ (kg m$^{-3}$) and the psychrometer constant $\gamma$ (hPa K$^{-1}$). $R_n$ was computed from
the global radiation, $GR$, using an empirical regression equation derived from measurements of global and net radiation over grass at the experimental field 'Ruthe':

$$R_n = 0.6494 \cdot GR - 18.417 \quad (8-9)$$

Potential evaporation is the sum potential transpiration, $T_p$, potential evaporation, $E_p$, and of interception evaporation, $I$:

$$ET_p = T_p + E_p + I \quad (8-10)$$

Interception evaporation kg m$^{-2}$d$^{-1}$ is assumed to take place from a storage pool, $IP$, (kg m$^{-2}$) situated on the surface of the canopy. The capacity of this storage pool, $CIP$, kg m$^{-2}$ is calculated from a specific interception capacity, $SIC$, (kg m$^2$m$^{-2}$) and the leaf area index $LAI$ m$^2$m$^{-2}$.

$$CIP = SIC \cdot LAI \quad (8-11)$$

Interception is the minimum of the sum of the maximum possible change of the interception pool and the precipitation rate, $Pr$, kg m$^{-2}$d$^{-1}$ and the potential Evapotranspiration:

$$I = \min \left( \frac{dIP}{dt} + \min(Pr, CIP - IP), ET_p \right) \quad (8-12)$$

The change of the storage pool is calculated from the minimum of the precipitation rate and the actual unused capacity of the precipitation pool, $CIP$-$IP$:

$$\frac{dIP}{dt} = \min(Pr, CIP - IP) - I \quad (8-13)$$

The potential evaporation rate is determined by the fraction of radiation energy which is reaching the soil surface, $R_{ns}$. This fraction can be calculated using an analogue of the Lambert-Beer law:

$$R_{ns} = R_n \cdot e^{-k_G LAI} \quad (8-14)$$

Were $k_G$ is the extinction coefficient for global radiation, which was set to a value of 0.5.
The potential evaporation then gets:

\[ E_p = (ET_p - I) \frac{R_{ns}}{R_n} \quad (8-15) \]

Actual evaporation was determined from an empirical function using potential evaporation and the water potential in 10 cm depth as input parameters ((Beese et al., 1978)). The potential transpiration is calculated as the remaining part of the potential evapo-transpiration after subtracting potential evaporation and interception and taking also into account an empirical crop resistance.

### 8.3.4. Soil nitrogen balance

Since in well aerated soils the concentration of ammonium compared to the concentration of nitrate is usually very low, only nitrate nitrogen is considered for in the model.

### 8.3.5. Vertical nitrate transport

Vertical nitrate transport in the soil profile is described by the convection-dispersion equation (Addiscott and Wagenet, 1985):

\[
\frac{\partial (\theta C_l)}{\partial t} = \frac{\partial}{\partial Z} \left( \theta \cdot D_s \frac{\partial C_l}{\partial Z} \right) - \frac{\partial F_w}{\partial Z} C_l - S(z,t) + P_m \quad (8-16)
\]

where \( Q_l \) is the nitrate concentration of the soil solution, g cm\(^{-3}\), \( D_s \) is the apparent dispersion coefficient (cm\(^2\) d\(^{-1}\)) \( F_w \) is the water flow rate (cm\(^3\) cm\(^{-2}\) d\(^{-1}\)), \( S(z,t) \) is the nitrate uptake rate of the roots and \( P_m \) is the production rate of nitrate nitrogen from organic matter (g cm\(^{-3}\) d\(^{-1}\)), which was input here.

The term \( D_s \) is the sum of the dispersion coefficient \( D_h(v) \), which is a function of pore water velocity, \( v \), and the effective diffusion coefficient, \( D_e(\theta) \), which is a function of the volumetric soil water content (Beese and Wierenga, 1980):

\[
D_s = D_h(v) + D_e(\theta) \quad (8-17)
\]
The apparent dispersion coefficient was assumed to be proportional to the pore water velocity, calculated from volumetric water content, $\theta$, and water flow rate, $F_w$, with the dispersion length $\lambda$ set to 0.5 (cm):

$$D_n = \lambda \frac{F_w}{\theta}$$  \hspace{1cm} (8-18)

Equation (8-16) is solved numerically using the Crank-Nicholson procedure (Remson et al., 1971). The same discretisation as for equation (8-6) is used. The upper boundary condition of equation (8-16) is a zero flow rate, for the lower boundary condition a zero gradient in 200 cm depth was assumed. The initial condition was the measured nitrate concentration from 0 to 120 cm, which was determined in a spatial resolution of 30 cm. Since no $N_{\text{min}}$-measurements were available for depths below 120 cm, all layers from 100 to 200 cm were initialised with the measured $N_{\text{min}}$-content of the layer 90-120 cm depth.

### 8.3.6. Nitrate uptake by plant roots

It is assumed that the nitrate uptake by the plants root system $U_{R_{\text{act}}}$ (g N m$^{-2}$ d$^{-1}$) is determined either by the nitrogen demand of the plants $N_{\text{dem}}$ or the maximum nitrate transport rate to the root system $U_{R_{\text{max}}}$:

$$U_{R_{\text{max}}} < N_{\text{dem}}: \quad U_{R_{\text{act}}} = U_{R_{\text{max}}}$$
$$U_{R_{\text{max}}} > N_{\text{dem}}: \quad U_{R_{\text{act}}} = N_{\text{dem}}$$  \hspace{1cm} (8-19)

Nitrogen demand of plants is derived from the sum of demand of the plant organs.

$$N_{\text{dem}} = \sum N_{\text{dem},i}$$  \hspace{1cm} (8-20)

The latter is computed from their growth rate and their nitrogen content under optimal N supply as described in chapter 9.

### 8.3.7. Nitrogen transport to roots

The maximum nitrogen transport rate to roots, $h_{\text{max}}$, (g N cm$^{-1}$ d$^{-1}$) is calculated using the single root model approach (Gardner, 1960). The nitrate transport to a single root
located in the centre of a cylindrical flow domain may be described by the following partial differential equation (Nye and Spiers, 1964):

\[
\frac{\partial C_l}{\partial t} = \frac{1}{r} \cdot \frac{\partial}{\partial r} \left( r \cdot D_l \cdot f(\theta) \cdot \frac{\partial C_l}{\partial r} + r \cdot J_w \cdot C_l \right)
\]  

(8-21)

where \( r \) is the distance to the root centre (cm), \( D_l \) is the diffusion coefficient of nitrate in water (cm\(^2\)d\(^{-1}\)), \( f(\theta) \) is the tortuosity factor (-) and \( J_w \) is the water flux density (cm\(^3\)cm\(^{-2}\)d\(^{-1}\)).

Baldwin et al. (1973) developed an analytical solution of equation (8-21) assuming steady state conditions. A modified version of this equation was used in this study. For details of the derivation of this equation see Kage (1997).

In this equation a minimum concentration \( C_{l\text{min}} \) is used, defined as the lowest concentration where nitrate uptake matches transport to roots (De Willigen and Van Noordwijk, 1987a). Since most plant species (Peuke and Kaiser, 1996) are very efficient in nitrate uptake, this value will be usually very low (\(< 10^{-7}\) mol·cm\(^{-3}\)), which is equivalent to less than 1 kg N in a 30 cm soil layer a volumetric water content of 30 %. Therefore the exact value of this parameter is not very important and can be set to zero, as it was done in this study, in order to calculate the maximum uptake rate.

The factor \( f \) in equation (8-21) stands for the tortuosity of the diffusion pathway in the soil. This parameter is a function of the soil water content \( \theta \). In the model the empirical relationship:

\[ f = 3.35 \cdot \theta^2 \]  

(8-22)

derived from experimental data of Barraclough and Tinker (1981) was used.

For each rooted soil layer \( i \) the maximum nitrate uptake rate \( AR_{\text{max},i} \) (g·cm\(^{-2}\)d\(^{-1}\)) is computed from the maximum nitrate influx rate \( I_{\text{max},i} \) (g·cm\(^{-1}\)d\(^{-1}\)) and the root length in that particular layer \( RL_i \) (cm·cm\(^{-2}\)):

\[ AR_{\text{max},i} = I_{\text{max},i} \cdot RL_i \]  

(8-23)
The maximum N supply rate \( (N_{\text{sup}})\) \( (g \cdot m^{-2} \cdot d^{-1})\) then simply is the sum of all maximum uptake rates corrected for the changed units of area:

\[
N_{\text{sup}} = \sum AR_{\text{max}} \cdot 10^4
\]  
(8-24)

The sink term of equation (8-16) then is computed either from the nitrogen demand and the proportion of the maximum nitrate uptake rate to the sum of the maximum uptake rate in all rooted soil layers or if the sum of the maximum uptake rates is smaller than the nitrogen demand the sink term is simply the maximum uptake rate itself:

\[
S_i = \begin{cases} 
AR_{\text{max}}, & N_{\text{dem}} \geq N_{\text{sup}} \\
N_{\text{dem}} \cdot 10^{-4} \cdot \frac{\sum_{i=1}^{z_{\text{z}}=2} AR_{\text{max}}}{\sum_{i=1}^{z_{\text{z}}=2}} & N_{\text{dem}} < N_{\text{sup}} 
\end{cases}
\]  
(8-25)

The total N uptake rate, \( UR_{\text{act}} \), from the soil then is the sum of the sink terms in all soil layers.

8.3.8. Parameter estimation and statistics

The whole model is implemented within the HUME modelling environment (Kage and Stützel, 1999a). This modelling environment supports parameter estimation based on the Marquardt algorithm (Marquardt, 1963). The parameter estimate for \( f_{R\text{max}} \) (Eqn. 8-5) was obtained by minimising the squared sum of differences between measured and simulated RLD values from the annual experiment in 1996.

For evaluation the goodness of fit of the model output linear regression analysis and the statistical measures modelling efficiency (EF) and root mean square error (RMSE) used. For definition see chapter 4.

8.4. Results

There is a tendency of decreasing net mineralisation rates with increasing nitrogen fertilisation (Table 8-3) in the annual experiments. For the rotation experiment no clearly
Nitrate availability for cauliflower

Influence of nitrogen fertilisation could be found on calculated net mineralisation. For the second cauliflower crops, however, clearly higher net mineralisation rates were calculated (Table 8-4).

The RLD values of the different N treatments in 1996 and 1997 differed not substantially (Fig. 8-2, Fig. 8-3), despite the indication of a more pronounced root distribution of the N0 treatment in 1996 compared to the N2 treatment. This indicates that the fraction of dry matter allocated to the fine root fraction was elevated under nitrogen deficiency. The parameter $f_{R\text{max}}$ (Eqn. 8-5) was estimated by adjusting to the 1996 data at a value of

Table 8-3: Calculated average net mineralisation rate (kg N ha$^{-1} \cdot$ d$^{-1}$) during crop growing period in two experimental years under four different nitrogen supply rates (N0..N3).

<table>
<thead>
<tr>
<th>N supply rate</th>
<th>1996</th>
<th>1997</th>
</tr>
</thead>
<tbody>
<tr>
<td>N0</td>
<td>0.728</td>
<td>1.173</td>
</tr>
<tr>
<td>N1</td>
<td>0.014</td>
<td>0.835</td>
</tr>
<tr>
<td>N2</td>
<td>-0.168</td>
<td>0.709</td>
</tr>
<tr>
<td>N3</td>
<td>1.276</td>
<td>0.386</td>
</tr>
</tbody>
</table>

Table 8-4: Calculated average net mineralisation rate (kg N ha$^{-1} \cdot$ d$^{-1}$) in three experimental years under two different nitrogen supply rates ($N_{\text{norm}}, N_{\text{red}}$).

<table>
<thead>
<tr>
<th>Year</th>
<th>1994</th>
<th>1995</th>
<th>1996</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Planting</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early</td>
<td>Late</td>
<td>Early</td>
<td>Late</td>
</tr>
<tr>
<td>$N_{\text{norm}}$</td>
<td>0.517</td>
<td>5.389</td>
<td>0.241</td>
</tr>
<tr>
<td>$N_{\text{red}}$</td>
<td>0.242</td>
<td>3.414</td>
<td>0.650</td>
</tr>
</tbody>
</table>
Using this parameter value the RLD data of the N deficient treatments N0 and N1 in 1996 could be described with sufficient accuracy (8-2). Also the prediction for the 1997 data was acceptable, with some minor discrepancies between simulated and measured values for the somewhat deeper distributed root system of the N0 treatment (Fig. 8-3).

The high amount of rainfall at the beginning of the experiment in 1997 (Fig. 8-4a) lowered the soil water potential down to values close to field capacity up to a soil depth of 90 cm (Fig. 8-4c). Due to soil evaporation and plant transpiration (Fig. 8-4b) the simulated absolute values of soil water potential rises to about 1500 hPa in the topsoil but remained at about 700 hPa in the subsoil. Also for the other evaluated crops a sufficient description of soil water tensions was achieved (Table 8-5).

Table 8-5: Parameters of a linear regression analysis between measured and simulated soil water tensions (hPa) as well as residual mean square error (RMSE) and modelling efficiency (EF). Data are from the 1997 annual experiment and from the early planted crops of the long term experiment.

<table>
<thead>
<tr>
<th>Soil depth</th>
<th>Slope</th>
<th>Intercept</th>
<th>$r^2$</th>
<th>n</th>
<th>RMSE</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td>20 cm</td>
<td>1.1724</td>
<td>-58.1560</td>
<td>0.6214</td>
<td>38</td>
<td>106.8452</td>
<td>0.5962</td>
</tr>
<tr>
<td>40 cm</td>
<td>2.5354</td>
<td>-278.7340</td>
<td>0.5753</td>
<td>38</td>
<td>99.8982</td>
<td>0.3637</td>
</tr>
<tr>
<td>70 cm</td>
<td>1.9471</td>
<td>-155.0777</td>
<td>0.3509</td>
<td>38</td>
<td>66.0248</td>
<td>0.1525</td>
</tr>
</tbody>
</table>

0.201 (±0.004). Using this parameter value the RLD data of the N deficient treatments N0 and N1 in 1996 could be described with sufficient accuracy (8-2). Also the prediction for the 1997 data was acceptable, with some minor discrepancies between simulated and measured values for the somewhat deeper distributed root system of the N0 treatment (Fig. 8-3).
Nitrate availability for cauliflower

The soil nitrate content in 1996 changed substantially only in the upper 30 cm of the profile, where the fertilised nitrogen was exhausted rapidly after onset of plant nitrogen uptake (Fig. 8-5; see also Chapter 9). Due to the low N contents of the deeper soil

**Fig. 8-2:** Measured and simulated root length density (RLD) vs. soil depth at end of the growing period for cauliflower crops grown under 4 different N supply treatments (N0 ..N3) in 1996. Simulated RLD is shown for total (RLD) and effective root length density (RLDeff). Error bars indicate standard error of the mean. The linear regression equation between measured and simulated RLD is $y = 0.17 (\pm 0.0884) + 0.95(\pm 0.12)x$, $r^2=0.75$, $n=24$. 

The soil nitrate content in 1996 changed substantially only in the upper 30 cm of the profile, where the fertilised nitrogen was exhausted rapidly after onset of plant nitrogen uptake (Fig. 8-5; see also Chapter 9). Due to the low N contents of the deeper soil
layers and the absence of leaching during the 1996 vegetation period, changes of soil nitrate in deeper soil layers (>30 cm) were small. The excess of rainfall at around DOY 210 in 1997 (Fig. 8-4a) induced downward water movement, which transported some nitrate nitrogen from the upper 30 cm of the soil profile to the layer 30-60 cm (Fig. 8-6). However, due to the high water capacity of the loess loam this leaching process did not affect soil nitrate contents below 60 cm depth (Fig. 8-6). With the exception of the N3 treatment the soil mineral N content was exhausted down to values less than 50 kg N during the growing period. Simulated and measured values for the different soil layers agreed sufficiently well also for the other evaluated crops (Table 8-6).

The simulated N uptake rates of the N2 and N3 treatments were during the time of highest N demand above 8 kg N ha\(^{-1}\) d\(^{-1}\) (1996: Fig. 8-7, 1997: data not shown). However, due to the high N amounts (Fig. 8-5) in the comparably dense rooted topsoil (Fig. 8-2), calculated maximum nitrate transport rates to the root system were always (N3) or until a few day before final harvest (N2) higher than calculated N uptake. This indicates unrestricted (N3 treatment) or almost unrestricted (N2) N availability for the crops. The suboptimal (N2) and unfertilised (N0) treatments, however, were calculated to be limited in N uptake by N availability in the second half of the growing period (N1) or throughout the growing period (N0) (Fig. 8-7). The N1 treatment was calculated to became N limited on DOY 210 at a soil nitrate content 0-60 cm of 67 kg N ha\(^{-1}\) (Fig. 8-5) assuming an active uptake period of 10 days (Eqn. 8-1). The calculation using the assumption of an unrestricted uptake period, however, indicated an N limitation on DOY 218 at a soil mineral N content of 18 kg N ha\(^{-1}\) (Fig. 8-7).
Fig. 8-3: Measured and simulated root length density (RLD) vs. soil depth at end of the growing period for cauliflower crops grown under 2 different N supply treatments (N0 and N2) in 1997. Simulated RLD is shown for total (RLD) and effective root length density (RLDeff). Error bars indicate standard error of the mean. The linear regression equation between measured and simulated RLD is $y=0.132 (\pm 0.116) + 1.036 (\pm 0.1641) x$, $r^2=0.80$, n=12.

The calculated apparent mass flow rates were close to the calculated plant uptake rate for first half of the growing period in the case of the super optimal fertilised N3 treatment. For all other treatments actual N uptake rates were generally much lower than calculated apparent mass flow rates (Fig. 8-7). Average nitrogen influx rates are subsequent to a phase of increase shortly after planting steadily decreasing. Peak values are higher than $5 \times 10^{-12}$ mol N cm$^{-1}$s$^{-1}$ if calculated with total root length and about $15 \times 10^{-12}$ mol N cm$^{-1}$s$^{-1}$ if calculated with an ‘effective’ root length (Fig. 8-8).
Fig. 8-4: Precipitation and irrigation during experimental period, calculated soil evaporation and plant transpiration as well as measured and simulated soil matrix potential head in different soil depths from transplanting to last harvest of the optimal fertilised (N2) cauliflower treatment in 1997.
Fig. 8-5: Measured and simulated soil mineral nitrogen content of the 1996 cauliflower experiment of the 4 N treatments. Error bars indicate the standard error of the mean.
Fig. 8-6: Measured and simulated soil mineral nitrogen content of the 1997 cauliflower experiment of the 4 N treatments. Error bars indicate the standard error of the mean.
A scenario calculation was carried out for the N2 treatments of both years using soil hydraulic parameters of a sandy soil instead of the parameters for the loess soil (Table 8-2). All other input values were left unchanged. Due to the lower water capacity of this soil type (Fig. 8-1) the calculated downward movement of nitrate during the vegetation periods of both years was more pronounced than was measured and simulated at the loess loam location (Fig. 8-5, Fig. 8-6). But the rainfall induced downward movement of water and nitrate was limited to a soil depth of about 60 cm (Fig. 8-9). This limited translocation of nitrate, however, increased the amount of unused of soil mineral nitrogen left in the soil at 30-60 cm compared to the loess loam soil conditions, especially under 1997 weather conditions (Fig. 8-9).

A further scenario calculation was carried out to obtain response curves of residual soil nitrate at harvest from 0-120 cm soil depth to N fertilisation. Again, two different set of hydraulic parameters were used, the parameter set for the loess soil of the experimental field and another of a sandy soil (Table 8-2). On the sandy soil also effects of a split nitrogen application were evaluated assuming a fixed nitrogen application at planting of 100 kg N ha\(^{-1}\) and varied secondary application 4 weeks after planting. For N mineralisation rate the same values as shown in Table 8-3 for the N2 treatment in 1997 were used.

Residual soil nitrate values remain at low values of about 20 kg N ha\(^{-1}\) up to a N fertilisation of about 200 kg N ha\(^{-1}\) for the loess loam soil conditions and up to 150 kg N ha\(^{-1}\) fertilisation for the sandy soil, however, starting from a higher level of about 50 kg N ha\(^{-1}\) (Fig. 8-10). Split nitrogen application on the sandy soil is calculated to delay the increase of residual soil nitrate towards a higher level of N supply. Starting at about a N fertilisation of about 250 kg N ha\(^{-1}\), the sink capacity of the cauliflower is saturated and residual soil nitrate levels are increasing linearly for all conditions considered in the calculation.
Fig. 8-7: Simulated maximum nitrate transport rates to the root system, apparent mass flow and actual N uptake rates of cauliflower from the 1996 experiment for 4 different N treatments.
8.5. Discussion

The aim of the presented work was to quantify the nitrogen availability for cauliflower crops grown under different nitrogen supply using a mechanistic simulation model. Furthermore scenario calculations were carried out to estimate effects of altered soil conditions.

The adopted root growth module from chapter 7 sufficiently well described the temporal-spatial pattern of root length density (Fig. 5-6, Fig. 8-3). The discrepancy of measured and simulated RLD in 75-90 cm depth of the N0 treatment in the annual experiment of 1996, however, indicates that even small amounts of nitrogen in the sub soil (Fig. 8-6) may induce local deviations of the root profile from the negative exponential shape predicted by the model if nitrogen is in deficiency. Such 'irregular' root growth patterns

---

*Fig. 8-8: Calculated N influx (N uptake per units root length) using either simulated total (WL) or effective root length (effWL) for the N2 treatment of the 1996 annual experiment.*
may be much more severe if roots of N deficient plants trap into sub soil regions with high N nitrate concentrations (Drew and Saker, 1975; Burns, 1991). Our approach to account for a changing assimilate partitioning between roots and shoots under nitrogen deficiency (Eqn. 8-5) accurately described our data (Fig. 5-6, Fig. 8-3) even under a quite extreme variation of N supply. But it may fail to predict responses of rooting intensity under different soil conditions, because the beneficial effect of an increased root growth on N uptake depends clearly on the particular soil conditions like water content and the vertical distribution of nitrate in the soil profile. Teleonomic approaches, explaining shoot-root partitioning with growth maximising principles (Johnson and Thornley, 1987; Kleemola et al., 1996; Thornley, 1972) may be superior for this purpose. However, their elaboration and parameterisation calls for more detailed data, than those which are presented here.

The good agreement between simulated and measured soil nitrate in different soil layers (Fig. 8-5, Fig. 8-6) is mainly due to the good description of the time course of crop nitrogen uptake by the model modules presented in chapter 9 because net mineralisation was input and downward movement of nitrate was even in 1997 of limited importance for soil nitrogen dynamics (Fig. 8-6). As shown in Table 8-3 and Table 8-4 there is a substantial variation of net mineralisation depending presumably on seasonal variations of soil temperature, the preceding crop (Greenwood et al., 1996) and the amount of N fertilisation (Blankenau and Kuhlmann, 2000).
The calculation presented in (Fig. 8-7) clearly demonstrates that mass flow is only able to contribute substantially to the nitrate transport to roots if the soil nitrate concentration is very high, as already stated by Strebel and Duynisveld (1989) and Kage (1996). The estimated nitrate influx rates for the whole root system are about one order of magnitude higher than values reported for winter wheat (Barraclough, 1986; Robinson et al., 1994) and winter rape (Barraclough, 1989). This is due to an additive effect of higher uptake nitrogen uptake rates of cauliflower per unit of ground area (Fig. 8-7) and a lower total root length (Fig. 5-6, Fig. 8-3, Chapter 7) compared to both agricultural crops. Influx rates are almost doubled for the calculated effective root length. These
high influx values are the prerequisite for the reproduction of the high critical soil nitrate values found in the field (Chapter 6) by the single root model (Eqn. 8-21).

The scenario calculation for the sandy soil (Fig. 8-9, Fig. 8-10) indicates that even for this soil type leaching losses of nitrogen out of the root zone during the growing period of cauliflower are limited. It has, however, to be stated that at the beginning of the growing period nitrate nitrogen was situated predominantly in the upper 30 cm of the soil in both years. But even the limited calculated downward movement of nitrate lowers the availability because of the lower rooting density in the subsoil (Fig. 8-1, Fig. 5-6), resulting in somewhat increased residual soil nitrate level in the depth 30-60 cm (Fig. 8-9). Due to the different water content-soil water potential characteristic of the sandy soil (Fig. 8-1) the calculated water contents are lower in the sandy soil compared to the loess loam. This also reduces nitrate availability because nitrate diffusion is closely dependent on the soil water content (Eqn. 8-21, 8-22). Critical soil nitrate levels and consequently residual soil nitrate levels are therefore higher for sandy soils than on loamy soils (Fig. 8-10). For both soil types residual soil nitrogen values are increasing only after the N uptake capacity of the cauliflower crop is reached. This behaviour has also been found for other crops like winter wheat (Chaney, 1990).

Table 8-6: Parameters of a linear regression analysis between measured and simulated soil nitrate nitrogen in different soil layers as well as residual mean square error (RMSE) and modelling efficiency (EF). Data are from the 1996 and 1997 annual experiments and from the early plantings of the long term experiment.

<table>
<thead>
<tr>
<th>Soil depth</th>
<th>Slope</th>
<th>Intercept</th>
<th>$r^2$</th>
<th>n</th>
<th>RMSE</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-30 cm</td>
<td>0.9819</td>
<td>5.8324</td>
<td>0.9336</td>
<td>47</td>
<td>28.0339</td>
<td>0.9319</td>
</tr>
<tr>
<td>30-60 cm</td>
<td>0.5309</td>
<td>5.8549</td>
<td>0.4380</td>
<td>47</td>
<td>12.2148</td>
<td>0.0251</td>
</tr>
<tr>
<td>60-90 cm</td>
<td>1.1340</td>
<td>0.0772</td>
<td>0.7274</td>
<td>47</td>
<td>3.5219</td>
<td>0.6855</td>
</tr>
<tr>
<td>90-120 cm</td>
<td>1.0726</td>
<td>0.2127</td>
<td>0.7670</td>
<td>47</td>
<td>3.8381</td>
<td>0.7499</td>
</tr>
<tr>
<td>0-120 cm</td>
<td>0.9575</td>
<td>8.4942</td>
<td>0.9303</td>
<td>47</td>
<td>32.0057</td>
<td>0.9278</td>
</tr>
</tbody>
</table>
The postulation of a limited active duration of root functioning used in this study is a very crude approach to bridge the gap between observed critical soil nitrate concentrations (Chapter 6) and the predictions obtained using an unrestricted functional time of roots (Fig. 8-7). The estimation of this active duration by adjustment with respect to measured and simulated critical soil nitrate values lumps the effects of all unrealistic simplifications of the model into one causal factor. Consequently, a presumably much too low value of 10 day period of N uptake was found to give an acceptable prediction of critical soil nitrogen content (Fig. 8-8, Fig. 8-5). Other candidates for explaining too high predictions of the model for maximum nitrate uptake rates of the root system are: a) horizontally uneven root distribution (Baldwin et al., 1972; De Willigen and Van Noordwijk, 1987b; Kage, 1992; Droogers et al., 1997), b) limited soil root contact (De Willigen and Van Noordwijk, 1987a; Herkelrath et al., 1977), c) locally decreased soil water contents around water absorbing roots (Hainsworth and Aylmore, 1986; Herkelrath et al., 1977;
Kage, 1994), d) horizontally uneven distribution of soil nitrate (Hodge et al., 1999; Van Noordwijk and Wadman, 1992). The incorporation of these effects into the model may reduce the contradiction between the functional time of roots in the model and physiological realistic values, but would also increase the number of unknown and hardly measurable model parameters. The approach of an effective root length presented here may therefore be regarded as acceptable, since it preserves the mechanistic character of the single root model and should therefore give realistic predictions even when extrapolated to other experimental conditions. However, it also clearly focuses the knowledge gap between empirically determined critical soil nitrogen contents and the prediction of mathematical models of root functioning.

8.6. Conclusions

Root growth of cauliflower under nitrogen deficiency could successfully described increasing the fraction of dry matter allocated to the fine root fraction. Rooting depth and vertical root distribution were obviously not severely affected. A mechanistic model of nitrate availability calculated lower critical soil nitrogen contents than were empirically derived. Critical soil nitrate values may be higher for sandy than for soils with a higher water holding capacity.
Chapter 9

9. Aspects of nitrogen use efficiency of cauliflower II. Productivity and nitrogen partitioning as influenced by N supply

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Abstract

Based on previously presented studies concerning dry matter partitioning, dry matter production, root growth, N contents of cauliflower organs and soil nitrate availability (first part of the paper) an integrated simulation model for the cauliflower/soil system is constructed, parameterised and evaluated using data from field grown crops.

Dry matter production of cauliflower was described and predicted using a simple light use efficiency, LUE, based approach assuming a linear decrease of light use efficiency with increasing differences between actual, NCA\textsubscript{Prot}, and 'optimal', NCA\textsubscript{optProt} area based leaf protein concentrations. For two experimental years the decline of LUE with decreasing leaf area was estimated by model adjustment to be 0.82 and 0.75 (g DM \textsubscript{g N}^{-1} \textsubscript{MJ}^{-1} m^{-2}).

Using this approach and the parameters obtained from the first experimental year shoot dry matter production data of cauliflower from 5 independent experiments with varied N supply containing intermediate harvests could be predicted with a residual mean square error (RMSE) of 72 g m\textsuperscript{-2}. Nitrogen uptake and partitioning of cauliflower was simulated using functions describing an organ size dependent decline of N content. Leaf nitrate was considered explicitly as a radiation intensity dependent pool, mobilised first under N deficiency. The curd was assumed to have a sink priority for nitrogen. The model predicted shoot N uptake including data of intermediate harvest with a RMSE of 2.4 g m\textsuperscript{-2}. N uptake of cauliflower at final harvest was correlated to final leaf number.

A long term scenario simulation analysis was carried out to quantify seasonal variation of N uptake cauliflower cultivars under unrestricted N uptake. Due to variations of the vernalisation phase simulated shoot N uptake varied from about 260 kg N ha\textsuperscript{-1} for spring planted crops to about 290 kg for summer planted crops of the cultivar 'Fremont'. The cultivar 'Linday', which shows a more severe delay under high temperatures, shows on average a higher shoot N uptake for summer planted crops of about 320 kg N ha\textsuperscript{-1} and a much higher variation of shoot N uptake.
9.1. Introduction

One of the prerequisites for efficient nitrogen use within intensive cropping systems is to achieve a close agreement between crop nitrogen demand and nitrogen supply (Stockdale et al., 1997). N fertilisation thereby should be adjusted to complement the N supply from the soil resources. Empirical methods to derive N fertilisation recommendations, like the $N_{\text{min}}$ method (Scharpf and Wehrmann, 1975), rely on a static analysis of yield response to total N supply from a larger group of experiments. Thereby the term N supply summarises N fertilisation and soil mineral nitrogen down to a soil depth which can almost completely exhausted by the root system. This approach has been applied to cauliflower (Everaarts et al., 1996; Everaarts and Van den Berg, 1996) taking mineral nitrogen down to a depth of 60 cm into account. This method intrinsically considers N supply from mineralisation of soil organic matter, but only as an average value of the experiments included in the analysis. Also the N demand of the crop is considered only as an average value. The actual N demand of cauliflower, however, can differ substantially, because a delayed vernalisation may increase the growth duration (Kage and Stützel, 1999b; Wiebe, 1980; Wurr et al., 1994).

Approaches based on mechanistically models possibly will help to calculate N demand more precisely and thereby minimise amounts of residual soil nitrate and leaching losses of nitrogen from the production system. Such a model based procedure for calculating N demand of a crop should consist of three parts: a) the calculation of the dry matter production per time b) the nitrogen content of this produced dry matter c) the growth period from sowing/transplanting to physiological/commercial maturity.

A model module for calculating dry matter production under unstressed conditions based on the light use efficiency approach has been presented in Chapter 4 and was slightly enhanced regarding to the method of light interception calculation (chapter 5). Nitrogen contents of cauliflower organs have successfully described using empirical functions of organ weight (chapter 6). An approach for calculating the partitioning of dry matter between the different plant organs as well as the length of the growth period has been presented in chapter 2 and chapter 5.

These model modules for modelling cauliflower growth and development were combined and used to predict the N demand of cauliflower under varying environmental
conditions. Additionally, the effects of limited N supply on the dry matter production and nitrogen partitioning will be included into the model. In that way, also the amount of N in crop residues can be predicted which contain more the 50% of total N uptake of cauliflower (Rahn et al., 1992; Everaarts et al., 1996). This high N amounts seriously affect the N supply of a succeeding crop (Rahn et al., 1998) and/or the possible N losses through leaching (De Neve and Hofman, 1998) and denitrification (Schloemer, 1991).

9.2. Material and methods

9.2.1. Field experiments

The field experiments are essentially the same as described in the first part of this paper. The planting and harvest dates as well as some other important parameters are shown in Table 9-1. The annual experiments were laid out as split plots with two different light environments, i.e. shaded and unshaded, as main plots and four different nitrogen-fertiliser levels as sub-plots. In the analysis presented here, only the unshaded treatments are considered. Nitrogen fertilisation was given as ammonium nitrate at the time of transplanting. Soil nitrate content of 10-15 kg N ha\(^{-1}\) in 1996 and 1997 in 0-60 cm were subtracted from the 150 (N1), 300 (N2) and 450 kg ha\(^{-1}\) (N3) target values. The N0 treatment received no N fertiliser.

The experiment at ‘Ruthe’ is a long-term rotational experiment consisting of two crop rotations, two tillage regimes, and two nitrogen fertilisation levels with three replications. For the analysis presented here, only data from the mouldboard tillage plots are used. A nitrogen fertilisation schedule according to the KNS system (Lorenz, et al. 1989) was applied here, defining two target values of 130 kg N ha\(^{-1}\) from 0-30 cm soil depth at transplanting and of 270 kg N ha\(^{-1}\) from 0-60 cm soil depth about 4 weeks after transplanting. The two N treatments received either 100 % of this recommended N supply level or a reduced N supply of 70% of this level in 1994 and 1995 and of 50% of this level in 1996. The planting density was 4 plants m\(^{-2}\) in a 0.5’0.5 m pattern for the spring planing dates and 3.3 plants m\(^{-2}\) (0.5’0.6m) for the summer planting dates. The cultivar “Fremont” was used in all experiments. General crop husbandry was as described in Chapter 2 and 8.
Additionally an annual experiment already described in using two cultivars (chapter 2), Linday and Fremont, having different vernalisation parameters (chapter 2) was used to evaluate developmental effects on N uptake of cauliflower.

### 9.2.2. Plant growth analysis

On several intermediate harvests six plants per plot in the annual experiments and 8 plant per plot in the final harvests of the long term experiment were collected and separated into stem, leaf including petioles, and curd. Leaves were considered and counted down to a size of approximately 1 cm². Stems were cut 1 cm below field level and at the onset of curd. Leaf area was measured with a LICOR 3100 leaf area meter (LI-COR Inc., Lincoln, NE, USA).

The samples of all plant compartments were oven dried and weighed. In the annual experiment total nitrogen and nitrate nitrogen was determined by the micro-Kjeldahl

<table>
<thead>
<tr>
<th>Type</th>
<th>Usage</th>
<th>Year</th>
<th>Planting Date</th>
<th>Harvest Date</th>
<th>Avg. I (MJ m² d⁻¹)</th>
<th>Avg. Temp. (°C)</th>
<th>No. of N Treatments</th>
</tr>
</thead>
<tbody>
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<td>240</td>
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<td>16.08</td>
<td>4</td>
</tr>
<tr>
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<td>E</td>
<td>1997</td>
<td>190</td>
<td>258</td>
<td>7.23</td>
<td>18.56</td>
<td>4</td>
</tr>
<tr>
<td>LT</td>
<td>E</td>
<td>1994</td>
<td>97</td>
<td>185</td>
<td>8.13</td>
<td>13.12</td>
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<td>LT</td>
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<td>1994</td>
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<td>293</td>
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</tr>
<tr>
<td>LT</td>
<td>E</td>
<td>1995</td>
<td>94</td>
<td>187</td>
<td>7.59</td>
<td>12.13</td>
<td>2</td>
</tr>
<tr>
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<td>E</td>
<td>1995</td>
<td>200</td>
<td>291</td>
<td>6.10</td>
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<td>2</td>
</tr>
<tr>
<td>LT</td>
<td>E</td>
<td>1996</td>
<td>200</td>
<td>284</td>
<td>6.18</td>
<td>14.34</td>
<td>2</td>
</tr>
<tr>
<td>A</td>
<td>E</td>
<td>1994</td>
<td>152</td>
<td>236</td>
<td>9.24</td>
<td>18.31</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 9-1: Type of experiment, annual (A), long term (LT), usage for parameterisation (P) for evaluation (E), year, planting and harvest dates, average incident photosynthetic active radiation and average temperature during the growth period of the cauliflower experiments used in this study.
method and a nitrate sensitive electrode, respectively. In the long term experiment total N concentrations of plant organs were determined by near-infrared spectrometry.

9.2.3. Model

The whole model used in this study consists of several parts, i.e. algorithms for describing dry matter partitioning, nitrogen partitioning and dry matter production. Generally, the model outlines in the following hypotheses:

- Total nitrogen content of cauliflower organs is independent of nitrogen supply rate above a certain critical threshold level.
- Total nitrogen contents of cauliflower organs decline during growth because an increasing portion of assimilated carbon is allocated to structural parts of organs.
- The nitrate fraction of leaf N content under unrestricted nitrogen supply is controlled by the intensity of incident radiation.
- Generative organs have a higher sink priority for nitrogen than vegetative organs.
- Light use efficiency decreases proportionally to increasing differences between optimal and actual protein contents per unit leaf area.

Dry matter partitioning

The dry matter partitioning part of the model is described in chapter 2 and chapter 5. However, according to the results of Alt (1999) and chapter 5 the development of the sink strength of the curd is delayed for slowly growing crops, caused either by shading or N deficiency. Therefore, the parameter \( r_f \) of Eqn. 2-21 from Chapter 2 which describes the rapidity of the increase of the fraction of dry matter allocated to the curd is now assumed to be a function of the average relative growth rate \( \bar{rgr} \) during the last 10 days of the vernalisation period:

\[
r_f = r_{fa} \cdot e^{\bar{rgr} \cdot r_{fb}}
\]  

(9-1)

The parameters \( r_{fa} \) and \( r_{fb} \) were estimated from the data 1997 field experiment with 0.01 and 2.21, respectively and were used for all experiments except the annual experiment in 1996 and the late planted 1996 crop of the rotational experiment. For these experiments the values 0.0087 and 7.26 were used for \( r_{fa} \) and \( r_{fb} \), respectively.
Nitrogen contents under sufficient N supply

An analysis of the dependency of the N content of cauliflower organs under sufficient N supply was presented in chapter 6. In the study presented here the same functional dependencies are used, however, the parameters are derived from the data of the 1996 annual experiment only, to retain a sufficiently large independent data set for the evaluation of the model.

Total leaf nitrogen contents of individual leaves under ample nitrogen supply, NCoptSL, (% N DM) are calculated from the weight of individual leaves, WSL, (g pt⁻¹) and the number of the actual leaf, i, using the following equation:

\[
NCopt_{SL,i} = 6.99 \cdot 0.1875 \cdot W_{SL,i} - 0.08 \cdot i
\]  \hspace{1cm} (9-2)

For derivation of optimal curd nitrogen contents NCoptc (% N DM) the following equation with curd weight WC (g pt⁻¹) as independent variable is used:

\[
NCopt_c = 6.6 \cdot e^{-0.0076 \cdot WC}
\]  \hspace{1cm} (9-3)

The optimal stem nitrogen content, NCoptS, (% N DM) is also calculated from the actual weight of the organ, WS (g pt⁻¹):

\[
NCopt_S = 3.45 - 0.346 \cdot \ln(W_S)
\]  \hspace{1cm} (9-4)

For the tap root the equation from Fig. 6-4 in Chapter 6 was used.

\[
NCopt_tr = 2.65 - 0.0381 \cdot W_{tr}
\]  \hspace{1cm} (9-5)

For the fine root fraction an N content of 1% in DM was assumed.

Calculation of nitrogen demand

The optimal N amount, Nopt, of all plant organs, i, from leaf1..leafn, curd, stem and tap root is derived from the optimal nitrogen content, Ncopti (% N DM) and their actual weight, Wi, (g pt⁻¹):

\[
Nopt_i = NCopt_i \cdot W_i
\]  \hspace{1cm} (9-6)
Nitrogen demand $N_{dem_i}$ ($g \text{ N pl}^{-1} \text{d}^{-1}$) then is determined from the difference of the actual nitrogen amount $N_i$ ($g \text{ pl}^{-1}$) and the optimal nitrogen amount, $N_{opt_i}$ ($g \text{ N pl}^{-1}$) at the end of the current time step, time step length, $\Delta t$, being 1 day:

$$N_{dem_i} = \frac{(N_{opt_i} + \Delta t - N_i)}{\Delta t} \tag{9-7}$$

The rate of change of the optimal nitrogen content of an organ may be calculated from:

$$\frac{dN_{opt_i}}{dt} = \frac{dW_i}{dt} \cdot \left( N_{C_i} + W_i \cdot \frac{dN_{opt_i}}{dW_i} \right) \tag{9-8}$$

For leaves, also the nitrate fraction of total leaf nitrogen demand is calculated. Therefore the equation shown in Fig. 6-11 (chapter 6), also derived from data of the 1996 field experiment was used:

$$f_{NO_3} = 0.2456 \cdot 0.0023 \cdot I_{av} \tag{9-9}$$

where $I_{av}$ is the 10 day running average of radiation intensity incident on a particular leaf. This value is calculated using sum of the simulated leaf area of all leaves younger than the particular leaf under consideration and the right hand bracket of Eqn. (2-10).

The total nitrogen demand, $N_{demp_l}$, is simply the sum of the nitrogen demand of all plant organs:

$$N_{demp_l} = \sum N_{dem_i} \tag{9-10}$$

From the nitrogen demand of the leaves and their nitrate fractions the total N demand of the nitrate pool of the canopy, $N_{demNO_3}$ ($g \text{ N pl}^{-1} \text{d}^{-1}$), is calculated:

$$N_{demNO_3} = \sum N_{dem_i} \cdot f_{NO_3} \tag{9-11}$$
The protein demand of the canopy, \( N_{dem}^{prot} \), then simply is the total nitrogen demand minus the leaf nitrate demand:

\[
N_{dem}^{prot} = N_{dem}^{can} - N_{dem}^{NO_3}
\]  

(9-12)

**Nitrogen remobilization and N-loss due to leaf drop**

A certain amount of nitrogen from senescing leaves is remobilized and acts therefore as an additional N source for the nitrogen demand of other organs. This remobilisation rate, \( N_{Rem} \) (g N.pl\(^{-1}.d^{-1}\)) is calculated from the sum of the senescence rates of all leaves \( \frac{dT_{SLW_i}}{dt} \) (g DM.pl\(^{-1}.d^{-1}\)) and the nitrogen content of the translocated dry matter \( NC_{Trans} \) (g N g DM\(^{-1}\)).

\[
N_{Rem} = NC_{Trans} \sum_{j=1}^{n} \frac{dT_{SLW_i}}{dt}
\]  

(9-13)

The senescence rate is calculated as described in chapter 5 and for \( NC_{Trans} \) a value of 0.1 is assumed. N-loss due to leaf drop is calculated using the dry weight of the dropped leaves times an assumed residual nitrogen content of 0.05 g N g DM\(^{-1}\).

**Nitrogen partitioning**

A nitrogen deficit, \( N_{def} \) (g N.pl\(^{-1}.d^{-1}\)), is calculated by subtracting the maximum uptake rate of the root system (\( N_{up}^{max} \)), corrected for the planting density, PD (pl m\(^{-2}\)), calculated as described in Chapter 8 and the amount of nitrogen which is remobilized from senescing leaves (Eqn. 9-13) for the plant nitrogen demand:

\[
N_{def} = N_{dem} - N_{up}^{max} / PD - N_{REM}
\]  

(9-14)

Under ample nitrogen supply (\( N_{def} < 0 \)), the nitrogen content of all organs equals their optimum nitrogen contents \( NC_{opt_i} \) as described in Eqs. 9-2 – 9-5. The change of their nitrogen amount then is calculated according to:

\[
\frac{dN_i}{dt} = \frac{dW_i}{dt} \left( NC_{opt_i} + W_i \frac{dNC_{opt_i}}{dW_i} \right)
\]  

(9-15)
If the actual supply rate is lower than the nitrogen demand (Ndef > 0) first the nitrate pool of the leaves is made available for the protein N demand of the leaves and the N demand of the other organs. However, transport and assimilation of this nitrate nitrogen are thought to limit the fraction of available N from this pool. Simple first order kinetics is used to describe this assumption, calculating a maximum leaf nitrate mobilisation rate, NO3\_mobmax (g N m\(^{-2}\) d\(^{-1}\)):

\[
NO3_{\text{mobmax}} = k_{NO3} \cdot NO3_L
\]  \hspace{1cm} (9-16)

where \(k_{NO3} (d^{-1})\) is a parameter determining the rapidity of the mobilisation process, set to 0.1 and \(NO3_L\) is the nitrate pool of the canopy (g N pl\(^{-1}\)).

The change of the leaf nitrate pool then is calculated according to the following equation:

\[
\frac{dNO3_L}{dt} = \begin{cases} 
Ndem_{NO3} & \text{Ndef < 0} \\
Ndem_{NO3} - Ndef - NO3_{\text{mobmax}} & \text{Ndef} - NO3_{\text{mobmax}} < 0 \\
NO3_{\text{mobmax}} & \text{Ndef} > NO3_{\text{mobmax}} 
\end{cases}
\]  \hspace{1cm} (9-17)

If the nitrogen amount available from soil uptake, N remobilisation from senescing leaves and the leaf nitrate pool to satisfy the N demand of the curd, \(N_{dem_{curd}} (g N pl^{-1} d^{-1})\), then the change of the curd nitrogen amount, \(dN_{curd}/dt\) is calculated according to Eqn. 9-15, if less nitrogen is available, all nitrogen is allocated to the curd:

\[
\frac{dN_{curd}}{dt} = \max(N_{dem_{curd}}, N_{rem} + NO3_{\text{mobmax}} + N_{up_{max}})
\]  \hspace{1cm} (9-18)

The change rate of the nitrogen pools of the other organs, \(dN_{i}/dt\) (g N pl\(^{-1}\) d\(^{-1}\)), is calculated according to the ratio of the remaining available nitrogen to their nitrogen demand:

\[
\frac{dN_i}{dt} = N_{dem_i} \frac{N_{up_{max}} + N_{rem} - \Delta N_{\text{curd}} / \Delta t}{N_{dem}}
\]  \hspace{1cm} (9-19)

**Dry matter production**

The dry matter production module used in this study is an extension of the approach described in chapter 4. Additionally the effect of sub-optimal leaf protein nitrogen
contents are considered assuming a linear decrease of the light use efficiency, LUE, (g MJ$^{-1}$) with increasing deviations of leaf protein content per area from optimal protein contents:

$$\text{LUE} = (\text{LUE}_0 - a_{\text{LUE}} \cdot (1 - b_{\text{LUE}})) f_{\text{Temp}}$$ (9-20a)

with:

$$b_{\text{LUE}} = \text{Nimp}_{\text{LUE}} \cdot (\text{NCAopt}_{\text{Prot}} - \text{NCA}_{\text{Prot}})$$ (9-20b)

where NCAopt$_{\text{Prot}}$ is the average nitrogen content of the canopy per canopy area (g protein N m$^{-2}$) and NCA$_{\text{Prot}}$ is the actual protein content of the canopy. The parameter Nimp$_{\text{LUE}}$ (g MJ$^{-1}$ gN$^{-1}$ m$^2$) thereby describes the decrease of LUE with decreasing area based protein nitrogen contents.

9.2.4. Parameter estimation and statistics

The whole model is implemented within the HUME modelling environment (Kage and Stützel, 1999a). This modelling environment supports parameter estimation based on the Marquardt algorithm (Marquardt, 1963) and allows easily sub-model exchange because of its modular object oriented structure. For this study the parameters $r_{fa}$ and $r_{fb}$ (Eqn. 9-1) were adjusted separately for the 1996 annual together with the late planted 1996 crop from the long term experiment and all other experiments, respectively. The parameters LUE$_0$ (Eqn. 9-20a) Nimp$_{\text{LUE}}$ (Eqn. 9-20b) were estimated for the 1996 and 1997 annual experiments separately. The parameter values obtained from the 1996 experiment then were used for the evaluation of the model using all other data (Table 9-1). Always un-weighted square sum of differences between simulated and measured model variables were used as objective function.

9.3. Results

The measured dry matter production of the N2 and N3 treatments at the final harvest of the 1996 annual experiment were at about 800 g m$^{-2}$ and not statistically different (Fig. 9-1). The DM production of the N1 treatment was only at the final harvest significantly lower than those of the N2 and N3 treatments (Fig. 9-1).
Estimates for the parameters $LUE_0$ and $N_{impLUE}$ of the dry matter production module did not vary considerably for both annual experiments (Table 9-2). The model described the 1996 dry matter data for different plant organs almost perfectly (Fig. 9-1, Table 9-3). Uptake and partitioning of nitrogen between the plant organs is also described quite good, however, the shoot N uptake of the N3 treatment was somewhat underestimated. This was mainly caused by a too low curd N uptake (Fig. 9-2, Table 9-3). Leaf nitrate under different nitrogen regimes was described quite good by the model (Fig. 9-3, Table 9-3). The model calculated an amount of N-loss due to leaf dropping of about 1 g N m$^{-2}$ for the N2 and N3 treatment and a N translocation of about 6 g N m$^{-2}$ (Fig. 9-3).

Despite the intensive N translocation, about two thirds the shoot N uptake remain in the not or only partially harvested plant parts stem and leaves (Fig. 9-2, Fig. 9-5). An additional amount of N of about 10% of shoot N remains in the root system (data not shown). Thereby N harvest index increased with decreasing fertilisation rates (Fig. 9-2, Fig. 9-5).
Chapter 9

Table 9-2: Estimates of parameters $LUE_0$ ($gMJ^{-1}$) and $N_{impLUE}$ ($gMJ^{-1}gN^{-1}m^2$) from the dry matter production model module as determined from adjustment to data of the both annual experiments.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Year</th>
<th>Value</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>$LUE_0$</td>
<td>1996</td>
<td>6.94</td>
<td>0.032</td>
</tr>
<tr>
<td>$N_{impLUE}$</td>
<td>1996</td>
<td>0.82</td>
<td>0.048</td>
</tr>
<tr>
<td>$LUE_0$</td>
<td>1997</td>
<td>7.03</td>
<td>0.056</td>
</tr>
<tr>
<td>$N_{impLUE}$</td>
<td>1997</td>
<td>0.75</td>
<td>0.094</td>
</tr>
</tbody>
</table>

Fig. 9-1: Measured and simulated dry matter production and partitioning of cauliflower under 4 different N supplies from the annual experiment in 1996 (parameterisation).
Fig. 9-2: Measured and simulated N uptake and partitioning of cauliflower under 4 different N supplies from the annual experiment in 1996 (parameterisation).
The model was evaluated using the parameters obtained from the 1996 annual experiment and the data of the 1997 annual experiment as well as data from the long term field experiment (Table 9-1). As already indicated by the estimated parameter values shown in Table 9-2, the model using the parameter values obtained from the 1996 annual experiment underestimated to some extend the dry matter production of the 1997 experiment (Fig. 9-4). Also the simulated N uptake of the N2 and N3 treatments was lower than the measured values (Fig. 9-5). The prediction for the whole evaluation data set seem to be less biased (Table 9-4, Fig. 9-6a), but again final values of shoot N uptake were underestimated to some extend (Fig. 9-6b). Considerable lower
amounts of leaf nitrate were simulated than measured in the 1997 annual experiment (Table 9-4).

Even for the crops grown under optimal N supply, there is a large difference of N uptake at final harvest ranging from about 200 kg N ha\(^{-1}\) to about 300 kg N ha\(^{-1}\) (Fig. 9-6b). This variation, however, is caused by two distinct data sub-sets, consisting of the spring planted (low N uptake) and the summer planted (high N uptake) crops. Much of this variation in N uptake could be explained due to differences in final leaf number (Fig. 9-7). Higher leaf numbers of summer planted crops are thereby caused by delayed vernalisation (data not shown). Such differences in leaf number and N uptake can be even larger for varieties which show a more delayed vernalisation at higher temperatures than the cultivar 'Fremont'. Under warm summer conditions the cultivar

![Graph showing measured and simulated dry matter production and partitioning of cauliflower under 4 different N supplies from the annual experiment in 1997 (evaluation).](image-url)
'Linday' needs about 27 days for vernalisation compared to about 15 days of the cultivar 'Fremont' (Fig. 9-8a) and to about 9 days under optimal vernalisation conditions. The continued leaf initiation during the delayed vernalisation phase resulted in final leaf numbers of about 31 for Fremont and 46 for Linday (Fig. 9-8b). But also curd initiation is delayed and a marketable curd size is reached at a later stage (Fig. 9-8c). The simulated shoot N uptake therefore was 32 g N m\(^{-2}\) for cultivar 'Linday' instead of 27 g N m\(^{-2}\) for cultivar 'Fremont' at a similar curd N uptake of 8.2 g N m\(^{-2}\) (Fig. 9-8d).

The temperature conditions presented in Fig. 9-8a are at the higher range of values which are typical for northern Germany. However, even under the quite maritime climatic conditions of this location a quite substantial variation of N uptake at curd maturity between different planting dates and for the both cultivars 'Fremont' and 'Linday' over period of 20 years was calculated (Fig. 9-9). For the cultivar Fremont average value for N uptake of the shoot ranging from about 25 g N m\(^{-2}\) for early planting dates up to 29 g N m\(^{-2}\) for late planting dates were simulated (Fig. 9-9). Exceptionally for

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Slope</th>
<th>Intercept</th>
<th>(r^2)</th>
<th>n</th>
<th>RMSE</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM Leaf</td>
<td>0.9161</td>
<td>10.1445</td>
<td>0.9854</td>
<td>12</td>
<td>23.2950</td>
<td>0.9742</td>
</tr>
<tr>
<td>DM Curd</td>
<td>1.1433</td>
<td>-3.9892</td>
<td>0.9886</td>
<td>8</td>
<td>22.1058</td>
<td>0.9671</td>
</tr>
<tr>
<td>DM Stem</td>
<td>0.8964</td>
<td>3.1760</td>
<td>0.9860</td>
<td>12</td>
<td>5.4007</td>
<td>0.9720</td>
</tr>
<tr>
<td>DM Shoot</td>
<td>0.9678</td>
<td>7.7180</td>
<td>0.9937</td>
<td>12</td>
<td>22.8977</td>
<td>0.9925</td>
</tr>
<tr>
<td>LAI</td>
<td>1.0054</td>
<td>-0.1231</td>
<td>0.9755</td>
<td>12</td>
<td>0.2536</td>
<td>0.9696</td>
</tr>
<tr>
<td>N Leaf</td>
<td>1.0188</td>
<td>-0.0276</td>
<td>0.9891</td>
<td>12</td>
<td>0.6085</td>
<td>0.9884</td>
</tr>
<tr>
<td>Leaf Nitrate</td>
<td>0.9943</td>
<td>0.0240</td>
<td>0.9334</td>
<td>12</td>
<td>0.2372</td>
<td>0.9329</td>
</tr>
<tr>
<td>N Curd</td>
<td>0.9260</td>
<td>0.0551</td>
<td>0.9825</td>
<td>12</td>
<td>0.1051</td>
<td>0.9763</td>
</tr>
<tr>
<td>N Stem</td>
<td>1.2739</td>
<td>-0.3244</td>
<td>0.9855</td>
<td>8</td>
<td>1.2348</td>
<td>0.9277</td>
</tr>
<tr>
<td>N Shoot</td>
<td>1.0895</td>
<td>-0.3083</td>
<td>0.9920</td>
<td>12</td>
<td>1.2658</td>
<td>0.9814</td>
</tr>
</tbody>
</table>

Table 9-3: Results of linear regression analysis (slope, intercept, \(r^2\), n) as well as the residual mean square error and the modelling efficiency for a number of state variables from the parameterisation of the model using the data of the 1996 annual field experiment.
the last planting date, the calculated standard deviation of N uptake was at around 2.5 g N m\(^{-2}\) (Fig. 9-9). For the cultivar 'Linday', however, the calculated average values of shoot N uptake were only slightly higher for early planting dates, but exceeded the average values of 'Fremont' by up to 2.5 g N m\(^{-2}\) for summer plantings (Fig. 9-9). Also the calculated standard deviation of N uptake was higher for this cultivar with values from 2.9 to 3.4 g N m\(^{-2}\) (Fig. 9-9). About 2.5-4.5 g N m\(^{-2}\) of shoot N is calculated to be situated within the leaf nitrate pool (Fig. 9-9).

A similar scenario calculation as presented in Chapter 8 was carried out to obtain N response curves for dry matter production and shoot N uptake. The obtained response curves for shoot dry matter are characterised by a higher DM yield at zero N fertilisation for the loess loam soil and a more rapid approach to maximum DM yield for the loess loam soil compared to the sandy soil (Fig. 8-10a). A split application of nitrogen on the sandy soil only partly reduced the differences between both soils. N uptake of

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**Table 9-4: Results of linear regression analysis (slope, intercept, \(r^2\), n) as well as the residual mean square error (RMSE) and the modelling efficiency (EF) for a number of state variables from the evaluation of the model using the data of the 1997 annual field experiment and of 6 crops from the long term experiment (see Table 9-1).**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Slope</th>
<th>Intercept</th>
<th>(r^2)</th>
<th>n</th>
<th>RMSE</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM Leaf</td>
<td>0.9956</td>
<td>13.9984</td>
<td>0.9116</td>
<td>51</td>
<td>62.1031</td>
<td>0.9076</td>
</tr>
<tr>
<td>DM Stem</td>
<td>0.9241</td>
<td>4.4996</td>
<td>0.6683</td>
<td>51</td>
<td>27.2220</td>
<td>0.6634</td>
</tr>
<tr>
<td>DM Curd</td>
<td>1.1044</td>
<td>2.0846</td>
<td>0.8293</td>
<td>35</td>
<td>41.9739</td>
<td>0.8104</td>
</tr>
<tr>
<td>DM Shoot</td>
<td>1.0357</td>
<td>7.5372</td>
<td>0.9530</td>
<td>51</td>
<td>72.0527</td>
<td>0.9477</td>
</tr>
<tr>
<td>LAI</td>
<td>1.0312</td>
<td>0.2490</td>
<td>0.8328</td>
<td>42</td>
<td>0.9611</td>
<td>0.8091</td>
</tr>
<tr>
<td>N Leaf</td>
<td>1.0585</td>
<td>-0.3842</td>
<td>0.8833</td>
<td>51</td>
<td>2.0622</td>
<td>0.8805</td>
</tr>
<tr>
<td>Leaf Nitrate</td>
<td>1.7691</td>
<td>0.1739</td>
<td>0.9398</td>
<td>12</td>
<td>1.6130</td>
<td>0.5904</td>
</tr>
<tr>
<td>N Stem</td>
<td>0.8457</td>
<td>0.1202</td>
<td>0.7471</td>
<td>51</td>
<td>0.3874</td>
<td>0.7217</td>
</tr>
<tr>
<td>N Curd</td>
<td>0.9246</td>
<td>-0.1824</td>
<td>0.8156</td>
<td>31</td>
<td>1.3815</td>
<td>0.7871</td>
</tr>
<tr>
<td>N Shoot</td>
<td>1.0239</td>
<td>-0.3814</td>
<td>0.9240</td>
<td>51</td>
<td>2.3635</td>
<td>0.9233</td>
</tr>
</tbody>
</table>
cauliflower shoots responds more linearly to an increased N supply than dry matter (Fig. 8-10b) but the differences between the soil types and the single and split application on the sandy soil are similar.

9.4. Discussion

The presented study aims to quantify dry matter production and nitrogen uptake and partitioning of cauliflower crops grown under varying climatic conditions and nitrogen supply. This may facilitate more precise fertilisation recommendations and thereby help to minimise potential harmful leaching of nitrate into the groundwater.

Fig. 9-5: Measured and simulated N uptake and partitioning of cauliflower under 4 different N supplies from the annual experiment in 1997 (evaluation).
Fig. 9-6: Measured and simulated shoot N uptake of cauliflower under different supplies, grouped into optimal N supply ($N_{\text{opt}}$) and reduced N supply ($N_{\text{red}}$). Figure (a) is for all harvests, and figure (b) only for final harvests. For parameters of the regression lines shown in (a) see (Table 9-4) for (b): $y = -4.192 \pm 2.68 + 1.20(\pm0.13)x$, $r^2=0.87$, $n=14$. All evaluation experiments except the 1994 annual experiment were used.
The simple LUE based approach for calculating dry matter production was quite successful in describing (Fig. 9-1, Table 9-3) and predicting (Fig. 9-4, Table 9-4) dry matter production of cauliflower under a varied N supply. The influence of protein nitrogen content per leaf area on light use efficiency is depicted in our model with a kind of a linear response plateau approach, because the linear increase of LUE with a increasing $\text{NCA}_{\text{Prot}}$ from sub optimal values (Eqn. 9-20) is cut off by the upper limit of $\text{NCA}_{\text{Prot}}$ resulting from Eqn. 9-2 and 9-8. Non-linear saturating response functions of LUE on $\text{NCA}_{\text{Prot}}$ (Muchow and Sinclair, 1994; Bange et al., 1997; Sinclair and Horie, 1989) may be more realistic. The principle shape of such curves may be derived from up-scaling of single leaf photosynthesis to the canopy level. Their parameters may then be estimated directly from field experiments using parameter estimation procedures. Generally, canopy aggregated LUE approaches are not able to predict effects of an changing nitrogen distribution within the canopy (Hirose and Werger, 1987; Bindraban, 1999). Theoretical studies indicate a strong impact of nitrogen distribution on the functional relationship between LUE and $\text{NCA}_{\text{Prot}}$ (Alt et al., 2000d). However, the N distribution within the canopy of cauliflower seems to be not seriously influenced by either N deficiency or radiation intensity (Chapter 6). This may explain the quite satisfying predictive quality of the LUE approach presented here.

The estimated values of $\text{LUE}_0$ (Table 9-2) are somewhat lower than reported in Chapter 7. This may at least partly caused by the use of a modified light interception module described in Chapter 5, which takes a value of 0.75 for the extinction coefficient for photosynthetic radiation instead of 0.65 used in Chapter 7. Recently, Olesen and Greven (2000) published a LUE approach for calculating dry matter production also assuming a linear decrease of LUE with increasing levels of radiation intensity. Their value of $\text{LUE}_0$ is much lower (5.44 g MJ$^{-1}$) but they assumed only a slightly decrease of LUE with PAR resulting in very similar predictions of both approaches at daily radiation levels of about 6-7 MJ PAR m$^{-2}$ d$^{-1}$. 


Adjusted initial values for shoot dry matter were used for the early plantings of the rotational experiment. The reasons for this procedure have been discussed in Chapter 4. Briefly, the model has problems to predict dry matter production of early plantings because the leaf area loss due to frost and the sometimes severe transplanting shock are not considered for in the model. This shortcoming may be handled by initialising the model and starting the simulation after complete establishment of the crop and not at transplanting.
Fig. 9-8: Daily average air temperature, simulated vernalisation state (a), measured and simulated number of visible leaves (b), measured and simulated shoot and curd dry matter (c) and simulated shoot and curd nitrogen for a field experiment with two cauliflower cultivars ('Fremont' and 'Linday') carried out in 1994.
The reasons for the different rapidity of curd growth for the later planted crops in 1996 are still not clear. There seems to be an influence of assimilate supply on curd initiation and/or growth. This is described by Alt (1999) with a function enhancing curd sink size more rapidly with higher values of leaf N per leaf area. Nowbuth and Pearson (1998) found an influence of assimilated supply on curd initiation. However, there was no indication of such an influence which should affect final leaf number in our experiments.

Fig. 9-9: Simulated shoot N and leaf nitrate N at curd maturity (marketable size: 180 mm diameter) of two different cauliflower cultivars (Fremont, Linday) for different planting dates calculated over a time period of 20 years using weather data from Hannover, Germany. Error bars indicate the standard error.
Further research seems therefore needed to address this problem more thoroughly.

The results presented in Fig. 9-3 demonstrate the high amount of leaf nitrate in cauliflower plants accumulated under high N supply and indicate a high importance of N translocation from senescing leaves to younger plant parts during the later growth stage of cauliflower. The latter result, however, relies on estimates about the onset of leaf senescence described in Chapter 5 and measured N contents of senescent leaves. Direct measurements of N translocation using isotopes (Ma et al., 1998) or of leaf N content with high temporal resolution may be used to further substantiate the estimates presented here.

The low nitrogen harvest index (Fig. 9-2, Fig. 9-5) of cauliflower we observed is in accordance with other data from the literature (Everaarts et al., 1996; Greenwood et al., 1996; Rahn et al., 1992; Van den Boogaard and Thorup-Kristensen, 1997). Low values of N harvest index are common for vegetable crops were immature generative organs are harvested, like brussels sprouts (Booij et al., 1997) and broccoli (Bowen et al., 1999). For late harvested crops these high N amounts in crop residues represent a substantial leaching risk (De Neve and Hofman, 1998).

The calculated relatively small effect of the split nitrogen application (Fig. 8-10) on shoot dry matter and shoot N uptake is in accordance with results of Everaarts et al. (1996). It can be explained by the dominating effect of soil water contents on the differences in uptake efficiency between the sandy and the loess loam soil and by the absence of N-losses due to leaching out of the rooted soil volume. The response of N uptake to increasing N supply is similar to a linear response-plateau, with two segments of the linear phase. The second segment of the linear phase with a smaller slope is the resulting from the fact that increasing portions of the N uptake are calculated to be allocated to the nitrate fraction, which the model considers as not productive. The plateau level clearly is the consequence of the saturated sink capacity of the cauliflower crop. Greenwood et al., 1989 compared the N response of vegetable and gramineous crops and found a linear response plateau response more typical for gramineous than for vegetable crops where quadratic response function gave a better fit to the data. He interpreted this as the consequence of a restricted N availability especially during early growth stages of vegetable crops, where rooting density is much lower than for
N demand of cauliflower

Thereby N application rates exceeding the N demand of the shoot are still increasing crop productivity of vegetables by increasing the N availability at early growth stages. The model approach used here calculated not such a limitation of N availability during early growth stages (Fig. 8-7, Chapter 8), but this may be due to the neglection of the spatial heterogeneity of the root system during early growth stages of cauliflower.

The presented results can be used to implement a more specific N fertilisation recommendation system for cauliflower. Summer planted crops generally seem to have a 30-40 kg N ha\(^{-1}\) higher N demand and show a higher variation of N demand because of variations in vernalisation time. Because daily mineralisation rates are usually substantially lower than crop N uptake this causes an increased demand for fertiliser N. The model approach presented here is able to quantify this additional N demand and to

Fig. 9-10: Simulated shoot dry matter and shoot nitrogen under varying nitrogen fertilisation rates for a loess loam soil, a sandy soil and a sandy soil with split N application. All other input variables as in the 1997 annual experiment.
adjust a second N application immediately after completion of the vernalisation (Fig. 9-8). Further development is needed to include suitable estimations of net mineralisation into the model calculations.

There is a discrepancy between the fertilisation recommendations between several countries in Western Europe. Whereas Everaarts et al., (1996) recommends based on experiments in the Netherlands a target value of 224 kg N ha\(^{-1}\) minus soil nitrate from 0-60 cm at planting, the KNS system advises higher values of 270 kg N ha\(^{-1}\) 4 weeks after planting (Lorenz et al., 1989), equivalent to about 300 kg N ha\(^{-1}\) at planting. Some of this differences may be explained by differing soil conditions including differing typical mineralisation rates. However, also a contribution of a higher vernalisation risk at more continental climates may be included in the German recommendations.

9.5. Conclusions

The observed and predicted differences in shoot N content at curd maturity (Fig. 9-6, Fig. 9-9) give indications for a specific N fertilisation regime for different a) climatic conditions, b) cultivars and c) soil types. Summer planted crops with a usually increased number of leaves take up about 30-40 kg N ha\(^{-1}\) more than early planted crops. A better adaptation of N fertilisation and N demand of cauliflower may be achieved by split application of N. A second N fertilisation after the end of the vernalisation period should be increased after periods of high temperatures resulting in an increased number of leaves and a longer growth period. For sandy soils a somewhat higher level of soil nitrate is needed to sustain maximum growth rates. On this soil type, split nitrogen applications may also marginally enhance nitrogen availability and partly reduce N leaching losses.
Demand of cauliflower
Chapter 10

10. Using deep rooting cereal crops for enhancing nutrient efficiency of intensive production systems I. Quantification of root growth of late sown winter wheat using a simple descriptive model

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Abstract

Root observations on winter wheat grown on a loess loam soil during three consecutive years were carried using the minirhizotron and the soil core method. There was a good \( r^2 = 0.92 \) correlation between the minirhizotron and the soil core method for the sub-soil data (>30 cm soil depth), whereas the minirhizotron method gave unrealistically low values of rooting intensity for the top soil. Rooting depth development could be described using a linear function of temperature sum with an increase of rooting depth of 0.11 \(( \pm 0.01 \) cm \( ^\circ C^{-1} d^{-1} \).

A simple descriptive root growth model based on the assumptions of a negative exponential decline of root length density (RLD) with soil depth, and of a fixed ratio of RLD at the top of the soil profile and at rooting depth \( r_{RLD} \) was used to describe the temporal and spatial variation of RLD found in the field. Two hypotheses on the allocation of dry matter into the fine root fraction thereby were proven. Hypothesis H1 postulated a constant and hypothesis H2 a linearly with temperature sum decreasing fraction of dry matter allocated to fine roots. The H2 hypothesis performed much better than the H1 hypothesis and explained about 90% of the total variance found for RLD values from all years and all soil depths.
Chapter 10

10.1. Introduction

The prediction of rooting depth and rooting intensity is the prerequisite for any mechanistically approach aiming to predict nutrient and water uptake processes. Such models incorporated within crop crops model may strongly facilitate the adaptation and optimisation of production systems over a wider range of environmental conditions with respect to environmental and economic objectives (Klepper and Rickman, 1990). Thereby especially intensive production system are of concern, because unused amounts of nitrate may be leached down to soil depths were rooting intensity is low (Kuhlmann et al., 1989; Hähndel and Dressel, 1996). The prediction of rooting depth and rooting intensity in the sub soil then is an inevitable requirement for the development of appropriate fertilisation regimes which have to ensure high yields and an effective use of sub-soil N reserves.

Root growth of winter wheat has been studied using several different approaches and under quite contrasting production situations (Barraclough and Leigh, 1984; Gregory et al., 1978; Belford et al., 1987; Vincent and Gregory, 1989; Hamblin et al., 1990). Rooting depth of winter wheat may reach depths > 150 cm, but late sowing and unfavourable soil conditions may limit the rooting depth of winter wheat.

The aim of the paper presented therefore is to quantify root growth of late sown winter wheat grown on a loess soil in succession of cauliflower crops, which leave large amounts of residual nitrogen as soil nitrate and crop residues in the field. In a succeeding paper the soil nitrogen dynamics in the soil plant system will be further analysed.

Root growth models differ widely in their level of detail (see Van Noordwijk and Van den Geijn (1996) for recent review) and thereby in the number of input parameters which have to be estimated from experimental data. In Chapter 7 and Chapter 8 a quite simple approach was presented which successfully described the spatial and temporal dynamics of cauliflower root systems. Data from 3 years of a long term field experiment were used to adopt and to parameterise this root growth model for winter wheat.
10.2. Material and Methods

The rooting data were obtained from a long-term rotational experiment carried out at the experimental station ‘Ruthe’, located about 15 km south of Hanover. The soil there is a silty clay loam (typical hapludalf) with 0.8 % C, 10 sand, 80 % silt and 10 % in the plough layer of 30 cm depth. The experiment includes two crop rotations, two tillage regimes and two nitrogen fertilisation levels with three replications. In this experiment root data were only collected from the conventional mouldboard tillage plots. The experiment was set up as a split-plot design with 3 replications as blocks, tillage and rotation as main plots and nitrogen fertiliser rate as subplots. The first rotation includes mainly vegetable crops, lettuce and celery in the first year, two crops of cauliflower in the second year followed by winter wheat and spinach in the third year. The second rotation includes mainly agricultural crops, faba beans in the first year, winter barley and cauliflower in the second year followed by winter wheat and mustard (green manure). Plots were 16 m in width and 8 m in length, with sampling areas of 2x8 m$^2$ for the $N_{\text{min}}$ probes and 2x8 m$^2$ for final harvest.

Winter wheat cv. *Xanthos* was sown at a density of 350 m$^2$ using a seed drill with 12.5 cm row width. Sowing dates are summarised in Table 10-1. Weeds, fungal diseases and insects were controlled chemically. The P and K levels in the soil were kept at levels ensuring optimal growth (>20 mg/100 g soil), the soil pH was at 7.1.

The weather during winter was quite contrasting in the three experimental years with 94/95 being warmer and more humid than the long-term average, 95/96 being colder and dryer than average and 96/97 again somewhat warmer more humid than the long term average (Fig. 10-1, Table 10-2). Spring and early summer temperatures as well as precipitation values were not substantially deviating from the long term average, except for the low rainfall in 1996.
Table 10-1: Planting dates and dates of root observations in the field experiments used in this study.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Year</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sowing</td>
<td>94/95</td>
<td>November 6</td>
</tr>
<tr>
<td>Installation of tubes</td>
<td></td>
<td>March 2</td>
</tr>
<tr>
<td>Minirhizotron observations</td>
<td></td>
<td>April 26</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 13</td>
</tr>
<tr>
<td>Soil core extractions</td>
<td></td>
<td>20.6.95</td>
</tr>
<tr>
<td>Sowing</td>
<td>95/96</td>
<td>November 2</td>
</tr>
<tr>
<td>Installation of tubes</td>
<td></td>
<td>March 26</td>
</tr>
<tr>
<td>Minirhizotron observations</td>
<td></td>
<td>April 30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 28</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 18</td>
</tr>
<tr>
<td>Soil core extractions</td>
<td></td>
<td>June 26</td>
</tr>
<tr>
<td>Sowing</td>
<td>96/97</td>
<td>November 5</td>
</tr>
<tr>
<td>Installation of tubes</td>
<td></td>
<td>March 13</td>
</tr>
<tr>
<td>Minirhizotron observations</td>
<td></td>
<td>April 15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 16</td>
</tr>
<tr>
<td></td>
<td></td>
<td>May 30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June 19</td>
</tr>
<tr>
<td>Soil core extractions</td>
<td></td>
<td>June 16</td>
</tr>
</tbody>
</table>

Nitrogen was given in all experiments as ammonium nitrate according to the $N_{\text{min}}$ fertilisation schedule (Scharpf and Wehrmann, 1975). For winter wheat this defines a target supply level of 120 kg N/ha including soil nitrate from 0 to 90 cm depth that has to be adjusted by fertilisation. Reduced fertilised plots received 70% of this supply in 1995 and 1996 and 50% in 1997. In addition about 30 kg N were given at shooting and about 50 kg at ear emergence only at the normal fertilised plots.
Fig. 10-1: Weekly average air temperature from beginning of September to end of August in the three growing seasons 1994/95, 1995/96 and 1996/97 and from the long term average 1970-1995 (Lt. av.).

Table 10-2: Cumulative rainfall (mm) during the winter and spring/early summer periods in the three experimental years at the station Ruthe.

<table>
<thead>
<tr>
<th>Period</th>
<th>94/95</th>
<th>95/96</th>
<th>96/97</th>
<th>avg. 1970-1995</th>
</tr>
</thead>
<tbody>
<tr>
<td>November 1 – March 31</td>
<td>349</td>
<td>110</td>
<td>247</td>
<td>203</td>
</tr>
<tr>
<td>April 1 - July 15</td>
<td>201</td>
<td>158</td>
<td>241</td>
<td>197</td>
</tr>
</tbody>
</table>
Soil cores were extracted on one sampling date per experiment (Table 10-1) with an special root auger of 8 cm diameter (Eijkelkamp Agriresarch Equipment, Giesbeek, The Netherlands) down to a depth of 120 cm within a spatial resolution of 15 cm. Samples were taken at two positions within a field plot, one directly on a winter wheat row and one in a mid row position. Soil cores were stored at 4°C until roots were washed out over a 1.25 mm sieve and root length was determined after removing organic debris from the sample using the method of Newman (1966).

Two minirhizotron tubes made from polyacryl with an outer diameter of 4.6 cm and a total length of 180 cm were installed per plot at an angle deviating 30° from the vertical direction to avoid preferential root growth along the tubes (Bragg et al., 1983). The upper parts of the tubes were painted black and closed with a rubber stopper to avoid incidence of light (Levan et al., 1987). Holes for the tubes were made by hand driven soil corers in a two step procedure. At first an auger of a diameter of 4 cm was used for a pilot hole followed by a second spiral auger of 4.5 cm diameter. The minirhizotron tubes usually could be installed manually into the resulting hole with slight pressure indicating a close fit of the tube to the soil without severe soil compaction in the vicinity of the tube.

For root observations an endoscope equipped with a glas fiber light source (Richard Wolf GmbH, Knittlingen, Germany) of a total length of 180 cm and a diameter of 1.8 cm was used. The view of the endoscope was at the right angle to ist main axis and the aperture angle of the endoscope was 60°. To ensure a constant distance between the endoscope lens and the tube surface the endoscope was fixed within the tube by means of two PVC rings attached 15 cm from the bottom of the endoscope in 10 cm distance. The endoscope was marked with rings in 5.77 cm spacing to facilitate an inspection of the minirhizotron tube in effective soil depth increments of 5 cm. Tube inspection of the tubes was carried out for every tube in two view directions each deviating 45° out of the perpendicular in effective vertical increments of 5 cm. Root observations were directly converted into root scores according to Maertens (1987) at the field plot. For correlation notation values were pooled according to the spatial aggregation of soil core data.
10.3. Model

The model approach used to describe and interpolate root growth of winter wheat is essentially the same as presented in chapter 7. However, because some modifications are introduced, the basic equations are presented again.

10.3.1. Fine root growth

If the fraction of dry matter increase attributed to fine root growth, \( f_{Rf} \), is known, the increase of total fine root length \( dR_L/dt \) (cm \( m^{-2} \cdot d^{-1} \)) may simply be calculated from the total dry weight increase \( dW_t/dt \) (g \( m^{-2} \cdot d^{-1} \)) and the average specific root length \( SRL \) (cm \( g^{-1} DM \)).

\[
\frac{dR_L}{dt} = \frac{dW_t}{dt} \cdot f_{Rf} \cdot SRL \tag{10-1}
\]

The value of \( f_{Rf} \) may be assumed to be constant or to decrease during the plant’s development from the vegetative to the generative phase with a minimum value of zero. As a simple approximation a linear decrease of \( f_{Rf} \) with temperature sum since emergence may be assumed:

\[
f_{Rf} = \max(0, f_{Rf0} - f_{Rfdec} \cdot TS) \tag{10-2}
\]

where \( f_{Rf0} \) is the initial fraction of dry matter allocated to the root fraction and \( f_{Rfdec} \) (\( °C^{-1} \cdot d^{-1} \)) is the decrease of this fraction per unit of accumulated temperature.

The value of \( SRL \) may regarded as a parameter or be calculated from the average diameter of the roots and the average dry matter content of the roots. We used a constant value of 7000 cm g \( DM^{-1} \). We did not measure specific root length within our experiments. Our estimate is mainly based on the results of Barraclough and Leigh (1984), nevertheless, also much lower values have been reported from soils with a quite high clay content (Siddique et al., 1990; Savin et al., 1994).

The total dry matter production rate may be estimated from the shoot dry matter increase if one considers only a fine root pool as below-ground biomass:

\[
\frac{dW_t}{dt} = \frac{1}{(1 - f_{Rf})} \frac{dW_{sh}}{dt} \tag{10-3}
\]
Chapter 10

Shoot dry matter increase may be obtained from a crop growth model or may be derived from an appropriate function fitted to experimental data. In this study we followed the second approach, using the Richards-function (Thornley and Johnson, 1990):

$$\frac{dW_{sh}}{dt} = r_{Ws} \cdot T_{eff} \cdot W_{sh} \cdot \left( \frac{W_{shmax}^{\cdot rf} - W_{sh}^{\cdot rf}}{rf \cdot W_{shmax}^{\cdot rf}} \right)$$  \hspace{1cm} (10-4)

Where $r_{Ws}$ is a growth rate parameter, $T_{eff}$ is the effective temperature, $W_{shmax}$ is the maximum attained shoot dry matter and $rf$ is form parameter. This function was integrated numerically, using a value for $W_{sh}$ at sowing of 10 g m$^{-2}$. The effective temperature was calculated from:

$$T_{eff} = \max(0, (T_a - T_b))$$  \hspace{1cm} (10-5)

Where $T_a$ is the daily average air temperature $T_b$ is a base temperature, assumed to be 4°C.

10.3.2. Rooting depth

Rooting depth $z_r$ (cm) is often found to increase linearly with accumulated temperature sum within certain development stages, but lag phases in rooting depth increase (Thorup-Kristensen, 1998; Thorup-Kristensen and Van den Boogaard, 1998) as well as diminishing rooting depth increases during maturity (Jaafar et al., 1993) have been observed.

Rooting depth increase (cm d$^{-1}$) therefore simply is:

$$\frac{dz_r}{dt} = b_{zr} \cdot T_{eff}$$  \hspace{1cm} (10-6)

Where $b_{zr}$ (cm°C$^{-1}$·d$^{-1}$) is a constant. The base temperature for root growth was set to 0°C.
10.3.3. Vertical root distribution

The root length density, RLD, (cm·cm⁻³) of many annual arable and vegetable crops decreases approximately exponentially with soil depth (Barraclough, 1984; Gerwitz and Page, 1974; Greenwood et al., 1982):

\[
\text{RLD} = \text{RLD}_0 \cdot e^{-k_r z} \tag{10-7}
\]

where the constant \( k_r \) (cm⁻¹) is the fractional decrease in RLD per unit increase of soil depth and \( \text{RLD}_0 \) is the root length density at zero soil depth.

Integration of Eqn. 10-7 from \( z=0 \) to a depth \( z=z_r \) where the root length density is very low yields the root length RL (cm·cm⁻²):

\[
\text{RL} = \int_{z=0}^{z=z_r} \text{RLD}_0 \cdot e^{-k_r z_r} \cdot dz = \frac{\text{RLD}_0}{k_r} \cdot (1 - e^{-k_r z_r}) \tag{10-8}
\]

The second term of Eqn. 10-8 becomes very small if the product of \( k_r \) and \( z_r \) is high enough.

If RL and \( z_r \) are known, and if one assumes a certain ratio, \( r_{RLD} \) (-), between the RLD at \( z_r \), \( \text{RLD}_{z_r} \), and \( \text{RLD}_0 \) the value of \( k_r \) (cm⁻¹) then can be calculated from:

\[
k_r = -\ln\left(\frac{\text{RLD}_{z_r}}{\text{RLD}_0}\right) = -\frac{\ln(r_{RLD})}{z_r} \tag{10-9}
\]

Knowing this value the root length density at the soil surface can be calculated:

\[
\text{RLD}_0 = \text{RL} \cdot k_r \cdot \frac{1}{1 - e^{-k_r z_r}} \tag{10-10}
\]

The average rooting density \( \text{RLD}_{av} \) (cm·cm⁻³) within a certain soil layer located between two soil depths \( z_1 \) and \( z_2 \), \( z \) then becomes:

\[
\text{RLD}_{av} = \frac{\text{RLD}_0 \cdot (e^{-k_r z_1} - e^{-k_r z_2})}{k_r \cdot (z_2 - z_1)} \tag{10-11}
\]
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10.4. Model implementation and statistics

The above algorithms were implemented as sub-models within the HUME modelling environment (Kage and Stützel, 1999a). The HUME modelling environment supports parameter estimation based on the Marquardt algorithm (Marquardt, 1963) using an algorithm from Press et al. (1986). We used the un-weighted square sum of differences between simulated and measured values of all available RLD values as the objective function for estimating the parameters $f_R$ (Eqn. 10-1), $f_{R_0}$, $f_{R_{dec}}$ (Eqn. 10-2) and $\alpha_{RLD}$ (Eqn. 10-9). All other statistical analysis were done using the procedures ANOVA, REG and NLIN from the SAS system (SAS Institute, 1988).

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

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

(10-12)

Where $y_i$ is the value of the $i^{th}$ observation, $\hat{y}_i$ is the $i^{th}$ model prediction and $\bar{y}$ is the average of the observations. The maximum value of the EF is one for complete agreement between simulated and measured values, but also negative values are possible if the model describes the data less well than the observation mean.

Comparing models having different numbers of parameters by solely by their EF value, however, is not appropriate since no correction for parameter number is included within these measure. An approach to overcome this problem is the Akaike information criterion AIC (Akaike, 1969).

$$
AIC = n \cdot \ln\left(\frac{\sum (y_i - \bar{y}_i)^2}{n}\right) + 2 \cdot p
$$

(10-13)

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

\[
RMSE = \sqrt{\frac{1}{n} \sum (y_i - \hat{y}_i)^2}
\]  
(10-14)

giving the average model prediction error.

### 10.5. Results

Due to the high amount of crop residues from the previous cauliflower crops, the nitrogen supply level in the experiment was high, even for the reduced fertilised winter wheat as indicated by the soil mineral nitrogen found in spring (Table 10-3). Therefore, there were no significant differences in shoot dry matter production between the two crop rotations, where either winter barley and cauliflower or two cauliflower crops were grown in the previous year (data not shown). Consequently, the data from both treatments were pooled for further analysis. Also the differences in shoot dry matter production of normal and reduced plots were not significant except for the last sampling date in 1996 (Fig. 10-2, Table 10-4). The values for root length density obtained from the soil core method at around ear emergence to flowering were therefore very similar for both nitrogen supply regimes (Fig. 10-3). The absolute values in the upper 15 cm were from about 1.6 cm cm\(^{-3}\) for the normal fertilisation in 1995 in minimum to 3.8 cm cm\(^{-3}\) for the reduced fertilisation treatment in 1996 in maximum. At 105-120 cm the absolute values were at around 0.05 to 0.15 cm cm\(^{-3}\). A fit of a negative exponential equation (Eqn. 10-7) to the data explained usually more than 90 % of the total variation caused between different soil depths (Table 10-5). The RLD\(_0\) values are substantially higher than averages over the upper 15 cm and the variation found in the parameter k\(_r\) was comparable small. The estimates of total root length, however, varied considerably between years, 1995 having the lowest values, despite the fact that shoot dry matter was comparable high at sampling date in this year. Therefore, the root length to shoot dry matter ratio RL/W\(_{sh}\) was lowest in this year. There was no clear effect of nitrogen fertilisation level on this ratio.
Table 10-3: Soil mineral nitrogen (kg N/ha) at spring sampling dates in winter wheat for three different years and from two nitrogen supply levels, “Norm”, 100% of recommended and “Red” 70% (1995) and 50% (1996-1997) of the supply level.

<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Norm</td>
<td>Red</td>
<td>Norm</td>
</tr>
<tr>
<td>0-30</td>
<td>13.4</td>
<td>12.3</td>
<td>43.5</td>
</tr>
<tr>
<td>30-60</td>
<td>16.5</td>
<td>16.4</td>
<td>80.6</td>
</tr>
<tr>
<td>60-90</td>
<td>56.8</td>
<td>51.3</td>
<td>32.7</td>
</tr>
<tr>
<td>90-120</td>
<td>63.4</td>
<td>57.5</td>
<td>19.0</td>
</tr>
<tr>
<td>Σ0-120</td>
<td>150.1</td>
<td>137.5</td>
<td>175.8</td>
</tr>
</tbody>
</table>

Table 10-4: Parameter values and standard errors (±) estimated for the Richards-equation fitted to data of shoot dry matter (g/m²) of winter wheat with normal (Norm) and reduced (Red) fertilisation in three consecutive years.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Experimental year</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Norm</td>
<td>Red</td>
<td>Norm</td>
<td>Red</td>
</tr>
<tr>
<td>W_{smax}</td>
<td>1703.0</td>
<td>1696.4</td>
<td>1341.1</td>
<td>1124.4</td>
</tr>
<tr>
<td></td>
<td>(±89.6)</td>
<td>(±89.3)</td>
<td>(±39.3)</td>
<td>(±10.5)</td>
</tr>
<tr>
<td>r_{Ws}</td>
<td>0.00715</td>
<td>0.00753</td>
<td>0.01609</td>
<td>0.02074</td>
</tr>
<tr>
<td></td>
<td>(±0.00394)</td>
<td>(±0.00457)</td>
<td>(±0.03727)</td>
<td>(±0.02511)</td>
</tr>
<tr>
<td>rf</td>
<td>0.964</td>
<td>1.046</td>
<td>2.485</td>
<td>3.267</td>
</tr>
<tr>
<td></td>
<td>(±0.743)</td>
<td>(±0.856)</td>
<td>(±6.212)</td>
<td>(±4.186)</td>
</tr>
</tbody>
</table>
Table 10-5: Parameters $RLD_0$ and $k_r$ of the negative exponential function describing the decrease of root length density with soil depth, $r^2$ of the fit, corresponding calculated total root length RL ($RLD_0/k_r$) and shoot dry matter, $W_{sh}$, of the winter wheat at sampling date in three years with two different N-supply levels (normal/reduced).

<table>
<thead>
<tr>
<th>Year</th>
<th>Fert.</th>
<th>$RLD_0$ (cm$^3$cm$^{-3}$)</th>
<th>$k_r$ (cm$^{-1}$)</th>
<th>$r^2$</th>
<th>RL (cm$^2$cm$^{-2}$)</th>
<th>$W_{sh}$ (g m$^{-2}$)</th>
<th>RL/WS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>Norm</td>
<td>2.13 (±0.29)</td>
<td>0.026 (±0.005)</td>
<td>0.90</td>
<td>80.6</td>
<td>1117.8</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Red</td>
<td>2.44 (±0.13)</td>
<td>0.038 (±0.003)</td>
<td>0.99</td>
<td>64.1</td>
<td>1110.3</td>
<td>0.06</td>
</tr>
<tr>
<td>1996</td>
<td>Norm</td>
<td>4.74 (±0.64)</td>
<td>0.034 (±0.006)</td>
<td>0.92</td>
<td>138.2</td>
<td>748.5</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>Red</td>
<td>5.42 (±0.79)</td>
<td>0.031 (±0.006)</td>
<td>0.90</td>
<td>175.4</td>
<td>701.3</td>
<td>0.25</td>
</tr>
<tr>
<td>1997</td>
<td>Norm</td>
<td>3.57 (±0.50)</td>
<td>0.027 (±0.005)</td>
<td>0.89</td>
<td>134.6</td>
<td>1093.4</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>Red</td>
<td>3.62 (±0.57)</td>
<td>0.026 (±0.006)</td>
<td>0.86</td>
<td>140.4</td>
<td>1211.0</td>
<td>0.12</td>
</tr>
</tbody>
</table>

Also the data obtained from the minirhizotron observations showed no significant differences between the nitrogen treatments (data not shown). Therefore, all scores for one soil depth class were pooled giving one value for each observation date and depth class. The root scores increased from 0 to about 40 cm soil depth and decreased from there on. This decrease was strongly dependent on sampling date (Fig. 10-4). The absolute values of the root scores and the observed rooting depth increased substantially with time for the sub soil except for the last sampling in 1997, which was already within the ripening phase of the wheat crop. The increase of rooting depth could well be described using Eqn. 10-6, indicating a linear increase with temperature sum (Fig. 10-5). There were no significant differences in this relationship between years.

A highly significant relationship between the minirhizotron root scores below 30 cm soil depth and the corresponding RLD values from the soil cores could be found (Fig. 10-6). Again, there were no significant differences between years.
Chapter 10

The function shown in Fig. 10-6 was used to convert the root scores from soil depths > 30 cm into root length density values for all sampling dates where no core measurements were available. These RLD's and the available soil core data were used to estimate the fraction of dry matter increase attributed to the fine-roots, $f_r$, and the ratio of RLD at the rooting depth to the RLD at the soil surface, $r_{RLD}$. 
Fig. 10-2: Shoot dry matter measured (points) and predicted by a fitted Richards-equation for winter wheat with normal and reduced nitrogen fertilisation and from three consecutive years.
Fig. 10-3: Root length densities of winter wheat at ear emergence to flowering grown in 3 consecutive years on a loess loam soil in northern Germany under 'normal' (Norm) and 'reduced' (Red) nitrogen fertilisation. Dates were determined using the soil core method. Error bars indicate standard error of the sample.

Fig. 10-4: Root length density scores of winter wheat observed in minirhizotrones from three years in northern Germany.
Table 10-6: Parameter values estimations for two hypotheses concerning the fine root fraction $f_R$, being either constant or linearly decreasing with temperature sum (explained in text). Also given are standard errors, SE, of the estimate and the Akaike information criterion (AIC) as well as modelling efficiency, EF.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Parameter name</th>
<th>Value</th>
<th>SE</th>
<th>AIC</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Const. fR</td>
<td>$f_R$</td>
<td>0.142</td>
<td>0.00854</td>
<td>-115.9</td>
<td>0.735</td>
</tr>
<tr>
<td></td>
<td>$r_{RLD}$</td>
<td>0.0155</td>
<td>0.00731</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Decr. fR</td>
<td>$f_{R0}$</td>
<td>0.653</td>
<td>0.114</td>
<td>-178.0</td>
<td>0.903</td>
</tr>
<tr>
<td></td>
<td>$f_{R_{dec}}$</td>
<td>0.000501</td>
<td>0.000133</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$r_{RLD}$</td>
<td>0.0125</td>
<td>0.00361</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 10-7: Parameters slope and intercept of the linear regression of calculated vs. observed root length density values (cm cm$^{-3}$) of winter wheat plants for different soil depths from the parameterisation procedure as well as $r^2$ of the linear regression, residual mean square error, RMSE, and modelling efficiency, EF.

<table>
<thead>
<tr>
<th>Soil depth (cm)</th>
<th>slope</th>
<th>intercept</th>
<th>$r^2$</th>
<th>n</th>
<th>RMSE</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-15</td>
<td>0.85</td>
<td>0.18</td>
<td>0.99</td>
<td>3</td>
<td>0.28</td>
<td>0.85</td>
</tr>
<tr>
<td>15-30</td>
<td>1.84</td>
<td>-0.88</td>
<td>0.98</td>
<td>3</td>
<td>0.78</td>
<td>0.21</td>
</tr>
<tr>
<td>30-45</td>
<td>0.83</td>
<td>0.04</td>
<td>0.76</td>
<td>12</td>
<td>0.23</td>
<td>0.68</td>
</tr>
<tr>
<td>45-60</td>
<td>0.64</td>
<td>0.14</td>
<td>0.61</td>
<td>12</td>
<td>0.19</td>
<td>0.42</td>
</tr>
<tr>
<td>60-75</td>
<td>0.71</td>
<td>0.09</td>
<td>0.40</td>
<td>12</td>
<td>0.18</td>
<td>0.33</td>
</tr>
<tr>
<td>75-90</td>
<td>1.02</td>
<td>-0.03</td>
<td>0.70</td>
<td>10</td>
<td>0.09</td>
<td>0.67</td>
</tr>
<tr>
<td>90-105</td>
<td>1.38</td>
<td>-0.06</td>
<td>0.82</td>
<td>9</td>
<td>0.06</td>
<td>0.75</td>
</tr>
<tr>
<td>105-120</td>
<td>0.28</td>
<td>0.04</td>
<td>0.09</td>
<td>8</td>
<td>0.07</td>
<td>-1.11</td>
</tr>
</tbody>
</table>
Fig. 10-5: Rooting depth ($z_r$) of winter wheat as a function of temperature sum (TS) since day of transplanting. Data are from three years 1995-1996 on a loess loam soil. The regression line shown is $z_r = -2.56 (±7.76) + 0.11 (±0.009) \cdot TS$, $r^2=0.96$.

The two simple hypotheses we evaluated concerning the behaviour of the fraction of dry matter increase attributed to fine roots, assuming either a constant or a linearly decreasing fraction were quite different in their ability to describe the experimental data (Fig. 10-7). Whereas the assumption of a constant root dry matter fraction was only poorly able to describe the data, the assumption of a decreasing root fraction was able to explain 90% of the total variance caused by years, time and soil depth. The estimated parameters are given in Table 10-6. The lower value of the Akaike information criterion indicates that the additional parameter introduced for the second hypothesis successfully enhanced the model performance. Much of the variance accounted for, however, is caused from differences in RLD between the soil depths. The goodness of fit of the model within certain soil depth classes was lower (Table 10-7). No clear trend between soil depth class and model performance is obvious. The time course of root length density development is quite different between years,
(Fig. 10-8), with a continuous increase of root length density and rooting depth in 1995 in contrast to marked phases without root growth in 1996 and 1997 due to low winter temperatures. The available three values of total root length, RL, from the monolith sampling however, were very good reproduced from the model $RL_{meas} = 1.03 \cdot RL - 7.43$, $r^2=0.99$ (data not shown).

### 10.6. Discussion

It was the aim of the work presented to evaluate the temporal and spatial dynamics of rooting intensity of winter wheat grown within an rotation including vegetable crops leaving high amounts of residual nitrogen and to summarise the data using a simple empirical model. For this purpose a combination of the non-destructive minirhizotron method and the soil core method were used. The model approach was chosen to...
give enough flexibility to describe the data but using only a limited amount of
parameters thereby enabling the estimation of the parameters with conventional non-
linear parameter estimation methods.

Fig. 10-7: Calculated vs. measured root length density (RLD) of winter wheat using
two different hypotheses, i.e. assuming either a constant fraction of dry
matter allocated to the fine roots (Const.) or a linearly with accumulation of
temperature sum decreasing fraction of dry matter allocated to fine root
(Dec.). Regression lines shown are (—) \( y = -0.0106 (\pm 0.0378) + 1.0083 \\
(\pm 0.0420) \cdot x, \hat{r} = 0.90, n=65 \) for a decreasing fraction of fine root growth
and (·) \( y=0.0736 (\pm 0.0602) + 0.9504 (\pm 0.0714) \cdot x, \hat{r}=0.74 \) for a constant
fraction of fine root growth.
Fig. 10-8: Simulated and measured root length densities (RLD) of winter wheat grown on a loess loam soil in three consecutive years and in different soil depths.
The results of this study further confirms the well known fact that vertical root length distribution under favourable growth conditions (no water and nutrient limitations, no compacted soil layers) could successfully described assuming negative exponential decline of RLD with soil depth. Even the quite contrasting distribution of soil nitrate nitrogen between the three experimental years (Table 10-3) did not influence root distribution seriously (Table 10-5). The values found for the parameter $k_r$ (Eqn. 10-7), are in good agreement with the results of Barraclough and Leigh (1984). The assumption of Eqn. 10-9, that $k_r$ is decreasing with ongoing plant development is also supported by the results of Barraclough and Leigh (1984). Our absolute values of RL and RLD0, however, seem to be somewhat lower than those of Barraclough and Leigh (1984). Our data probably did not show influences of nitrogen supply shoot to root ratio's (Table 10-5), simply because the overall differentiation of the N-supply was too low (Table 10-3).

The estimated decrease of root dry matter fraction with ongoing plant development is in accordance with findings of several other authors (Barraclough, 1984; Gregory et al., 1978; Hamblin et al., 1990). Also the absolute values of this function seem to be realistic (Barraclough, 1984; Hamblin et al., 1990). From the parameter $f_{R0}$ and $f_{Rdec}$ it follows that fine root growth ceases at around $1300 ^\circ$C·d after sowing. According to the linear relationship between rooting depth and temperature sum the rooting depth should be around 140 cm. This value may be used as an estimate of maximum rooting depth, however, this implies an extrapolation of the presented data, as our maximum observation depth was 120 cm. Masse et al., 1991 found a decreasing rooting depth development at around $800^\circ$C·d for late sown and at about $1000^\circ$C·d for early sown winter wheat. The increase of rooting depth per degree day of 0.12 cm$^\circ$C·d presented in Masse et al., 1991, however, is close to our estimate (Fig. 10-5). Rooting depth increase per unit temperature sum seems to be generally not too variable between species (Barraclough and Leigh, 1984; Pellerin and Pages, 1994; Thorup-Kristensen, 1998; Thorup-Kristensen and Van den Boogaard, 1998, Chapter 7). A somewhat better description of this partitioning pattern between aboveground and below-ground plant organs may be achieved using more detailed models of wheat development, which also include the effects of vernalisation and photo-periodism. However, our approach may be sufficient for a first approximation.
The root length densities at the deepest observed soil layer, 95-120 cm were quite low (Fig. 10-3). From theoretical considerations (de Willigen and Van Noordwijk, 1987 Kage, 1997), however, it seems that even this low rooting density may be high enough for an efficient exhaustion of soil nitrate if it is sustained over a longer time period. Our simulated RLD’s (Fig. 10-7) indicate that in 1996 the time integral of root length density in the 95-120 cm soil layer was lower than in 1995 and 1997. But one has to notice that the reason for this reduced root length density duration are the low winter temperatures, which are in 1995/96 as usually associated with low rainfall values and a restricted downward water movement due to frozen soil regions. This resulted in low leaching depths and comparable low sub soil nitrate values (Table 10-3).

The quite contrasting root length to shoot dry matter ratios between the different years (Table 10-5) could be reproduced because of their differing winter temperatures. In the case of the year 94/95 with the highest winter temperatures the value of $f_R$ dropped down before substantial shoot growth started in spring, resulting in low RL/Wsh ratios. Also Barraclough (1984) reported from quite contrasting RL/Wsh ratios between different years but explained them by differences between potential growth rates in spring, which were supposed to influence root growth rates more seriously than shoot growth. From the limited data base of this study no final conclusion may be drawn, but it seems to be plausible that for root to shoot ratios decreasing within plant development, high development rates at early stages combined with unfavourable growth conditions during winter may finally result in low root to shoot ratios. If this causes a higher susceptibility to drought stress, however, remains unclear, as rooting depth on the other hand may be higher in spring and early summer after warm winters.

The presented relatively simple model clearly has several shortcomings. The basic approach of negative exponentially decreasing RLD’s may not be able to describe the reality under situations were either local growing conditions within the soil profile vary substantially or under severe water and nitrogen shortage. A limited flexibility to include effects of water and nitrogen within the presented model approach is given trough rising $f_R$ values under water or nitrogen limitation. Also rooting depth may develop faster under water stress (increase of $b_{zr}$ in Eqn. 10-6). Relatively more roots may be allocated deeper in the soil profile by making the value of $f_{RLD}$ (Eqn. 10-9) dependent on the actual nitrogen and water supply. It remains therefore to be proven if more complex models perform better than the approach presented here.
10.7. Conclusions

Rooting depth of late sown winter wheat reached soil depths > 120 in spring time and higher rooting depths were presumably reached during later growth stages. Winter wheat or similar cereals may therefore be regarded to be specifically suitable for making effective use of deeply leached nitrogen. The quite simple model presented here may be used to predict the time when such N resources become available to this crop.
11. Using deep rooting cereal crops for enhancing nutrient efficiency of intensive production systems: II. Uptake of deeply leached nitrogen by winter wheat

Abstract 258

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Abstract

Results from four years of a long term crop rotation experiment on a loess loam soil in northern Germany are presented where late harvested cauliflower is followed by winter wheat under two contrasting crop rotations and fertilisation regimes. The N uptake of cauliflower at final harvest was about 300 kg N ha$^{-1}$ if curds reached a marketable size and N supply was optimal. About two thirds of this nitrogen was contained in un-harvested plant material. Additionally about 80 kg nitrate N ha$^{-1}$ was left in the soil from 0-120 cm, with large variations between years.

Experimental results indicate that only in one of four years winter rainfalls translocated substantial amounts of residual soil nitrate and mineralised nitrate from crop residues deeper than the final rooting depth of the following winter wheat. The winter wheat exhausted the sub soil very effectively from nitrate during ear emergence to grain filling if no late N dressings were applied.

A simulation model consisting of modules describing crop N uptake, mineralisation of soil organic matter and crop residues, the soil water balance and vertical nitrate movement was used to further analyse the dynamics of soil mineral nitrogen. The model was also used to estimate the N leaching losses of a cauliflower/winter wheat sequence on a sandy soil and N-losses of an alternative sequence of cauliflower followed by two lettuce crops in the succeeding year. N-losses on the sandy soil were higher than on the loess loam soil and higher for two lettuce crops than for wheat succeeding the late harvested cauliflower. Sowing winter wheat reduced N-losses on the sandy soil compared to the cropping sequence cauliflower/lettuce/lettuce.
11.1. Introduction

Many vegetable crops leave large amounts of crop residues in the field (Rahn et al., 1992), which are usually rapidly decomposed. Thereby large amounts of nitrate nitrogen may be produced which are subject to leaching if not taken up by a succeeding crop (Whitmore, 1996a). Residual soil nitrate and nitrate produced from decomposing crop residues might be prevented from leaching by uptake through succeeding crops. Such succeeding crops could be main crops planted and harvested in the same year, catch crops particularly established to conserve excess amounts of residual nitrogen and main crops harvested in the next year.

The success of catch crops in conserving excess soil nitrate, however, may sometimes be limited by the amount of dry matter which can be produced until the end of the vegetation period. Catch crops may therefore not able to conserve large amounts of soil nitrate nitrogen residues in late harvested crops (Everaarts, 1993b; Vos and van der Putten, 1997). Furthermore, only a part of the nitrogen taken up by the catch crop is re-mineralised during the growing period of the next main crops (Harrison and Peel, 1996; Thorup-Kristensen, 1993b). At least a part of the re-mineralisation possibly will happen during un-cropped periods and therefore may enlarge the leaching potential of the field (Catt et al., 1998).

An alternative strategy to minimise the loss of residual nitrogen within vegetable cropping systems can be the use of deep rooting succeeding crops for recycling of leached nitrate nitrogen. This approach may be successful if the average leaching depth does not exceed the rooting depth of the succeeding crop. There seems to be considerable variation within the rooting depth of vegetable crops (Greenwood et al., 1982), however, due to their longer vegetation period winter sown cereals generally have higher rooting depths (Barraclough and Leigh, 1984) than vegetable crops. In the previous chapter it has been shown that rooting depth of late sown winter wheat on a loess loam exceeds 120 cm.

The aim of the work presented here was to investigate the fate of residual soil nitrate nitrogen and nitrogen from crop residues of late harvested cauliflower within the soil-plant system of following wheat. Data of four years from a long term field experiment were compared with the outcome of a mechanistic simulation model. For this purpose
Chapter 11

the root growth model for winter wheat presented in chapter 10 was combined with a simple model of the C/N dynamics of the soil organic matter and the crop residues, a water budget, a leaching model and modules for calculating plant N uptake (Kage, 1997).

11.2. Material and Methods

The experimental data were obtained from a long term rotational experiment carried out at the experimental station ‘Ruthe’, located about 15 km south of Hanover. The soil there is a silty loam (typical hapludalf) with 10 % sand, 80 % silt and 10 % clay in the plough layer of 30 cm depth. Carbon and nitrogen contents of the soil are given in Table 11-1. The experiment includes two crop rotations, two tillage regimes and two nitrogen fertilisation levels with three replications. In this study only data from the conventional mouldboard tillage plots are presented. The experiment was set up as a split-plot design with 3 replications as blocks, tillage and rotation as main plots and nitrogen fertiliser rate as subplots. The first rotation includes mainly vegetable crops, lettuce and celery in the first year, two crops of cauliflower in the second year followed by winter wheat and spinach in the third year. The second rotation includes mainly agricultural crops, faba beans in the first year, winter barley and cauliflower in the second year followed by winter wheat and mustard (green manure). Plots were 16 m in width and 8 m in length, with sampling areas of 2x8 m² for the $N_{\text{min}}$ probes and 2x8 m² for final harvest. The experiment was set up in autumn 1993.
Table 11-1: Total soil organic nitrogen and carbon content as well as the C\textsubscript{r}/N\textsubscript{r} ratio of the experimental site at the station Ruthe.

<table>
<thead>
<tr>
<th>Soil depth</th>
<th>N\textsubscript{r} (%)</th>
<th>C\textsubscript{r} (%)</th>
<th>C\textsubscript{r}/N\textsubscript{r}</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-10</td>
<td>0.089 (±0.011)</td>
<td>0.82 (±0.12)</td>
<td>9.2</td>
</tr>
<tr>
<td>10-20</td>
<td>0.088 (±0.009)</td>
<td>0.80 (±0.11)</td>
<td>9.2</td>
</tr>
<tr>
<td>20-30</td>
<td>0.083 (±0.011)</td>
<td>0.74 (±0.11)</td>
<td>8.9</td>
</tr>
<tr>
<td>0-30</td>
<td>0.087</td>
<td>0.790</td>
<td>9.1</td>
</tr>
</tbody>
</table>

Seed of winter wheat c.v. *Xanthos* were sown 2-3 cm deep at a density of 350 m\(^2\) using a grain drill with 12.5 cm row width. Sowing dates are summarised in Table 10-1. Weeds, fungal diseases and insects were controlled chemically using appropriate pesticides. The P and K levels in the soil were kept at levels ensuring optimal growth (>20 mg/100 g soil), the soil pH was at 7.1.

The weather during winter was quite contrasting in the four experimental years with 94/95 being warmer and more humid than the long term average, 95/96 being colder and dryer than average and 96/97 again somewhat warmer more humid than the long term average (Fig. 11-1). Spring and early summer temperatures as well as precipitation values were not deviating substantially from the long term average, except for a too low rainfall in 1996.

Nitrogen was given in all experiments as ammonium nitrate according to the N\textsubscript{min}\textsuperscript{-} fertilisation schedule (Scharpf and Wehrmann, 1975). For winter wheat this defines a target supply level of 120 kg N/ha including soil nitrate from 0 to 90 cm depth in early spring that has to be adjusted by fertilisation. Reduced fertilised plots received 70% of this supply in 1995 and 1996 and 50% in 1997. In addition about 30 kg N were given at shooting and about 50 kg at ear emergence only at the normal fertilised plots. The dates and amounts of fertiliser N are summarised in Table 11-3.
Fig. 11-1: Cumulative climatic water budget and weekly average air temperature from beginning of September to end of August in the four growing seasons 1994/95, 1995/96, 1996/97 and 97/98.
Table 11-2: Time table of activities during the field experiments. Dates followed by (CF) are for the crops following cauliflower and dates followed by (WB) are for crops following winter barley.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Year</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Planting of Cauliflower</td>
<td>94/95</td>
<td>July 26 (CF)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August 10 (WB)</td>
</tr>
<tr>
<td>Harvest of Cauliflower</td>
<td></td>
<td>October 24</td>
</tr>
<tr>
<td>Sowing of winter wheat</td>
<td></td>
<td>November 6</td>
</tr>
<tr>
<td>Spring Nmin sampling</td>
<td></td>
<td>March 6</td>
</tr>
<tr>
<td>Harvest of W-Wheat</td>
<td></td>
<td>August 9</td>
</tr>
<tr>
<td>Planting of Cauliflower</td>
<td>95/96</td>
<td>July 19 (CF)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>July 26 (WB)</td>
</tr>
<tr>
<td>Harvest of Cauliflower</td>
<td></td>
<td>October 17 (CF)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>October 25 (WB)</td>
</tr>
<tr>
<td>Sowing of winter wheat</td>
<td></td>
<td>November 2</td>
</tr>
<tr>
<td>Spring Nmin sampling</td>
<td></td>
<td>March 20</td>
</tr>
<tr>
<td>Harvest of W-Wheat</td>
<td></td>
<td>August 27</td>
</tr>
<tr>
<td>Planting of cauliflower</td>
<td>96/97</td>
<td>July 18 (CF)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>August 1 (WB)</td>
</tr>
<tr>
<td>Harvest of cauliflower</td>
<td></td>
<td>October 14 (CF)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>October 29 (WB)</td>
</tr>
<tr>
<td>Sowing of winter wheat</td>
<td></td>
<td>November 5</td>
</tr>
<tr>
<td>Spring Nmin sampling</td>
<td></td>
<td>March 10</td>
</tr>
<tr>
<td>Harvest of W-Wheat</td>
<td></td>
<td>August 13</td>
</tr>
<tr>
<td>Planting of cauliflower</td>
<td>97/98</td>
<td>July 23 (CF)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>July 29 (WB)</td>
</tr>
<tr>
<td>Harvest of cauliflower</td>
<td></td>
<td>October 20 (CF)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>October 27 (WB)</td>
</tr>
<tr>
<td>Sowing of winter wheat</td>
<td></td>
<td>November 4</td>
</tr>
<tr>
<td>Spring Nmin sampling</td>
<td></td>
<td>March 26</td>
</tr>
<tr>
<td>Harvest of W-Wheat</td>
<td></td>
<td>August 8</td>
</tr>
</tbody>
</table>
Soil mineral N was determined down to a depth of 120 cm in 4 intervalls of 30 cm thickness. From every plot 4 auger samples were collected. Soil nitrate N was measured photometrically at 210 nm after extraction (Navone, 1964). Tensiometers were installed in the winter wheat plots around end of march.

On several intermediate harvests 0.5 m² per plot were collected and separated into stems, leaves, and ears. Leaf area was measured with a LICOR 3100 leaf area meter (LI-COR Inc., Lincoln, NE, USA). The samples of all plant compartments were oven dried and weighed. The N concentrations of plant organs were determined by near-infrared spectrometry.

Table 11-3: Dates and amounts of fertiliser N applied to the winter wheat.

<table>
<thead>
<tr>
<th>Development stage</th>
<th>Date</th>
<th>Normal N</th>
<th>Reduced N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early spring</td>
<td>23.03.1995</td>
<td>60</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td>Stem elongation</td>
<td>25.04.1995</td>
<td>40</td>
<td>40</td>
</tr>
<tr>
<td>Ear emergence</td>
<td>15.06.1995</td>
<td>44</td>
<td>-</td>
</tr>
<tr>
<td>Early spring</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Stem elongation</td>
<td>10.05.1996</td>
<td>40</td>
<td>-</td>
</tr>
<tr>
<td>Ear emergence</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Early spring</td>
<td>25.03.1997</td>
<td>50</td>
<td>30</td>
</tr>
<tr>
<td>Stem elongation</td>
<td>09.05.1997</td>
<td>40</td>
<td>40</td>
</tr>
<tr>
<td>Ear emergence</td>
<td>24.6.1997</td>
<td>50</td>
<td>-</td>
</tr>
<tr>
<td>Early spring</td>
<td>09.04.1998</td>
<td>30</td>
<td>-</td>
</tr>
<tr>
<td>Stem elongation</td>
<td>07.05.1998</td>
<td>40</td>
<td>40</td>
</tr>
<tr>
<td>Ear emergence</td>
<td>17.06.1998</td>
<td>50</td>
<td>50</td>
</tr>
</tbody>
</table>
11.3. Model

The soil water balance modules are the same as used in Chapter 8. Briefly, the Penman-Monteith equation (Monteith and Unsworth, 1990) is used for calculation of a reference evapotranspiration, the functional approach of Feddes et al. (1978) is used to calculate actual transpiration and a numerically solution of the soil water diffusivity based formulation of the Richards equation is used to calculate vertical water transport in the soil (Kage, 1992; Kage, 1997). The modules for calculation of nitrogen uptake of the plant roots in the different soil layers and the vertical nitrate movement are the same as described in (Kage, 1997) and chapter 8. Also all parameter values of the model are identical to the values presented in chapter 8.

11.3.1. N uptake of wheat

Shoot nitrogen increase may be calculated using a crop growth model or may be derived from an appropriate function fitted to experimental data. In this study we followed the second approach, using the Richards-function (Thornley and Johnson, 1990):

\[
\frac{dN_{sh}}{dt} = r_{Nsh} \cdot T_{eff} \cdot N_{sh} \left( \frac{N_{shmax}^r - N_{sh}^r}{r_f \cdot N_{shmax}^r} \right) \tag{11-1}
\]

Where \( r_{Ws} \) is a growth rate parameter, \( T_{eff} \) is the effective Temperature, \( N_{shmax} \) is the maximum attained shoot nitrogen amount and \( r_f \) is a form parameter. This function was integrated numerically, using a value for \( N_{sh} \) at sowing of 0.4 g m\(^{-2}\). The effective Temperature was calculated from:

\[
T_{eff} = \max(0, (T_a - T_b)) \tag{11-2}
\]

Where \( T_a \) is the daily average air temperature \( T_b \) is a base temperature, assumed to be 4°C.

A similar procedure was applied to fit measured data of leaf area index.
11.3.2. Mineralisation

The module for calculating mineralisation of soil organic matter and crop residues was a simplified version of the model of Verberne et al., (1990) with only four carbon pools \( C_i \) representing the carbon in the soil organic matter, \( C_{som} \), the microbial biomass, \( C_{biom} \), the easily decomposable crop residue fraction, \( C_{dpm} \), and a more stable crop residue fraction, \( C_{rpm} \). All these fractions have fixed C/N ratios and decompose by first order kinetic processes:

\[
\frac{dC_i}{dt} = -k_i C_if
\]  

(11-3)

where \( k_i \) represents the rate constants of the four pools (Table 11-4) and \( f \) is a factor (0< \( f \) <1) accounting for limitations of temperature, soil water content and mineral nitrogen which was taken from Verbruggen (1985). For the sake of simplicity air temperature was instead of soil temperature.

Nitrogen mineralisation of each pool is then obtained by multiplication with the N/C ratio:

\[
\frac{dN_i}{dt} = \frac{dC_i}{dt} \frac{N_i}{C_i}
\]  

(11-4)

Gross microbial growth is the product of the mineralisation rate and the efficiency \( E \) (Table 11-4) with which \( C \) is used for the synthesis of organic components. Subtracting the decomposition of the microbial biomass yields the net microbial growth:

\[
\frac{dC_{biom}}{dt} = E \sum k_i C_if - k_{biom} C_{biom}f
\]  

(11-5)

The net mineralisation rate of each pool \( i \) is the result of decomposition and biomass growth:

\[
\frac{dN_{mini}}{dt} = k_i C_if \left( \frac{N}{C} \right) - E \left( \frac{N}{C}_{biom} \right)
\]  

(11-6)

The parameter values for decomposition of all pools except the \( C_{som} \) pool were kept constant for all simulations.
The residue pools were initialised using the measured dry weight and nitrogen content of the cauliflower residues, assuming a C content of the residues of 43% (de Neve et al., 1994).

The fraction of decomposable C in plant residues \( f_{DPM} \) is calculated according to the following equation:

\[
f_{DPM} = \left( \frac{-N_{CR} \cdot CN_{DPM} \cdot CN_{RPM}}{C_{CR}} + CN_{DPM} \right) \cdot \frac{1}{-CN_{RPM} + CN_{DPM}} \quad (11-7)
\]

The soil carbon pool was initialised assuming 1.6 % C ha\(^{-1}\) (Table 11-1) and soil bulk density of 1.5 g cm\(^{-3}\). Soil microbial biomass is assumed to contain initially 0.01 % of total soil organic carbon.

### 11.3.3. Root growth and N uptake of lettuce

A preliminary version of model modules for calculating N uptake and root growth of lettuce was used for a scenario calculation, comparing N-losses of the crop sequence cauliflower/winter wheat with a sequence cauliflower followed by two lettuce crops in the next year. Dry matter production of lettuce is calculated using a simple light use efficiency approach as outlined in Chapter 2 and Chapter 4. The light use efficiency of lettuce was set to a constant value of 3 gMJ\(^{-1}\) and a value 0.5 was used for the

<table>
<thead>
<tr>
<th>Pool</th>
<th>Description</th>
<th>C/N ratio</th>
<th>( k ) (d(^{-1}))</th>
<th>Efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>( C_{som} )</td>
<td>soil organic matter</td>
<td>9</td>
<td>0.001</td>
<td>0.2</td>
</tr>
<tr>
<td>( C_{biom} )</td>
<td>microbial biomass</td>
<td>8</td>
<td>0.2</td>
<td>-</td>
</tr>
<tr>
<td>( C_{dpm} )</td>
<td>fraction of easily decomposable harvest residues</td>
<td>6</td>
<td>0.2</td>
<td>0.4</td>
</tr>
<tr>
<td>( C_{rpm} )</td>
<td>fraction of resistant harvest residues</td>
<td>60</td>
<td>0.007</td>
<td>0.4</td>
</tr>
</tbody>
</table>
extinction coefficient for photosynthetically active radiation. The specific leaf area SLA was assumed to decrease linearly with temperature sum from transplanting to maturity using a starting value of 300 cm$^2$g$^{-1}$ and a rate of decrease of 0.4 cm$^2$g$^{-1}$°C$^{-1}$d$^{-1}$. This decrease of SLA was used to account for the high self shading of lettuce leaves at later growth stages, which reduces their ‘effective leaf area’. A constant leaf/shoot dry matter ratio of 0.9 was assumed throughout the growing season.

The nitrogen content of the lettuce shoot was assumed to decrease from a value of 6% N at a dry matter of 1 g m$^{-2}$ to 3% at maturity assumed to be reached at 380 g DM m$^{-2}$. The planting density was set to 11 m$^{-2}$.

Root growth was modelled using the approach outlined in Chapter 7 for cauliflower. Thereby a fraction of 0.15 of the total dry matter production was assumed to be partitioned to the fine root fraction. The increase of rooting depth is also assumed exponential with an initially increase of rooting depth during the exponentially phase of 0.06 cm cm$^{-1}$°C$^{-1}$d$^{-1}$ and a further increase during the linear phase of 0.15 cm cm$^{-1}$°C$^{-1}$d$^{-1}$. Initial rooting depth was set to 3 cm. The parameter $r_{RLD}$ was left unchanged at the value used in Chapter 7. The parameter estimates are based on the results presented in (Wijaya, 1996) and own unpublished measurements.

The N fertilisation to lettuce was adjusted to 130 kg N ha$^{-1}$ at planting minus the simulated soil nitrate from 0-30 cm. The N fertilisation regime for the winter wheat in the long term scenario calculation was a fixed amount of 50 kg N ha$^{-1}$ at end of March followed by two variable dressings of 200 kg N ha$^{-1}$ and 220 kg N ha$^{-1}$ each minus the sum of the simulated soil nitrate from 0-120 cm and the simulated shoot nitrogen of winter wheat at end of April and begin of June, respectively.

11.4. Model implementation and statistics

The above algorithms were implemented as sub-models within the HUME modelling environment (Kage and Stützel, 1999a). The parameters of the mineralisation sub-model (Table 11-4) were taken in analogy to (Verberne, 1990) and were slightly adjusted using a trial and error approach controlled by comparison with the data of the 95/96 experimental year.
The descriptive and predictive power of a model can be evaluated by linear regression of output and measured data and several other statistical measures. One of them is the modelling efficiency EF (Smith et al., 1997):

\[
EF = 1 - \frac{\sum (y_i - \bar{y})^2}{\sum (y_i - \bar{y})^2}
\]  

(11-8)

Where \(y_i\) is the value of the \(i^{th}\) observation, \(\bar{y}_i\) is the \(i^{th}\) model prediction and \(\bar{y}\) is the average of the observations. The maximum value of the EF is one for complete agreement between simulated and measured values, but also negative values are possible if the model describes the data less well than the observation mean.

Another statistical parameter used in this study is the root mean square error RMSE:

\[
RMSE = \sqrt{\frac{\sum (y_i - \bar{y})^2}{n}}
\]  

(11-9)

giving the average model prediction error.

For analysis of variance the procedure GLM from the SAS system (SAS Institute, 1988) was used. For mean separation, the least significant differences were calculated using the appropriate error term.

11.5. Results

11.5.1. Experimental

The total nitrogen uptake of the 'normal' fertilised cauliflower crops from the CF/CF/WW sequence at final harvest was at around 300 kg N ha\(^{-1}\) (Fig. 11-2a). About two thirds of this nitrogen was situated within the plant residues. The crops from the WB/CF/WW sequence were later planted (Table 11-2) and therefore reached not always a marketable curd size and a N uptake comparable to the crops from the CF/CF/WW sequence (Fig. 11-2b). Due to the lower crop N uptake residual soil nitrate levels were substantially higher than for the CF/CF/WW cropping sequence (Fig. 11-2b). But also the residual soil nitrate levels of the normal fertilised treatment from the CF/CF/WW sequence exceeded 50 kg from 0-90 cm (Fig. 11-2a).
The spring nitrogen contents found below the following winter wheat were generally higher than autumn values (Fig. 11-3) indicating a substantial mineralisation of the cauliflower crop residues during winter time. However, also losses of N through leaching occurred simultaneously. Especially during the winter period 94/95 excessive rainfall (Fig. 11-1) transported much nitrogen down to the soil layer 90-120 cm and presumably also to deeper soil layers resulting in loss of N. During the much colder and dryer winter 95/96, however, leaching was less pronounced. Most of the nitrogen within the soil profile was in spring 1996 still situated within the 30-60 cm layer. The downward movement of nitrate of the two following winters 96/97 and 97/98 was higher than in 95/96 but affected the 90-120 cm region not as much as was found for the 94/95 winter.

N uptake of winter wheat at final harvest was about 200 kg N ha\(^{-1}\) (Fig. 11-4) with the highest values for 1995 following a relatively mild winter and the lowest values in 1996 following the coldest winter period (Fig. 11-1). About 80% of the nitrogen found at maturity of winter wheat was in the grain and was consequently removed from the field. Residual soil nitrate levels in all analyses soil layers were generally low for the reduced fertilised treatment, but were still comparably high for the normal fertilised treatment with the exception of 1995 were no nitrogen at ear emergence was applied for the normal N treatment.

The fitted parameter values for \(N_{sh\text{max}}\) and \(LAI_{\text{max}}\) growth curves (Table 11-6, Table 11-7) reflect the values of N uptake presented in Fig. 11-4. The differences in the growth rate parameters \(r_{Nsh}\) and \(r_{LAI}\) and the form parameters \(rf_{Nsh}\) and \(rf_{LAI}\) are not systematic. The parameter estimates for the form parameters \(rf_{Nsh}\) and \(rf_{LAI}\) show a quite high standard error.
Fig. 11-2: N amounts in different organs of cauliflower and soil nitrate nitrogen in different soil depths at final harvest of cauliflower in autumn for two different N supply rates and two different crop rotations. a) cf/cf/ww rotation b) wb/cf/ww rotation. An * indicates singificance at p=0.05.
Fig. 11-3: Soil nitrate nitrogen in early spring below winter wheat following late-harvested cauliflower in 4 experimental years and for two different crop rotations. a) cf/cf/ww rotation b) wb/cf/ww rotation. An * indicates significance at p=0.05.
**11. N uptake of winter wheat**

![Graph showing nitrogen amounts in grain and straw of winter wheat following late-harvested cauliflower and soil nitrate nitrogen at harvest for four experimental years and two crop rotations a) following two crops of cauliflower and b) following winter barley and cauliflower. A * indicates significance at p=0.05.](image)

*Fig. 11-4: Nitrogen amounts in grain and straw of winter wheat following late-harvested cauliflower and soil nitrate nitrogen at harvest for four experimental years and two crop rotations a) following two crops of cauliflower and b) following winter barley and cauliflower. A * indicates significance at p=0.05.*
### Table 11-5: Parameters of the Van Genuchten-Mualem equations found by fitting to data on soil water tension vs. soil water content.

<table>
<thead>
<tr>
<th>Soil Depth (cm)</th>
<th>Depth (cm)</th>
<th>( \theta_r ) (cm(^3) cm(^{-3}))</th>
<th>( \theta_s ) (cm(^3) cm(^{-3}))</th>
<th>( \alpha ) (cm(^{-1}))</th>
<th>( n )</th>
<th>( h^* ) (cm(^{-1}))</th>
<th>( K_s^* ) (cm(^{d^{-1}}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loess loam</td>
<td>0-30</td>
<td>0.0</td>
<td>0.4295</td>
<td>0.01479</td>
<td>1.276</td>
<td>0.5</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>30-80</td>
<td>0.0347</td>
<td>0.4367</td>
<td>0.00903</td>
<td>1.448</td>
<td>0.5</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>80-200</td>
<td>0.0</td>
<td>0.4485</td>
<td>0.00675</td>
<td>1.238</td>
<td>0.5</td>
<td>7</td>
</tr>
<tr>
<td>Sand (Scenario)</td>
<td>0-30</td>
<td>0.0</td>
<td>0.4429</td>
<td>0.0332</td>
<td>1.336</td>
<td>0.5</td>
<td>40.19</td>
</tr>
<tr>
<td></td>
<td>30-200</td>
<td>0.0</td>
<td>0.3800</td>
<td>0.01997</td>
<td>1.627</td>
<td>0.5</td>
<td>50</td>
</tr>
</tbody>
</table>

*) estimated value

### Table 11-6: Parameter values and standard errors (±) estimated for the Richards equation fitted to data of shoot nitrogen (g/m\(^2\)) of winter wheat with normal (Norm) and reduced (Red) fertilisation in the three years with .

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>WB/CF/WW ( N_{shmax} )</td>
<td>20.10 (±1.16)</td>
<td>19.65 (±0.53)</td>
<td>16.52 (±0.30)</td>
<td>12.43 (±0.85)</td>
<td>20.89 (±0.39)</td>
<td>12.60 (±0.39)</td>
</tr>
<tr>
<td>WB/CF/WW ( r_{Nsh} )</td>
<td>0.013 (±0.016)</td>
<td>0.016 (±0.019)</td>
<td>0.012 (±0.002)</td>
<td>0.007 (±0.003)</td>
<td>0.020 (±0.014)</td>
<td>0.008 (±0.002)</td>
</tr>
<tr>
<td>WB/CF/WW ( r_{fNsh} )</td>
<td>1.69 (±2.71)</td>
<td>2.33 (±3.11)</td>
<td>1.92 (±0.46)</td>
<td>0.75 (±0.68)</td>
<td>2.80 (±2.17)</td>
<td>1.35 (±0.49)</td>
</tr>
<tr>
<td>CF/CF/WW ( N_{shmax} )</td>
<td>21.91 (±0.73)</td>
<td>20.46 (±0.69)</td>
<td>18.84 (±0.18)</td>
<td>14.38 (±1.68)</td>
<td>21.92 (±0.68)</td>
<td>16.02 (±0.78)</td>
</tr>
<tr>
<td>CF/CF/WW ( r_{Nsh} )</td>
<td>0.014 (±0.012)</td>
<td>0.009 (±0.005)</td>
<td>0.012 (±0.003)</td>
<td>0.005 (±0.001)</td>
<td>0.012 (±0.005)</td>
<td>0.011 (±0.006)</td>
</tr>
<tr>
<td>CF/CF/WW ( r_{fNsh} )</td>
<td>1.81 (±1.82)</td>
<td>1.20 (±0.81)</td>
<td>2.19 (±0.59)</td>
<td>0.75 (±0.68)</td>
<td>1.58 (±0.85)</td>
<td>1.52 (±1.12)</td>
</tr>
</tbody>
</table>
11.5.2. Model analysis

The model was able to reproduce the soil mineral dynamics in all four experimental years with acceptable accuracy (Table 11-8). A detailed analysis is presented for the years with the most contrasting climatic conditions 94/95 and 95/96. The parameter values shown in Table 11-6 determine a rapid mineralisation of the nitrogen from the DPM pool in the first weeks after cauliflower harvest (Fig. 11-5, Fig. 11-6) which is somewhat delayed during the cold winter 95/96 (Fig. 11-7). The low calculated mineralisation rates in spring (Fig. 11-5, Fig. 11-6) are a consequence of nitrogen immobilisation by the more slowly decomposable RPM pool of the crop residues with a wide C/N ratio (Table 11-4). In 94/95 the soil nitrogen content in the 0-30 cm layer were after a short increase directly after incorporation of crop residues steadily decreasing until the first fertilisation in spring ‘95 due to the downward movement of nitrate in deeper soil layers (Fig. 11-5, Fig. 11-6). In early spring ‘95 the downward movement reaches the soil layer 90-120 cm and the cumulative N flow in 120 cm is steadily increasing. In 95/96 however, the low precipitation values (Fig. 11-1) caused only a limited downward movement of nitrate which affected only the 30-60 cm soil layer. Leaching losses were calculated to be negligible in this year (Fig. 11-7).
Table 11-7: Parameter values and standard errors (±) estimated for the Richards-equation fitted to data of leaf area index \((m^2/m^2)\) of winter wheat with normal (Norm) and reduced (Red) fertilisation in the three years.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Norm</td>
<td>Red</td>
<td>Norm</td>
</tr>
<tr>
<td>WB/CF/WW</td>
<td>LAI(_{\text{max}})</td>
<td>4.80 (±0.06)</td>
<td>4.40 (±0.21)</td>
<td>5.16 (±0.13)</td>
</tr>
<tr>
<td></td>
<td>r(_{\text{LAI}})</td>
<td>0.009 (±0.001)</td>
<td>0.008 (±0.003)</td>
<td>0.020 (±0.010)</td>
</tr>
<tr>
<td>WB/CF/WW</td>
<td>r(_{\text{LAI}})</td>
<td>0.56 (±0.12)</td>
<td>0.44 (±0.39)</td>
<td>1.27 (±0.74)</td>
</tr>
<tr>
<td>CF/CF/WW</td>
<td>LAI(_{\text{max}})</td>
<td>5.55 (±0.16)</td>
<td>4.91 (±0.12)</td>
<td>3.91 (±0.16)</td>
</tr>
<tr>
<td></td>
<td>r(_{\text{LAI}})</td>
<td>0.006 (±0.001)</td>
<td>0.007 (±0.001)</td>
<td>0.067 (±1.052)</td>
</tr>
<tr>
<td>CF/CF/WW</td>
<td>r(_{\text{LAI}})</td>
<td>0.17 (±0.19)</td>
<td>0.23 (±0.16)</td>
<td>4.98 (±82.20)</td>
</tr>
</tbody>
</table>

Table 11-8: Parameters slope and intercept of the linear regression of the calculated vs. observed soil nitrate nitrogen winter wheat plants for the different soil depths as well as \(r^2\) of the linear regression, residual mean square error, RMSE, and modelling efficiency, EF.

<table>
<thead>
<tr>
<th>Soil depth</th>
<th>slope</th>
<th>intercept</th>
<th>(r^2)</th>
<th>n</th>
<th>RMSE</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-30</td>
<td>0.7819</td>
<td>3.8020</td>
<td>0.7034</td>
<td>76</td>
<td>18.9167</td>
<td>0.6401</td>
</tr>
<tr>
<td>30-60</td>
<td>1.0511</td>
<td>-4.0110</td>
<td>0.7519</td>
<td>76</td>
<td>10.8289</td>
<td>0.7316</td>
</tr>
<tr>
<td>60-90</td>
<td>0.7939</td>
<td>3.4944</td>
<td>0.6305</td>
<td>76</td>
<td>11.0882</td>
<td>0.5833</td>
</tr>
<tr>
<td>90-120</td>
<td>1.2499</td>
<td>-1.1344</td>
<td>0.8009</td>
<td>76</td>
<td>13.2851</td>
<td>0.7381</td>
</tr>
<tr>
<td>0-120</td>
<td>0.9131</td>
<td>6.2198</td>
<td>0.7783</td>
<td>76</td>
<td>28.1417</td>
<td>0.7696</td>
</tr>
</tbody>
</table>
During the phase of high N uptake rates of the winter wheat, the soil was exhausted beginning in the upper layers followed by the deeper soil layers. The late N dressing applied in 1995 in the ‘normal’ fertilised treatment, however, prevented the winter wheat from fully exhausting also the soil layer 90-120 cm and furthermore increased residual soil nitrate values in the 0-30 cm region (Fig. 11-5).

11.5.3. Scenario calculations

Scenario calculations were carried out to compare the experimental and simulation results presented above with two alternative conditions. These are a) a soil with a lower water holding capacity than the loess soil of the experiment and b) an alternative more shallow rooted succeeding crop to cauliflower. For the alternative soil conditions we used a sandy soil using parameter values presented in Table 11-5 derived from data taken out of Wösten et al. (1986). As alternative crop lettuce was used, using the model approach presented in the material and methods section based on experimental results of Wijaya (1996). For all calculation otherwise unchanged initial and boundary conditions of the reduced fertilised treatment from the CF/CF/WW treatment in the year 94/95 were used.

The higher hydraulic conductivity in the near saturated range of the sandy soil together with the lower water holding capacity (Table 11-5) increased leaching rates compared to the situation of the loess loam soil from 50 to 117 kg N ha⁻¹ (Fig. 11-8, Fig. 11-5). However, still substantial increased soil nitrate values remained in the soil layer 60-120 cm. Much of this nitrogen could be taken up by the root system of the winter wheat during later growth stages (Fig. 11-8).
Fig. 11-5: Results from a simulation analysis of the N dynamics of the soil plant system in winter wheat following late harvested cauliflower for the ‘normal’ N fertilised treatment from the CF/CF/WW sequence in 94/95. Error bars indicate the standard error of the measurements for the particular soil depth, not the cumulative value.
Fig. 11-6: Results from a simulation analysis of the N dynamics of the soil plant system in winter wheat following late harvested cauliflower for the reduced N fertilised treatment from the CF/CF/WW sequence in 94/95. Error bars indicate the standard error of the measurements for the particular soil depth, not the cumulative value.
Fig. 11-7: Results from a simulation analysis of the N dynamics of the soil plant system in winter wheat following late harvested cauliflower for the reduced N fertilised treatment from the CF/CF/WW sequence in 95/96. Error bars indicate the standard error of the measurements for the particular soil depth, not the cumulative value.
For two lettuce crops following the late harvested cauliflower on the loess loam soil leaching over winter is similar as for the winter wheat as following crop, but due to the missing N uptake in the deeper soil layers, leaching continues at small rates during summer and finally reaches a total amount of 61 kg N ha\(^{-1}\). Also the large amounts of nitrogen situated end of August in the soil layers 60-120 cm have to be regarded as lost from the production system.

Long term calculations using weather data from the station 'Hannover-Herrenhausen' from 1971-1995 were used to estimate the long term probability of N-losses for alternative soil conditions and cropping systems. Thereby the cumulative nitrate flow at 120 cm soil depth and the soil nitrate content from 60-120 cm were defined as N-loss.

For the winter wheat following the late harvested cauliflower an average N-loss of 37 kg N ha\(^{-1}\) was calculated with a standard deviation of 23 kg N ha\(^{-1}\) (Fig. 11-10a). This is a lower value than for the scenario of two lettuce crops following cauliflower where an average N-loss of 85 kg N ha\(^{-1}\) was calculated (Fig. 11-10a). Average N-losses on the sandy soil were clearly higher (Fig. 11-10b), but still on this soil type a clear difference in N-losses between the deep rooting winter wheat and the shallow rooting lettuce crops is obvious.
Fig. 11-8: Results from a scenario calculation of the N dynamics of the soil plant system in winter wheat following late harvested cauliflower for a sandy soil.
Fig. 11-9: Results from a scenario calculation of the N dynamics of the soil plant system in two lettuce crops following late harvested cauliflower for a loess loam soil.
11.6. Discussion

The aim of the presented study was to quantify the nitrogen dynamics in the soil plant system after late harvested cauliflower. The main objective thereby was the determination of N-losses due to leaching. Leaching losses were calculated indirectly using a simulation model consisting of several modules which were mainly already used in previous studies (Kage, 1997; Stützel and Kage, 1998; Chapter 8).

As already shown in Chapter 8, the soil water diffusivity based approach for calculating vertical water transport in combination with the convection dispersion equation was well suited for calculating vertical nitrate transport on the quite homogenous experimental site. Due to the comparable low clay content macropores are at this experimental site restricted to a small amount of earth worm channels. We therefore had no indication for a more sophisticated leaching model (Brusseau and Rao, 1990). A further simplification of the model approach using a tipping bucket approach for soil water transport, however, considerably decreased the predictive quality of the model (data not shown).

Mineralisation of cauliflower residues has been modelled using first order kinetics under laboratory (de Neve and Hofman, 1996) and field (de Neve and Hofman, 1998) conditions. In these studies the fraction of nitrogen in the residues which was available for the decomposition process was quite low, 64 and 48 % for leaf blades and leaf stalks, respectively. We also tried to simulate the decomposition process of the crop residues using this approach, however, found that the C/N based model module presented here (Eq. 1-7) had a superior descriptive quality because it considers nitrogen immobilisation due to the definition of a second crop residue pool ($C_{rpm}$) with a lower decomposition rate constant and a wide C/N ratio (Table 11-4).

Gaseous N-losses due to denitrification were not considered in the model and were also not measured. Under favourable conditions like low oxygen concentrations this process may induce substantially N-losses (Schloemer, 1991, Lafolie, 1997). However, in absence of such extreme situations denitrification losses are rather small (Kaiser et al., 1998) compared to leaching losses ranging from 50 to >100 kg N ha⁻¹. Leaching losses seem therefore clearly be the dominating pathway of N-losses (Whitmore, 1996b). The successful simulation of the nitrogen balance in our simulations also indicates that no major error in the N balance was caused by neglecting denitrification losses.
The nitrogen amounts in the cauliflower crops which reached a marketable curd size (Fig. 11-2) were comparable to figures presented by (Everaarts, 2000; Everaarts et al., 1996; Chapter 9; Van den Boogaard and Thorup-Kristensen, 1997). The rapid mineralisation of cauliflower residues has (Fig. 11-5, Fig. 11-6, Fig. 11-7) previously been observed by Scharpf and Schrage (1988) and de Neve and Hofman (1998) and, indirectly, by Rahn et al. (1998). The magnitude of downward displacement of soil nitrate during winter on clearly depends on soil and weather conditions (Fig. 11-1, Fig. 11-3). However, it seems possible to make good estimates of it's magnitude using appropriate simulation models (Richter et al., 1980, Fig. 11-5, Fig. 11-6, Fig. 11-7). From the results presented here, it may be concluded that on loess loam soils under climates of moderate humidity (clim. water budget during winter < 200 mm) leaching depth does not exceed maximum rooting depths of winter sown cereals.

The complete exhaustion of the soil regions deeper than 90 cm of winter wheat in the reduced treatments is no uncommon result (Kuhlmann et al., 1989). The root length densities found at later growth stages in our experiment in the soil depth 90-120 cm (Chapter 10) and presumably in deeper soil layers (Barraclough and Leigh, 1984; Kuhlmann et al., 1989) are sufficient for are quite rapid exhaustion of soil mineral N (Kage, 1997). However, under super optimal N supply these resources are not used by winter wheat (Fig. 11-4). This clearly indicates the need for an appropriate fertilisation regime taking account of the sub soil nitrate. Addiscott and Darby (1991) calculated for UK conditions that soil mineral N should be considered down to depths of 160 m for determining the fertiliser optimum of winter wheat up to the mid of April.
Fig. 11-10: N-Loss probability after cauliflower for two different succeeding crops during a 24 year simulation period (1971-1995) on (a) a loess loam soil and (b) a sandy soil.
Regarding the scenario calculations made for the sandy soil (Fig. 11-8, Fig. 11-10) some uncertainty remains if a) the root growth is as assumed similar for this soil type as for the loess loam soil and b) the nitrogen uptake capacity is as high as on a loess loam. However, winter rye may be used instead of winter wheat, which has similar potential to achieve high rooting depths (Vos et al., 1998) and may take up sufficient amounts of nitrogen if modern hybrid varieties are used. The use of lettuce as an alternative to winter wheat is clearly a worst case scenario and other vegetable crops may make more efficient use of the N residues of cauliflower. However, reported maximum rooting depths of vegetables seldom exceed 100 cm (Greenwood et al., 1982; Chapter 7; Thorup-Kristensen and Van den Boogaard, 1999) and the time integral of rooting density may be too low for a complete uptake of sub soil nitrate (see also Chapter 8 for further discussion).

The use of catch crop has been intensively discussed as an option for decreasing leaching losses (Everaarts, 1993b; van Dam and Leffelaar, 1998; Vos and van der Putten, 1997; Stenberg, 1999). The main advantage of using appropriate full season crops instead catch crops is their long growing period which allows their root system to reach soil depths comparable deep or even deeper than the average displacement depth of residual soil nitrate from the upper soil layers or mineralised nitrate from crop residues. Alternatively to the use of full season crops one may try to allow winter cover crops like winter rye to grow until their root system has reached the desired soil depth and their shoot has absorbed sufficient amounts of nitrogen. However, when catch crops are incorporated in the soil, their re-mineralisation during the following growing season may be incomplete (Thorup-Kristensen, 1993b; Thorup-Kristensen and Nielsen, 1998) or even missing (Jensen, 1992; Sørensen and Thorup-Kristensen, 1993; Burket et al., 1997) especially if the C/N ratio of the catch crop plant material is low (Kuo and Sainju, 1998).

11.7. Conclusions

The introduction of deep rooting cereals into vegetable crop rotations can be an efficient measure for reducing leaching losses of nitrate. The presented results clearly demonstrates that residual soil nitrate is only an indicator of nitrate leaching losses. Depending on the soil type and the local climate large amounts of nitrogen transported into deeper soil regions may become potential available for deep rooting succeeding
crops like winter sown cereals during later parts of their growing season. An appropriate fertilisation regime has to consider this N source, because too high late dressings of N may suppress N uptake from the sub-soil. Simulation modelling may strongly support the derivation of such regimes, by estimating the amounts of nitrogen situated in the deeper sub soil after crops remaining large amounts of residual nitrogen.

Evaluations of nitrogen use efficiency should consider effects at the cropping system level. Negative effects of crops with a low nitrogen use efficiency may be compensated by appropriate succeeding crops which make effective use of residual nitrogen amounts.
12. Final discussion

The aim of this thesis was to analyse the determinants of nitrogen use efficiency in intensive vegetable cropping systems on the crop and cropping systems scale. Thereby, cauliflower was used as an example, because this crop represents some of the problems of N management in vegetable crops and cropping systems in a typical way. Simulation modelling was used as the methodological approach, as it allows the quantitative testing of hypotheses and offers the chance to use newly gained knowledge for predictive purposes.

12.1. Models as heuristic tools

The object oriented HUME class library (Fig. 12-1, Kage and Stützel, 1999a) which was used to implement the model modules presented in the previous chapters was especially designed to support the use of modelling as a heuristic tool.

Applying complex models like those of the CERES family (Jones and Kiniry, 1986) to an experimental data set is not a very efficient way for testing an hypothesis. Differences between measurement and simulation for complex parameters like grain yield may be caused by a huge number of processes simulated within the model. Without appropriate data and the possibility to exchange process formulations no meaningful information can be gained from experimental data as to whether a particular model describes reality adequately. The testing of hypotheses, the principal activity of scientific work, by comparison of simulation model output with experimental data calls for options to vary individual process formulations independently. However, the structure of most complex models of crop growth in combination with the water and nitrogen dynamics in the soil plant system does not allow this (Jones, 1998).

The Fortran based FSE modelling environment (van Kraalingen, 1995) was a promising effort to couple the flexibility of general-purpose programming languages with the effective use of overall similarities between simulation models, which all contain the steps of initialisation followed by repeated steps of rate calculation, integration and output until the final model condition is reached. Further steps towards a more structured modelling were done during the development of the Expert-N system (Engel...
and Priesack, 1992). The APSIM (McCown et al., 1996) system follows a similar way, however, it’s still using quite large buildings blocks or components usually not representing a single testable hypothesis.

Modular modelling approaches have recently been discussed (Acock and Reynolds, 1997; Chen and Reynolds, 1997; Reynolds and Acock, 1997; Porter et al., 1999) to overcome the shortcomings described. However, besides the introduction of modularity and genericness further efforts are needed to implement tools for parameter estimation and statistical model evaluation into simulation modelling environments.

![Schematic representation of the HUME-component library based upon the visual component library (VCL) of the Borland® Delphi/C++ Builder compiler technology.](image)

**Fig. 12-1:** Schematic representation of the HUME-component library based upon the visual component library (VCL) of the Borland® Delphi/C++ Builder compiler technology.

For smaller-scale problems commercial software products like ModelMaker® (Walker, 1997) and ACSL (MGA-software, 1999) are available which fulfil much of the above mentioned needs. For larger scale problems of crop modelling, however, such systems seem to be not yet very suitable.

A generic, object oriented model library supporting all important basic tasks of simulation modelling from effective integration methods to optimisation algorithms and consisting of the basic templates for standard processes and sub-systems seems to be
a promising tool to further enhance the capabilities of simulation modelling. The HUME component library, still under construction, allows to investigate the potentials of such an approach.

**12.2. Further aspects and future prospects of research on nitrogen use efficiency in intensive vegetable cropping systems**

This thesis has shown that many processes directly or indirectly affect the complex parameter of nitrogen use efficiency in crops and cropping systems.

Developmental processes (chapter 2) govern carbon (chapter 2 and 5) and nitrogen partitioning (chapter 9) between vegetative and generative plant parts and thereby dry matter and nitrogen harvest index. The light use efficiency i.e. the productivity per unit of intercepted radiation depends not only on the level of irradiance (chapter 3 and 4) and temperature (chapter 3), but also on the protein nitrogen content per unit leaf area (chapter 9). The rooting characteristics (chapter 7) determine together with soil properties (chapter 8) the uptake efficiency and thereby also the residual soil nitrate levels (chapter 8). Late autumn residual soil nitrate levels and mineralisation of nitrate from crop residues and soil organic matter determine together with the downward water movement leaching losses (chapter 11). Deep rooting cereal crops (chapter 10), however, may make effective use of deeply leached nitrate (chapter 11) thereby increasing the nitrogen use efficiency of the cropping system.

Many aspects of NUE have been covered in this thesis, however, some have been dealt with only on a limited level of detail and some were not yet discussed.

Further physiological aspects of the nitrogen-productivity relationship in cauliflower using a photosynthesis-respiration approach have been elaborated by (Alt, 1999; Alt et al., 2000b; Alt et al., 2000d). Besides the fact that the light-use efficiency-based approach for calculation of dry matter production showed good predictive quality (chapters 4 and 9), photosynthesis-respiration based approaches offer the possibility to investigate effects of certain physiological traits, like altered N distributions within the canopy and effects of varying N contents on the carbon loss by respiration losses.

Alt (1999) predicted seasonally changing N demands of cauliflower based on a temperature / radiation intensity induced change of optimal N contents. The analysis given in chapter 9 is based on the light use efficiency approach. It therefore neglects
such effects, but also predicts a considerable variation of the N demand depending on the climatic conditions during the growing season and for the cultivar used. Seasonal variations in the N demand of cauliflower therefore should be separated into effects caused by developmental processes and effects caused by a changing optimum N content of the canopy of cauliflower (Alt et al., 2000d). The results presented in chapter 6 indicate that there is no severe adaptation of N contents in cauliflower due to a changing light environment. Whether varying temperature conditions are able to induce such a change of optimal N-content as suggested by Alt (1999) remains to be proven.

High proportions of vegetable crops in the rotation leaving large amounts of N residues in the field and high inputs of organic fertilisers may in the long term increase soil organic matter and consequently nitrogen mineralisation. This long term effect further contributes to problems of N management in vegetable production systems. Introducing crops with harvest residues of a wide C/N ratio like cereals into vegetable production systems, is therefore likely to improve NUE of the production systems through mechanisms other than the uptake of deeply translocated nitrogen (chapter 10 and 11).

Tillage practices strongly influence soil structure and thereby many processes affecting the NUE at the crop and cropping systems scale. Increases in soil bulk density may reduce rooting intensity (Barraclough and Weir, 1988; Tardieu, 1988; Unger and Kaspar, 1994) and thereby the uptake efficiency of crops. However, reduced tillage practices not only lead to increased bulk densities of the soil, but also to a higher portion of macropores, enabling root systems to reach deeper regions of the soil (Ehlers, 1975), thereby increasing the availability of water and nutrients from the sub soil. Macropores increase infiltration capacity (Ehlers, 1975) and strongly affect the nutrient transport properties of the soil (Brusseau and Rao, 1990; Matthews et al. 2000). Tillage also influences mineralisation rates by effects on soil aeration, soil temperature and by reducing the degree of 'physical protection' (Verberne et al., 1990; Balesdent et al. 2000) of soil microbial biomass. Conservation tillage practices therefore may be used to slow down unwanted mineralisation during winter time thereby reducing leaching losses. However, after ploughing of previously direct drilled plots nitrate losses may rise (Catt et al., 2000). Higher reproduction rates of weeds under reduced tillage, however, may lead to increasing seed banks and over a longer run to hardly manageable problems of weed control.
Influences of water supply on dry matter partitioning and the productivity of the cauliflower crop are not covered directly in this thesis, chapter 8 only focuses on some possible effects of lower water contents of sandy soils on nitrogen availability. This is, however, not very critical because commercial cauliflower crops are usually grown under well watered conditions. Severe interactions between water supply and N availability, strongly affecting N demand and fertilisation practice are therefore probably of limited importance in present production cauliflower production systems. Under conditions of a restricted water availability, however, this issue may become increasingly important.

Mineralisation of nitrogen from the soil organic matter and the crop residues during the growing period of vegetable crops is still difficult to predict. The approach presented in chapter 11 therefore is more of descriptive rather than of highly predictive nature. The difficulties using mineralisation models in practice arise to a large extent from the problem of initialisation their different pools and the estimation of their rate parameters. Crop models may help to quantify the amounts nitrogen remaining as crop residues in the field. Fast and cheap methods to characterise the amount and quality of soil organic matter like the near infrared spectroscopy (Fox et al., 1993) may be seen as promising attempts to achieve this goal.

Site specific N management has become an intensively discussed option for increasing NUE. This is mainly because the technical prerequisites like global positioning systems coupled with yield mapping and remote sensing systems (Wollring et al., 1998) are now available at reasonable costs. Dynamic crop growth models may be used to derive site specific N fertilisation strategies (Matthews and Cosser, 1997; Braga et al. 1999). The model approach presented here for cauliflower is in principle suitable for such purposes, as it gives information about the N response of yield and about factors influencing spectral properties of the canopy. However, the comparably small vegetable production area may hinder the introduction of such techniques into practical farming. Furthermore, it may be speculated that much of the variation in N supply in vegetable fields is caused by an inhomogeneous incorporation of crop residues and therefore the spatial scale is less than 3-4 meters. Larger-scale variation in N supply due to differing pedogenic conditions may play a smaller role in vegetable production than in arable crops due to the higher N supply level.
It has been also shown that the N demand of cauliflower is influenced by developmental parameters which may vary between cultivars. The applicability of the model approach presented for advising purposes therefore depends on the availability of parameter values for changing cultivars. For a small scale crop like cauliflower this may cause serious problems simply because the possible benefits of sound fertilisation recommendations have at least to compensate the research efforts needed to obtain the desired information (see also Acock and Reynolds, 1989).
Epilogue

This thesis hopefully contributes some small bricks for a further increase of understanding of the nitrogen dynamics of the soil/plant system under conditions of intensive, vegetable production. Such knowledge is, as already stated in the introduction of this thesis, urgently needed to develop production techniques which are able to cope in parallel economical and environmental goals.

It is, however, at least a political issue if a society is willing and if it is efficient to further subsidise the development and dissemination of knowledge about environmentally safe production methods for agricultural and horticultural crops in general and especially for small scale crops in vegetable production systems. Strict legislative rules may be regarded cheaper than investments in knowledge acquisition and transfer. However, such legislation solutions may cause an increased ousting of vegetable production into less restrictive 'political environments' leading to an export of environmental problems and possibly to an import of problems of product quality. The development of science based, innovative production methods in agriculture therefore hopefully remains an accepted goal of the society because they are a prerequisite for a profitable and environmental safe food production.
Kurzfassung

Die vorgestellte Arbeit befasst sich mit dem Thema der Stickstoffnutzungseffizienz (SNE) in intensiven gemüsebaulichen Produktionssystemen des ungeschützten Anbaus. Hierbei wird ein systemtheoretischer Ansatz verfolgt, und die Simulationsmodellierung bildet zusammen mit als Datengrundbasis dienenden Feldversuchen die methodische Grundlage. Die Arbeit gliedert sich in 12 Kapitel, wobei neben einer allgemeinen Einleitung und der Gesamtdiskussion 10 Kapitel Grundlagen für die Modellierung und Aspekte der SNE behandeln.

In Kapitel 2 wird ein einfacher Modellansatz zur Simulation der Entwicklung und Stoffverteilung bei Blumenkohl unter Abwesenheit von Nährstoffmangel sowie Trockenstreuß vorgestellt. Das Modell ist eine Kombination einer empirischen Funktion zwischen Temperatursumme und Blattzahl, einem Vernalisationsmodell, einem allometrischen Ansatz zur Stoffverteilung zwischen Blatt und Strunk sowie einer logistischen Funktion, die den Anteil des Kopfes an der Gesamttrockenmassezuwachsrate nach Ende der Vernalisation beschreibt. Dieser Modellansatz wurde mit einem einfachen, auf dem Konzept der Lichtnutzungseffizienz (LUE) beruhenden Ansatz zur Modellierung der Stoffproduktion gekoppelt. Die Parameterwerte für die LUE und für die spezifische Blattfläche wurden für einzelne Experimente angepaßt, um eine genaue Beschreibung der Trockenmasseproduktionsrate zu erreichen.


Die rechtwinklige Hyperbel beschreibt die unter Variation von Strahlungsintensität und CO₂-Konzentration gewonnenen Daten zum Gaswechsel von Einzelblättern mit
hinreichender Genauigkeit. Die Werte für die initiale Lichtnutzungseffizienz, $\alpha$, wurden jedoch durch die geringe Flexibilität dieser Funktion mit Werten von ca. 25 µg·J$^{-1}$ zu hoch geschätzt. Die lichtgesättigte Photosyntheserate ($P_{\text{max}}$) zeigte eine Optimumreaktion bezüglich der Temperatur und war positiv mit den Blattstickstoffgehalten korreliert. Die initiale Lichtnutzungseffizienz zeigte dagegen keine konsistente Reaktion auf die Blattemperatur und die Blattstickstoffgehalte. Die Respiration pro Einheit Blattfläche zeigte einen exponentiellen Anstieg mit steigender Temperatur, der Q10 Wert wurde auf 1.86 geschätzt.

Die Modellanalyse zeigte, daß die LUE nur dann von einer Variation der Strahlungsintensität im Bereich 5-10 MJ·m$^{-2}$·d$^{-1}$ unbeeinflußt ist, wenn $P_{\text{max}}$ sich im Bestand und über die Zeit varierenden Strahlungsintensitäten anpaßt. Die Anpassung von $P_{\text{max}}$ an eine innerhalb des Bestandes variierende Strahlungsintensität allein, sowie höhere LAI Werte reduzieren tendenziell die Abnahme der LUE mit ansteigender Strahlungsintensität.

In Kapitel 4 werden sechs verschiedene Module für die Berechnung der Trockenmasseproduktion von Blumenkohl unter Benutzung einer Datenbasis von 22 Blumenkohlsätzen aus 15 unabhängigen Feldversuchen parameterisiert und evaluiert. Zunächst wurden ein Modul das eine konstante Lichtnutzungseffizienz sowie ein Modul das eine Abnahme der Lichtnutzungseffizienz mit ansteigendem täglichem Strahlungsintegral postuliert überprüft. Weiterhin wurden zwei Photosynthese/Respiration basierte Module benutzt, die auf einer analytischen Integration der rechtwinkligen Hyperbel zur Beschreibung der Einzelblattphotosynthese über den Bestand beruhen und jeweils einen konstanten bzw. einen proportional zur Strahlungsintensität im Bestand abnehmenden $P_{\text{max}}$-Wert annehmen. Darüberhinaus wurden noch zwei auf dem "SUCROS" Modell beruhende Module benutzt, bei denen die negative Exponentialfunktion zur Beschreibung der Einzelblattphotosynthese durch die rechtwinklige Hyperbel ersetzt wurde. Auch hier wurde jeweils ein konstanter $P_{\text{max}}$-Wert bzw. ein im Bestand abnehmender $P_{\text{max}}$ Wert angenommen.

Die Ergebnisse zeigen, daß eine konstante LUE (3.15 (±0.04) g·MJ$^{-1}$) nur schlecht in der Lage war, die Trockenmassproduktion von Blumenkohl eines unabhängigen Datensatzes zu prognostizieren (modelling efficiency $\text{EF} = 0.69$). Bei Annahme einer mit der Strahlungsintensität, $I$, abnehmenden LUE ($\text{LUE} = 6.66 (±0.80) - 0.36$...
(±0.08) l)) verbesserte sich die Prognosegüte drastisch (EF = 0.88). Die beschreibende und prognostische Güte der Photosynthese/Respiration basierten Modellmodule war höher, wenn eine Abnahme von $P_{\text{max}}$ im Bestand angenommen wurde. Unter dieser Voraussetzung war die Prognosegüte dieser Modellansätze höher, als die des einfachen, eine konstante LUE annehmenden LUE Ansatzes, jedoch nicht prinzipiell höher, als die desjenigen LUE Ansatzes, der eine Abnahme der LUE mit steigender Strahlungsintensität postulierte.


Das Modell war in der Lage, die Trockenmasse einzelner gemessener Blattgruppen, bestehend aus 3 bzw. 5 Blättern, zu beschreiben ($r^2=0.97$) und zu prognostizieren ($r^2=0.90$ und 0.87). Die gewonnenen Parameterwerte lassen erkennen, daß zwei bis drei Blätter gleichzeitig mit hoher Wachstumsrate wachsen. Die potentiellen Wachstumsraten der Blätter nehmen während der Entwicklung des Blumenkohls ab, wahrscheinlich wegen der Assimilatkonkurrenz durch den sich bildenden Kopf. Das gezeigte Modell kann als Grundlage für die Analyse und die Prognose von Translokationsprozessen dienen, welche den Stickstoffersatzindex und hierüber die Stickstoffeffizienz beeinflussen.

In Kapitel 6 werden Daten aus Feldversuchen aus 3 aufeinanderfolgenden Jahren, in denen Blumenkohl unter variierter Stickstoffdüngung kultiviert wurde, benutzt, um Funktionen zur Beschreibung der Abnahme der Stickstoffgehalte bei zunehmender Pflanzen-/Organgröße, aber optimaler N-Versorgung abzuleiten. Eine optimale N-Versorgung wurde bei Nmin-Gehalten von > 100 kg N ha$^{-1}$ von 0-60 cm unterstellt.
Zusätzlich wurde die Strahlungsintensität in 2 von 3 Jahren durch eine Netzbedeckung variiert, die jeweils die natürliche Strahlungsintensität um 40% reduzierte. Die Abnahme der mittleren Stickstoffkonzentration des Sprosses, \( Nc (%N \text{TM}) \), mit zunehmender Sproßtrockenmasse, \( W_{\text{sh}} (t \text{ha}^{-1}) \), von Blumenkohl (\( Nc = 4.84 \pm 0.071 \cdot W_{\text{sh}}^{-0.089} \pm 0.011 \), \( r^2 = 0.67 \)) ist geringer als für einige landwirtschaftliche Kulturen beschrieben wurde. Blattfläche und Blattgewicht waren gleichermaßen geeignet als unabhängige Variablen zur Beschreibung der Abnahme des Stickstoffgehaltes der Blätter mit zunehmender Blattgröße zu dienen. Die Strahlungsintensität hatte keinen signifikanten Einfluß auf die Gesamtstickstoffkonzentration der Blätter und nur einen geringen Einfluß auf die Proteinstickstoffgehalte in den unteren Blattetagen. Die Gesamtstickstoffgehalte von aus 5 Blättern bestehenden Blattgruppen, \( NLc \), unter optimaler N-Versorgung konnten durch eine multiple lineare Regression mit der Masse dieser Blattgruppe, \( W5L, (g \text{TM} 5 \text{Blätter}^{-1}) \) und der mittleren Blattnummer dieser Blattgruppe, \( nL, (-) \) als unabhängige Variablen beschrieben werden (\( NLc = 7.58-0.82 \cdot W5L-0.074 \cdot nL + 0.024 \cdot W5L \cdot nL, r^2 = 0.76, n=76 \)). Der Anteil an Nitratstickstoff, \( f_{\text{Nit}} (-) \), in den Blättern konnte zur mittleren auf einzelnen Blattetagen eintreffenden Strahlungsintensität, \( I_{\text{av}} (W \text{PARm}^{-2}) \), in Beziehung gesetzt werden (\( f_{\text{Nit}} = 0.2456 \pm 0.0188 - 0.0023 \pm 0.0004, r^2 = 0.67 \)).

Aus diesen funktionalen Beziehungen konnten Referenzstickstoffgehalte ermittelt und hiermit wiederum Differenzen zu gemessenen Stickstoffgehalten berechnet werden, wobei jetzt auch N-Mangel Bedingungen in die Betrachtung einbezogen wurden. Mit Hilfe dieser berechneten Differenzen wurden kritische Nmin-Gehalte des Bodens abgeleitet, bei denen die Stickstoffgehalte von Blumenkohl unter die Referenzgehalte abzusinken beginnen. Hierzu wurden Linear-Plateau Funktionen an Wertepaare aus errechneten N-Gehaltsdifferenzen und log-transformierten Boden- stickstoffgehalten von 0-60 cm angepaßt. Als kritische Nmin-Gehalte wurden 85, 93 und 28 kg Nha\(^{-1}\) für Blätter, Strunk und Kopf geschätzt. Die kritischen Nmin Werte waren für Blattprotein mit ca. 30 kg Nha\(^{-1}\) deutlich geringer als für den Gesamtstickstoffgehalt.

In Kapitel 7 werden Ergebnisse von Wurzelbeobachtungen mit der Minirhizotronmethode und der Bohrkernmethode an Blumenkohl dargestellt, die aus 4 Feldversuchen aus zwei Jahren und von 2 Standorten (Lößlehm / humoser Sand)
stammen. Die Gesamtwurzellänge (RL) (cm cm⁻²) von Blumenkohl war positiv mit der Sproßtrockenmasse von Blumenkohl (Wsh) (g m⁻²) korreliert RL= 0.0124(±0.005) Wsh, r²=0.76. Es ergab sich eine akzeptable Übereinstimmung (r²=0.88) von Minirhizotron- und Bohrkernmetode für den Unterboden, wohingegen für den Oberboden eine Unterschätzung der Durchwurzelungsintensität durch die Minirhizotronmethode festgestellt werden konnte. Die Entwicklung der Durchwurzelungstiefe konnte für beide Bodentypen durch eine segmentierte, aus einer exponentiellen und einer darauffolgenden linearen Phase bestehenden Funktion der Temperatursumme dargestellt werden. Während der linearen Phase betrug die Zunahme der Durchwurzelungstiefe 0.107(±0.01) cm °C⁻¹ d⁻¹.

Ein einfaches Wurzelwachstumsmodell beruhend auf den Annahmen einer negativ exponentiell mit der Bodentiefe abfallenden Durchwurzelungsintensität (RLD), einer konstanten Fraktion der Feinwurzeltrockenmasse an der Gesamttrockenmasse (frR) und einem konstanten Verhältnis zwischen der RLD an der Oberkante des Bodenprofils und der RLD an der aktuellen Durchwurzelungstiefe (rRLD) wurde benutzt, um die zeitliche und räumliche Entwicklung der RLD im Wurzelraum zu beschreiben. Für die unterschiedlichen Bodentypen konnten leicht abweichende Parameterwerte für fr und rRLD gefunden werden, die darauf hindeuten, daß auf dem Lößboden ein höherer Anteil an Trockenmasse in die Feinwurzeln verlagert wurde und das die Durchwurzelungsintensität auf dem humosen Sandboden in größeren Bodenschichten höher war. Eine Kreuzvalidation, bei der die Parameterwerte die durch Anpassung der auf einem Boden gewonnen Daten zur Prognose der Durchwurzelungsdaten auf dem anderen Boden benutzt wurden, zeigte aber, daß trotz der erwähnten Unterschiede der Parameterschätzer jeweils noch eine recht gute Prognose (r²= 0.91 und 0.95) erreicht werden konnte.

In Kapitel 8 werden Daten aus zwei einjährigen und einem mehrjährigen Feldversuch, die zusammen eine Datengrundlage von 7 unter jeweils varierter Stickstoffdüngung kultivierten Blumenkohlsätzen ergeben, benutzt, um in einer modellbasierten Studie die Verfügbarkeit des Bodenstickstoffs für Blumenkohl zu analysieren. Das hierzu benutzte Modell setzt sich zusammen aus Modulen für Wurzelwachstum, Nitrattransport zu den Wurzeln und vertikalem Nitrattransport im Bodenprofil. Die Netto-mineralisation wurde aus den Stickstoffbilanzen der jeweiligen Varianten berechnet und war eine Eingabegröße für das Modell. Die Stickstoffaufnahme der Pflanzen
Kurzfassung

wurde aus einem Pflanzenwachstumsmodell abgeleitet, das im folgenden Kapitel 9 beschrieben wird.

Aus zwei Jahren vorliegende Wurzelbeobachtungen ließen unter Stickstoffmangel einen erhöhten Anteil an Feinwurzeln relativ zur Gesamttdrogenmasse erkennen. Eine angepaßte Version des Wurzelwachstumsmodèles aus Kapitel 7, die diese Tatsache berücksichtigte, beschrieb die erhobenen Wurzeldaten mit hinreichender Genauigkeit ($r^2=0.75$ und 0.80). Basierend auf einer akzeptablen Beschreibung des Bodenwasserhaushaltes, wurde auch der vertikale Nitrattransport im Bodenprofil überwiegend korrekt beschrieben. Das Ausmaß der vertikalen Verlagerung während der Vegetationszeit war jedoch aufgrund der hohen Wasserspeicherkapazität des Lößbodens auf dem die Versuche durchgeführt wurden auf eine Tiefe von maximal 60 cm beschränkt. Eine Analyse der Faktoren die die Nitratverfügbarkeit beeinflussen zeigte, daß der scheinbare Massenfluß nur unter überdüngten Bedingungen, wenn während der gesamten Vegetationszeit sehr hohe Nitratmengen im Bodenprofil vorliegen von größerer Bedeutung für den Nitrattransport zur Wurzel ist. War dies nicht der Fall, so erfolgte der weit überwiegende Teil des N-Transportes zur Wurzel durch Diffusion. Das Einzelwurzelmodell zur Berechnung des maximalen Nitrattransportes zur Wurzel überschätzte die maximalen Nitrattransportraten. Dies konnte durch Vergleich der $N_{\text{min}}$-Werte, bei denen das Modell eine Transportbegrenzung der N-Aufnahme berechnete, mit empirisch ermittelten kritischen $N_{\text{min}}$-Gehalten (Kapitel 6) geschlossen werden. Um diesen Widerspruch zwischen theoretischen, berechneten und gemessenen kritischen $N_{\text{min}}$-Werten zu überbrücken, wurde daher eine Begrenzung der Aufnahmedauer der Wurzeln postuliert. Es war jedoch die Annahme einer unrealistisch kurzen aktiven Aufnahmeperiode der Wurzeln nötig, um eine hinreichende Übereinstimmung zwischen Modellergebnis und Messungen zu erreichen. Weiterhin wurden Szenariorechnungen durchgeführt, um funktionelle Beziehungen zwischen Düngungshöhe und Restnitratmengen zu ermitteln. Hierbei wurden auch hypothetische Bedingungen eines Sandbodens sowie mögliche Auswirkungen einer geteilten N-Gabe untersucht.

In Kapitel 9 wird basierend auf den bereits in Kapitel 2 - 8 gezeigten Ergebnissen zu Stoffverteilung, Stoffproduktion, Wurzelwachstum, N-Konzentrationen in verschiedenen Organen und zur Verfügbarkeit von Bodenstickstoff ein integriertes
Simulationsmodell für das System Blumenkohl/Boden vorgestellt. Diese Modell wurde anhand von Daten aus 7 Feldversuchen parameterisiert und evaluiert.

Die Trockenmasseproduktion wird in diesem Modell mit Hilfe eines einfachen, den in Kapitel 4 vorgestellten Lichtnutzungseffizienz basierten Ansatz um den Effekt von N-Mangel erweiterten Modul berechnet. Hierbei wird eine lineare Abnahme der Lichtnutzungseffizienz mit zunehmender Differenz zwischen aktuellem und unter-optimaler N-Versorgung realisiert, flächenbezogenem Proteinstickstoffgehalt, NCA_{Prot} (g N m⁻²), der Blätter angenommen. Für zwei Feldversuche wurde die Abnahme der LUE durch Parameterschätzung mit 0.82 und 0.75 (g DM MJ⁻¹ g N⁻¹ m²) ermittelt. Mit Hilfe dieses Ansatzes und auf einem experimentellen Jahr beruhenden Parameterschätzungen wurde die Trockenmasseproduktion von Blumenkohl von 5 unabhängigen Experimenten mit varierter N-Versorgung mit einem Bestimmtheitsmaß von 0,95 prognostiziert. Stickstoffaufnahme und -verteilung wurden mit Funktionen simuliert, die eine organgrößenabhängige Abnahme der Stickstoffgehalte annehmen. Ein Nitratstickstoffpool der Blätter wurde explizit berücksichtigt, dessen Größe von der Strahlungsintensität und der N-Versorgung abhängt. Bei N Mangel der Pflanze erfolgt zuerst eine Mobilisierung der Nitratreserven des Blattes. Es wird weiterhin angenommen, daß der Kopf die höchste Priorität bei der Stickstoffverteilung unter N-Mangel hat. Das Modell prognostizierte die N-Aufnahme des Sprosses unter Berücksichtigung von Zwischenernten mit einem \( r^2 \) von 0,92 und unter alleiniger Berücksichtigung der Endernten mit einem \( r^2 \) von 0,87. Die N-Aufnahme des Sprosses war dabei mit der Endblattzahl positiv korreliert.

Darüberhinaus wurde eine Langzeitszenarioanalyse durchgeführt um jahreszeitliche Schwankungen des N-Bedarfs zu quantifizieren. Durch Unterschiede in der Länge der Vernalisationsphase variierte die simulierte N-Aufnahme optimal N versorgt angenommener Bestände der Sorte 'Fremont' im Mittel von 260 kg N ha⁻¹ bei Frühjahrsätzen bis zu 290 kg N ha⁻¹ für Sommersätzen. Für die hinsichtlich der Vernalisation empfindlicher auf hohe Temperaturen reagierende Sorte 'Linday' nahm bei Sommerpflanzung die berechnete N-Aufnahme im Mittel auf 320 kg N ha⁻¹ zu, wobei gleichzeitig eine hohe jährliche Variation der N-Aufnahme berechnet wurde.

In Kapitel 10 werden Wurzelbeobachtungen vorgestellt, die an Winterweizen in 3 aufeinander folgenden Versuchs-session auf einem Lößlehmboden mit der Mini-
rhizotron- und der Bohrkernmethode durchgeführt wurden. Es ergab sich wie bereits für Blumenkohl (Kapitel 7) für den Unterboden eine gute Beziehung zwischen der Minirhizotron- und der Bohrkernmethode \((r^2=0.92)\), wohingegen die Minirhizotronmethode für den Oberboden unrealistisch geringe Durchwurzelungsintensitäten schätzte. Die Entwicklung der Durchwurzelungstiefe von Winterweizen konnte für alle 3 Jahre als linear mit der Temperatursumme ansteigend beschrieben werden, wobei die Zunahme der Durchwurzelungstiefe 0.11 (±0.01) cm°C⁻¹ d⁻¹ betrug.

Das in Kapitel 7 vorgestellte Wurzelwachstumsmodell wurde neu parameterisiert und zur Beschreibung der experimentellen Daten benutzt. Hierbei wurden zum einen wie beim Blumenkohl ein konstantes Verhältnis zwischen Feinwurzel- und Gesamttrockenmasse angenommen (Hypothese H1) bzw. es wurde ein linear mit der Temperatursumme abnehmender Anteil an Feinwurzeln postuliert (Hypothese H2). Hypothese H2 war weitaus besser in der Lage, die experimentellen Daten zu beschreiben. Es erklärte ca. 90% der gefundenen experimentellen Varianz.

In Kapitel 11 werden Ergebnisse aus einem langjährigen, auf einem Lößlehmstandort durchgeführten Fruchtfolgeversuch vorgestellt, in dem innerhalb zwei verschiedener Rotationen jeweils nach spät geerntetem Blumenkohl Winterweizen angebaut wurde. Die Gesamtstickstoffaufnahme des Blumenkohls zum Zeitpunkt der Ernte betrug ca. 300 kg N ha⁻¹ sofern eine marktfähige Kopfgröße erreicht wurde und die N-Versorgung optimal war. Etwa zwei Drittel des Stickstoffs der Blumenkohlpflanzen befand sich in den auf dem Feld verbleibenden Pflanzenteilen. Zusätzlich wurden ca. 80 kg N ha⁻¹ als Restnitratstickstoff von 0-120 cm Bodentiefe zum Zeitpunkt der Ernte gefunden, wobei es jedoch große Unterschiede zwischen den Jahren gab.


Ein Simulationsmodell bestehend aus Modulen die die Stickstoffaufnahme des Weizens, die Mineralisation von Stickstoff aus den Ernterückständen und der organischen Bodensubstanz, den Bodenwasserhaushalt und den vertikalen Nitrat-
Kurzfassung

## Abbreviations

### List of main symbols

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Units</th>
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<tr>
<td>AIC</td>
<td>Akaike information criterion</td>
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<tr>
<td>a\textsubscript{LU}E</td>
<td>light use efficiency parameter</td>
<td>g DM MJ\textsuperscript{-2} m\textsuperscript{2} d</td>
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<tr>
<td>a\textsubscript{zr}</td>
<td>rooting depth constant</td>
<td>°C\textsuperscript{-1} d\textsuperscript{-1}</td>
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<tr>
<td>b</td>
<td>leaf respiration rate</td>
<td>µg CO\textsubscript{2} m\textsuperscript{-2} s\textsuperscript{-1}</td>
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<tr>
<td>b\textsubscript{zr}</td>
<td>rooting depth constant</td>
<td>cm °C\textsuperscript{-1} d\textsuperscript{-1}</td>
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<tr>
<td>C</td>
<td>CO\textsubscript{2} concentration</td>
<td>mg m\textsuperscript{-3}</td>
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<tr>
<td>CD</td>
<td>curd diameter</td>
<td>mm</td>
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<tr>
<td>C\textsubscript{l}</td>
<td>concentration of soil solution</td>
<td>g kg\textsuperscript{-1}</td>
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<td>C\textsubscript{lf}</td>
<td>interception correction factor</td>
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<tr>
<td>D</td>
<td>plant diameter</td>
<td>m</td>
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<td>D\textsubscript{L}</td>
<td>daylength</td>
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<tr>
<td>D\textsubscript{s}</td>
<td>dispersion coefficient</td>
<td>cm\textsuperscript{2} d\textsuperscript{-1}</td>
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<tr>
<td>D\textsubscript{w}</td>
<td>diffusivity of soil water</td>
<td>cm\textsuperscript{2} d\textsuperscript{-1}</td>
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<tr>
<td>E</td>
<td>evaporation</td>
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<td>f</td>
<td>fraction of curd growth / total growth</td>
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<td>f\textsubscript{f}</td>
<td>tortuosity factor</td>
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<tr>
<td>f\textsubscript{av}</td>
<td>fraction of assimilates</td>
<td>-</td>
</tr>
<tr>
<td>f\textsubscript{fr}</td>
<td>fraction of fine roots</td>
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<td>f\textsubscript{NO3}</td>
<td>fraction of nitrate nitrogen</td>
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<tr>
<td>f\textsubscript{Temp}</td>
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<tr>
<td>h</td>
<td>allometric constant</td>
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<td>I</td>
<td>irradiance</td>
<td>W m\textsuperscript{2}, MJ m\textsuperscript{-2} d\textsuperscript{-1}</td>
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<tr>
<td>I\textsubscript{0}</td>
<td>irradiance on top of the canopy</td>
<td>W m\textsuperscript{2}</td>
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<tr>
<td>I\textsubscript{av}</td>
<td>average radiation intensity</td>
<td>MJ m\textsuperscript{-2} d\textsuperscript{-1}</td>
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<tr>
<td>I\textsubscript{max}</td>
<td>maximum nitrate influx</td>
<td>g N cm\textsuperscript{-1} d\textsuperscript{-1}</td>
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<td>k (θ)</td>
<td>unsaturated hydraulic conductivity</td>
<td>cm d\textsuperscript{-1}</td>
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<td>k</td>
<td>light extinction coefficient</td>
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<td>Variable</td>
<td>Description</td>
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<tr>
<td>$k_{dif}$</td>
<td>extinction coefficient for diffuse radiation</td>
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</tr>
<tr>
<td>$k_G$</td>
<td>extinction coefficient for global radiation</td>
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<td>$k_r$</td>
<td>root length density constant</td>
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<td>LAI</td>
<td>leaf area index, LAI</td>
<td>m$^2$ m$^{-2}$</td>
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<td>LUE</td>
<td>light-use efficiency</td>
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<td>light use efficiency parameter</td>
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<tr>
<td>Nc</td>
<td>nitrogen content</td>
<td>% DM</td>
</tr>
<tr>
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<td>nitrogen content per unit leaf area</td>
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<td>NC$_{opt}$</td>
<td>optimum nitrogen content</td>
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<td>N demand</td>
<td>g N.m$^{-2}$.d$^{-1}$, g N.pl$^{-1}$</td>
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<td>Canopy nitrate pool</td>
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<td>optimum nitrogen amount</td>
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<td>nitrogen in shoot</td>
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<td>N$_{sup}$</td>
<td>N supply</td>
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<td>o$_{tr}$</td>
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<td>PAR</td>
<td>photosynthetic active radiatiton</td>
<td>W m$^2$</td>
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<td>plant density</td>
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<td>PD</td>
<td>planting density</td>
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<td>light saturated photosynthetic rate on top of canopy</td>
<td>μg CO$_2$.m$^{-2}$.s$^{-1}$</td>
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<td>P$_n$</td>
<td>net photosynthetic rate</td>
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<td>rgc</td>
<td>relative ground cover</td>
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<tr>
<td>rgc</td>
<td>relative ground cover</td>
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<td>root length</td>
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<td>root length density</td>
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<tr>
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<td>RLD at zero soil depth</td>
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<tr>
<td>RLDₑff</td>
<td>density of effective roots</td>
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<tr>
<td>RLₑff</td>
<td>effective root length</td>
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<tr>
<td>Rₑm</td>
<td>maintenance respiration</td>
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<td>RMSE</td>
<td>residual mean square error</td>
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<td>Rₙ</td>
<td>net radiation</td>
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<td>S(ψ)</td>
<td>sink term</td>
<td>d⁻¹</td>
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<td>SLA</td>
<td>specific leaf area</td>
<td>m²·g⁻¹</td>
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<tr>
<td>sᵣ</td>
<td>senescence parameter</td>
<td>leaf°C⁻¹·d⁻¹</td>
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<tr>
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<td>specific root length</td>
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<tr>
<td>t</td>
<td>time</td>
<td>h, d</td>
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<tr>
<td>T</td>
<td>Temperature</td>
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<tr>
<td>Tₐcₜ</td>
<td>actual transpiration rate</td>
<td>kg·pl⁻¹·d⁻¹, kg·m⁻²·d⁻¹</td>
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<td>Tₑv</td>
<td>daily mean temperature</td>
<td>°C</td>
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<td>Tₑff</td>
<td>effective temperature</td>
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<td>TLW</td>
<td>translocable leaf dry matter</td>
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<td>Tₑₐ₀</td>
<td>reference temperature</td>
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<td>temperature sum</td>
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<tr>
<td>TS3</td>
<td>temperature sum since vernalisation</td>
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<td>Tₛₑₜₙ</td>
<td>temperature sum since onset of senescence</td>
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<tr>
<td>Tₑₚₑ</td>
<td>transpiration use efficiency</td>
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<tr>
<td>Tₑₜₚₑ</td>
<td>translocated leaf mass</td>
<td>g·pl⁻¹</td>
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### Abbreviations

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>URmax</td>
<td>maximum nitrate uptake rate of the root system</td>
<td>g N m⁻² d⁻¹</td>
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<td>V</td>
<td>vernalisation</td>
<td>-</td>
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<tr>
<td>WC</td>
<td>curd dry weight</td>
<td>g m⁻²</td>
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<td>WL</td>
<td>leaf dry weight</td>
<td>g m⁻²</td>
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<td>WS</td>
<td>stem dry weight</td>
<td>g m⁻²</td>
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<tr>
<td>WS_SH</td>
<td>shoot dry weight</td>
<td>g m⁻²</td>
</tr>
<tr>
<td>WSL</td>
<td>weight of individual leaf</td>
<td>g pl⁻¹</td>
</tr>
<tr>
<td>WT</td>
<td>total plant dry weight</td>
<td>g m⁻²</td>
</tr>
<tr>
<td>WT_TR</td>
<td>weight of tap root</td>
<td>g m⁻²</td>
</tr>
<tr>
<td>WV</td>
<td>vegetative dry weight</td>
<td>g m⁻²</td>
</tr>
<tr>
<td>z</td>
<td>soil depth</td>
<td>cm</td>
</tr>
<tr>
<td>z_r</td>
<td>rooting depth</td>
<td>cm</td>
</tr>
<tr>
<td>α</td>
<td>initial light use efficiency</td>
<td>µg J⁻¹</td>
</tr>
<tr>
<td>θ</td>
<td>volumetric soil water content</td>
<td>cm³ cm⁻³</td>
</tr>
<tr>
<td>τ</td>
<td>leaf conductance for CO₂</td>
<td>m s⁻¹</td>
</tr>
<tr>
<td>λ</td>
<td>latent heat of vaporisation of water</td>
<td>J kg⁻¹</td>
</tr>
</tbody>
</table>

Names and units of auxiliary variables are specified in the text.
References


References


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