Modelling Nitrogen Content and Distribution in Cauliflower (Brassica oleracea L. botrytis)

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A model of nitrogen uptake and distribution is presented which describes these processes in relation to the amount of available soil nitrate and the rate of plant growth. Nitrogen uptake is either sink or source limited. Sink limitation is based on maximum N-concentrations of plant compartments. The N-uptake model is combined with a photosynthesis model based on the productivity-nitrogen relationship at the single-leaf level. The model is parameterized using cauliflower as an example crop. Applied to an independent data set, the combined model was able to predict leaf, stem and inflorescence nitrogen concentrations with correlation coefficients between predicted and simulated values of 0.89, 0.66 and 0.86, respectively. The influence of nitrogen supply and light intensity on leaf nitrate-N could also be predicted with good accuracy ($r^2 = 0.87$). Dry matter production based on the productivity-N relationship and the partitioning into leaf, stem and inflorescence was also reproduced satisfactorily ($r^2 = 0.91, 0.93$ and $0.92$, respectively).

Key words: Brassica oleracea L. botrytis, cauliflower, nitrogen, nitrate, nitrogen supply, nitrogen uptake, nitrogen distribution, model.

INTRODUCTION

There are close positive relationships between nitrogen status and plant growth manifested by the close relationship between photosynthesis and nitrogen at the single-leaf level (Evans, 1983) as well as for relative growth rate of the whole-plant (Ågren, 1985). However, positive effects of high N-contents on productivity are accompanied by increased rates of respiration (Penning de Vries et al., 1974; Byrd et al., 1992; Alt et al., 2000) which may partly offset the benefits of high N-contents on net C-accumulation rates. A mechanistic understanding of the interactions between available nitrogen, plant nitrogen content and plant productivity will help to quantify crop N-demand under specific environmental and agronomic conditions. This knowledge will assist the development of fertilizer recommendations and may thereby help to avoid both the environmental risks of excess rates of fertilization and also the effects of N-deficiency in crops.

A decrease in plant nitrogen content per unit dry weight with increasing plant dry weight has been observed for many crops (Greenwood et al., 1990; Lemaire et al., 1992; Vos et al., 1996) and has been termed the ‘law of progressive decline’ in plant nitrogen concentration during crop growth (LeBot et al., 1998). Greenwood et al. (1990) empirically quantified, for many species, a critical nitrogen concentration, $n_{crit}$, required for maximum growth rate. A comparison of the plant nitrogen concentrations during crop growth with $n_{crit}$ may be used to identify nitrogen deficiency in plants (LeBot et al., 1998). This concept of critical nitrogen concentrations was also used by Greenwood et al. (1991) to predict crop growth under optimal and sub-optimal N-supply. However, it is based on plant weight as the only causal factor determining the change of optimal plant nitrogen concentrations during growth. It does not take into account possible effects of other environmental and agronomic conditions on $n_{crit}$. Such effects can, for example, be expected from the acclimatization of leaf nitrogen content to a changing radiation environment (Hirose and Werger, 1987). The $n_{crit}$ concept also neglects negative effects of luxury N-consumption on crop productivity, caused by an enhanced protein-turnover and, thereby, increased maintenance respiration.

In a previous paper (Alt et al., 2000), functional relationships between the fundamental physiological processes determining productivity, photosynthesis and respiration, and nitrogen content were established. These relationships were then used in a model-based analysis to quantify effects of given plant N-contents on crop productivity. However, prediction of crop nitrogen demand under certain environmental and agronomic conditions additionally requires prediction of plant nitrogen content and distribution during growth. The objective of the present work is, therefore, to elaborate relationships between nitrogen contents of cauliflower organs and environmental as well as morphological parameters, and to use these relationships in combination with the productivity—nitrogen-relationships presented in Alt et al. (2000) to predict nitrogen demand and to estimate crop productivity under different N-supplies.

MODEL

This study assumes that even under optimal N-supply daily nitrogen uptake by the plant is limited, and that this can be characterized by the maximum nitrogen concentrations of plant tissues and organs as they change...
with time. This is referred to as the plant's physiological upper limit or as the sink limitation of N-uptake. Source limited N-uptake due to restricted diffusion and mass flow to the roots, even under conditions of optimal water supply, is assumed to be related to the average NO₃-N concentration in the soil exploited by the roots ($N_{min}^{soil}$, kg ha⁻¹) (see Appendix for full list of symbols). A detailed mechanistic analysis of soil nitrate availability, taking into account the tempo-spatial variation of root length density (Kage et al., 1997), as well as of soil water and soil nitrate content such as in the approaches presented by De Willigen and Van Nordwijk (1987) and Kage (1997), is beyond the scope of this paper. For the sake of simplicity, and in a first-step analysis, it is postulated that source limitation can be expressed by a factor $f_{soil}$ ranging from one to the asymptotic value of zero as the available amount of nitrate in the soil decreases:

$$f_{soil} = \frac{N_{min}}{K_{Nmin} + N_{min}}$$

(1)

where $K_{Nmin}$ (kgN ha⁻¹) is the parameter influencing the curvature of the rectangular hyperbola. At a value of $N_{min}$ equal to $K_{Nmin}$ the value of $f_{soil}$ is 0.5. Thus, the amount of nitrogen taken up and accumulated in the leaves, $N_{leaf}$, is assumed to be the maximum N-content corrected for source limitation, i.e.

$$N_{leaf} = n_{max,leaf}W_{leaf}f_{soil}(N_{min})$$

(2)

where $n_{max,leaf}$ denotes the maximal N-concentration of the foliage under non-limiting N-supply and $W_{leaf}$ is leaf mass. Due to senescence and self-shading, nitrogen translocation and remobilization within the cauliflower canopy lead to a decreasing leaf N-concentration with increasing leaf area index (LAI) even under optimal N-supply, assuming continuously increasing leaf area and leaf dry matter until harvest. Thus, $n_{max,leaf}$ may be expressed as a function of LAI:

$$n_{max,leaf} = -m_{1}LA_{i} + b_{1}$$

(3)

where $-m_{1}$ denotes the decrease in $n_{max,leaf}$ with LAI under non-limiting N-supply, and $b_{1}$ is the physiological upper limit of the nitrogen concentration of well fertilized transplants.

The amount of nitrogen taken up per unit of time, $dN_{leaf}/dt$, is derived from eqn (2):

$$\frac{dN_{leaf}}{dt} = n_{max,leaf}f_{soil}(N_{min}) \frac{dW_{leaf}}{dt} + n_{max,leaf}W_{leaf} \frac{df_{soil}(N_{min})}{dt}$$

(4A)

where $dW_{leaf}/dt$ denotes the increase in leaf dry matter. Since $f_{soil}$ is assumed to be a continuous function depending on $N_{min}$ the last term in eqn (4A) is of major importance whenever nitrogen supply in the soil changes very rapidly with time. Since this is not the case in the present study the term will be neglected in what follows. N-accumulation in stem, root and inflorescence has the same form as the first term in eqn (4A) with N-concentrations in the stem, root and inflorescence, $n_{max,stem}$, $n_{max,root}$ and $n_{max,in}$ respectively:

$$\frac{dN_{stem}}{dt} = n_{max,stem}f_{soil}(N_{min}) \frac{dW_{stem}}{dt}$$

(4B)

$$\frac{dN_{root}}{dt} = n_{max,root}f_{soil}(N_{min}) \frac{dW_{root}}{dt}$$

(4C)

$$\frac{dN_{in}}{dt} = (n_{max,in}f_{soil}(N_{min}) + n_{red}) \frac{dW_{in}}{dt}$$

(4D)

The additional parameter $n_{red}$ in eqn (4D) represents nitrogen redistribution from vegetative into generative organs as observed for many field crops (Booij et al., 1997). All vegetative organs are supposed to contribute to the rate of nitrogen translocation, i.e. $n_{red}(dW_{in}/dt)$ [eqn (4D)], according to their proportion in the total amount of nitrogen stored in leaves, stem and root. The fraction translocated, e.g. from leaves, is given by $n_{red}(dW_{in}/dt)N_{leaf}/(N_{leaf} + N_{stem} + N_{root})$, which must be subtracted from eqn (4A) to give the correct total change in leaf N-content:

$$\frac{dN_{leaf}}{dt} = n_{max,leaf}f_{soil}(N_{min}) \frac{dW_{leaf}}{dt} - n_{red} \frac{dW_{in}}{dt} \frac{N_{leaf}}{N_{leaf} + N_{stem} + N_{root}}$$

(5)

It is assumed that 1% of the inflorescence nitrogen concentration results from N-redistribution within the plant, i.e. the value of $n_{red}$ is set to 0.01. Thus, a significant amount (about 1/3) of the total of N in the inflorescence is assumed to result from N-redistribution in the plant.

The profile of protein-nitrogen in the canopy has been examined in detail (Alt et al., 2000), based on the concept of optimal canopy N-distribution with respect to daily growth rate. The protein-N content per unit leaf area was observed to be more evenly distributed within the canopy than predicted by the optimized distribution which follows the life profile in the canopy closely. It is, therefore, assumed here that a linear relationship exists between nitrogen content per unit leaf area, $n_{a}$, and cumulative leaf area index, $L_{c}$, as determined from the top of the canopy. This relationship was also found in sunflower (Bang et al., 1997). Thus:

$$n_{a} = -m_{2}L_{c} + n_{a,\text{max}}$$

(6)

where $n_{a,\text{max}}$ is the maximum N-content at the top of the canopy and $-m_{2}$ denotes the decline with $L_{c}$.

Nitrogen contents based on dry weight and leaf area are inter-converted by using the specific leaf area, $sla$, which depends on the light environment during leaf growth (Björkman, 1981). The $sla$ of growing leaves is assumed to be a function of the daily total of photosynthetic photon flux (PPF) averaged over previous days, $I_{ave}$:

$$sla = \text{function}(I_{ave})$$

(7)
The nitrate-N concentrations in leaves depend on the light environment (Marschner, 1984). Therefore, the maximum nitrate-N concentration of the compartment leaf, \( n_{\text{max,NO}_3-N} \), is assumed to increase with increasing leaf area index due to decreasing average light intensity in the canopy. Thus, under non-limiting N-supply

\[
    n_{\text{max,NO}_3-N} = \frac{I_{\text{rel}}}{I_{\text{ave}}} \text{function(LAI)} \quad (8A)
\]

where the quotient \( I_{\text{rel}}/I_{\text{ave}} \) relates the average light intensity above the canopy to a reference value. This means that the function dependent on LAI in eqn (7A) is parameterized under a certain light condition \( (I_{\text{rel}}) \) and then adapted to different conditions \( (I_{\text{ave}}) \) by multiplying by the quotient. To account for a decrease in leaf nitrate concentrations, \( n_{\text{NO}_3-N} \), due to limiting N-supply (Marschner, 1984; Gardner and Roth, 1990) it is assumed that the change in the nitrate concentration of the plant correlates linearly with N-supply (Gardner and Roth, 1990; Bellaloui and Pilbeam, 1991; Burns, 1994) or, here, \( f_{\text{soil}} \) as the determinant of source limitation. This assumption predicts that the nitrate concentration of the plant itself, \( n_{\text{NO}_3-N} \), is proportional to \( (f_{\text{soil}})^2 \) rather than \( f_{\text{soil}} \):

\[
    n_{\text{NO}_3-N} = n_{\text{max,NO}_3-N} f_{\text{soil}}^2 (N_{\text{min}}) \quad (8B)
\]

This expression results in an asymptotic dependency of \( n_{\text{NO}_3-N} \) on N-supply.

**Cauliflower development**

Leaf development is described in the same way as described by Kage and Stützel (1999); visible leaf number is an expo-linear function of the temperature sum, with base temperature zero, having the two parameters \( k_1 \) and \( k_2 \). Parameter values were determined from an experiment in 1997, independent of the one described in this study, for the cultivar ‘Fremont’ to be \( k_1 = 0.0032 \) (°C)−1 and \( k_2 = 0.0350 \) (°C)−1 (unpubl. res.). The vernalization process was calculated according to Wiebe (1972) using a daily vernalization rate, \( dV/dt \), as a function of mean daily temperature, \( T \):

\[
    \frac{dV}{dt} = \begin{cases} 
    0 & T \leq T_1 \\
    v_{\text{max}} \left(1 - \frac{T_2 - T}{T_2 - T_1}\right) & T_1 < T \leq T_2 \\
    v_{\text{max}} \left(1 - \frac{T - T_3}{T_4 - T_3}\right) & T_2 < T \leq T_3 \\
    v_{\text{max}} \left(1 - \frac{T - T_4}{T_4 - T_3}\right) & T_3 < T \leq T_4 \\
    0 & T > T_4 
\end{cases} \quad (9)
\]

where \( v_{\text{max}} \) is the maximum vernalization rate set to 0.11 d−1. The four temperatures, \( T_1 \) to \( T_4 \), are cultivar dependent and assumed to be 0, 10, 13 and 28°C for ‘Fremont’ (Wiebe, pers. comm.). The vernalization phase is completed when the sum of daily vernalization rates is one.

**Photosynthesis**

Photosynthesis was calculated from leaf area and protein-nitrogen content and distribution within the canopy, as well as from the light and temperature environment as described in Alt et al. (2000). The instantaneous rate of whole-plant net CO₂-uptake, \( P_{\text{plant}} \), for a certain light environment, \( I \), is the integral of single-leaf photosynthesis on a leaf area basis, \( P_{\text{g}} \), over the leaf area, \( A_1 \), with whole-plant respiration, \( R_{\text{plant}} \), subtracted:

\[
    P_{\text{plant}} = \int_0^{A_1} dP_{\text{g}}(I, P_m) - R_{\text{plant}} \quad (10)
\]

\( P_{\text{g}} \) is given by the non-rectangular hyperbola,

\[
    P_{\text{g}} = \frac{zI + P_m - \sqrt{(zI + P_m)^2 - 4\Theta zIP_m}}{2\Theta} \quad (11)
\]

where \( \alpha \) and \( \Theta \) are two parameters describing the initial slope and curvature of the response curve, respectively. Their values were determined to be \( \alpha = 0.056 \) μmol CO₂ mmol⁻¹ PPF and \( \Theta = 0.899 \) (Alt, 1999). The single-leaf gross photosynthetic capacity, \( P_m \) (μmol CO₂ m⁻² s⁻¹), varies within the canopy according to the N-content per unit leaf area, \( n_a \) (g N m⁻²) (Alt et al., 2000):

\[
    P_m = 12.82 \times n_a - 5.07 \quad (12)
\]

\( R_{\text{plant}} \) (mg CO₂ per plant min⁻¹) has contributions from maintenance respiration, temperature, \( T \) (°C), dependent and associated with the amount of protein-N in plant dry matter, \( N_{\text{P,plant}} \) (g protein-N per plant), and from growth respiration, depending on the increase in dry mass per day, \( dW_{\text{plant}}/dt \) (g d. wt per plant d⁻¹) (Alt et al. 2000):

\[
    R_{\text{plant}} = 1.80 \times N_{\text{P,plant}} \times 2^{T-20/10} + 0.40 \times \frac{dW_{\text{plant}}}{dt} \quad (13)
\]

Respiration per unit leaf area, \( R_{\text{plant,a}} = R_{\text{plant}}/A_1 \), during the night is assumed to decrease linearly with the duration of darkness, \( t_n(h) \) (Alt et al., 2000):

\[
    R_{\text{plant,a}}(t_n) = R_{\text{plant,a}}(0) - (0.038 \times R_{\text{plant,a}}(0) - 0.042) \times t_n \quad (14)
\]

where the rate of decline depends on the initial respiration at the beginning of the night, \( R_{\text{plant,a}}(0) \), which is determined by eqn (13) divided by \( A_1 \).

**Light environment**

The diurnal course of the photosynthetic photon flux (PPF) above the canopy, \( I_0(t) \), with time, \( t \), is assumed to follow a sine-squared function:

\[
    I_0(t) = I_{\text{noon}} \sin^2\left(\frac{t}{d}\right) \quad (15)
\]

where \( d \) denotes the period between sun rise and set, and \( I_{\text{noon}} \) is the maximum PPF at solar noon calculated from the
daily total PPF, $I_{tot}$, by $I_{noon} = 2I_{tot}d^{-1}$. $I_{tot}$ is determined from the daily global radiation using a factor of 0.5. The light profile within the canopy is calculated by separating $I_0$ into diffuse, $I_{0,df}$, and direct, $I_{0,dr}$, components based on Spitters (1986). The profiles of the diffuse and direct component at a certain depth in the canopy expressed as cumulative leaf area index, $l_c$, can be calculated as:

\[
I_{df}(l_c) = I_{0,df}e^{-k_{df} \times l_c} \quad (16A)
\]
\[
I_{dr}(l_c) = I_{0,dr}e^{-(1-\sigma) \times k_{bl} \times l_c} \quad (16B)
\]

The values of the extinction coefficients for an approximated spherical leaf angle distribution are $k_{df} = 0.8(1-\sigma)^{0.5}$ and $k_{bl} = 0.5 \sin \beta^{-1}$ (Goudriaan, 1977) where $\sigma$ is the scattering coefficient, approximately 0.2, and $\beta$ the solar elevation angle. $I_{df}$ splits into diffuse, $I_{dr,df}$ and direct, $I_{dr,dr}$, components:

\[
I_{dr,df}(l_c) = I_{dr}(l_c) - I_{dr,dr}(l_c) \quad (17)
\]

The direct part is given as the profile of light in a non-scattering canopy:

\[
I_{dr,dr}(l_c) = I_{0,dr}e^{-k_{bl} \times l_c} \quad (18)
\]

The relevant light intensity, $I_{sh}$, absorbed by the shaded leaf area at canopy height $l_c$ is given by Spitters (1986):

\[
I_{sh}(l_c) = k_{df}I_{df}(l_c) + k_{bl}I_{dr,dr}(l_c) \quad (19)
\]

The sunlit leaf area at canopy height $l_c$ absorbs diffuse and non-scattered direct radiation:

\[
I_{df}(l_c) = I_{sh}(l_c) + (1-\sigma)k_{bl}I_{0,dr} \quad (20)
\]

The fractions of sunlit leaf area, $f_{sl}$, and shaded leaf area, $f_{sh}$, at canopy height $l_c$ are calculated according to the direct beam profile:

\[
f_{sl}(l_c) = e^{-k_{bl} \times l_c} \quad (21A)
\]
\[
f_{sh}(l_c) = 1 - f_{sl}(l_c) \quad (21B)
\]

The photosynthetic rate at canopy height $l_c$, $P_g(l_c)$ [eqn (11)], is the weighted sum of shaded and sunlit contributions:

\[
P_g(l_c) = f_{sl}(l_c)P(I_{sl}(l_c)) + f_{sh}(l_c)P(I_{sh}(l_c)) \quad (22)
\]

Dry matter partitioning

The increase in plant dry matter, $dW_{plant}/dt$, is the net CO$_2$-uptake $P_{plant}$ [eqn (10)] multiplied by the CO$_2$–CH$_2$O-conversion factor of 30/44, and is partitioned between stem, leaf and inflorescence according to Alt (1999). After vernalization has been completed, reproductive growth has priority over vegetative growth in the model in order to satisfy the potential sink capacity of the inflorescence which is the product of its dry matter, $W_{in}$, and its specific growth rate, $gr_{in}$ (d$^{-1}$). The dry matter increase of the inflorescence is limited by its sink capacity at the beginning and, later on, by total available assimilates:

\[
\frac{dW_{in}}{dt} = \min\left(1, \left(1 + f_{stem}\frac{dW_{plant}}{dt}\right)r_{gr_{in}}W_{in}\right) \quad (23)
\]

where $f_{stem}$ was experimentally determined to be 0.15 (Alt, 1999). Specific inflorescence growth rate, $r_{gr_{in}}$, is a function of the nitrogen content per unit leaf area, $n_{area}$, at the time of inflorescence initiation:

\[
r_{gr_{in}} = 0.18 \times n_{area} \quad (24)
\]

The growth rate of leaf dry matter is given by:

\[
\frac{dW_{leaf}}{dt} = \frac{1}{1 + a \times sla + f_{root}}\left(\frac{dW_{plant}}{dt} - (1 + f_{stem})\frac{dW_{in}}{dt}\right) \quad (25)
\]

where $a$ was determined from experiments to be 12.93 g stem d.wt m$^{-2}$ leaf area. The term sla denotes the specific leaf area of the newly produced leaf dry matter, and $f_{root}$ is the fraction of root growth rate to leaf growth rate. Thus, stem and root growth rates are given by:

\[
\frac{dW_{stem}}{dt} = a \times sla \times \frac{dW_{leaf}}{dt} + f_{stem}\frac{dW_{in}}{dt} \quad (26)
\]
\[
\frac{dW_{root}}{dt} = f_{root}\frac{dW_{in}}{dt} \quad (27)
\]

The partitioning coefficient $f_{root}$ is assumed to vary with nitrogen availability, $f_{root} = 0.15/f_{soil}$. The minimum value of 0.15 for $f_{root}$ was determined from a greenhouse experiment in 1997 (Alt et al., 2000) where cauliflower was cultivated in nutrient solution containing 145 mg N l$^{-1}$. A similar hyperbolic dependency of $f_{root}$ on N-supply was found for seedlings of different rice cultivars where $f_{root}$ varied from about 0.4 at very low, to about 0.16 at high N-supply (Cook and Evans, 1983).

**MATERIALS AND METHODS**

Two independent field experiments with cauliflower (Brassica oleracea L. convar. botrytis var. botrytis L. ‘Fremont’) were conducted on the institute’s experimental farm located 15 km south of Hannover, Germany on a typical hapludalf soil derived from loess. The 1996 experiment was used for derivation of model parameters and the 1997 experiment for model evaluation. Seeds were sown in 4 cm$^3$ peat cubes. When the plants had developed an average of 3.25 and 3.5 visible leaves on June 18 and July 9 in 1996 and 1997, respectively, they were transplanted into the field. The initial dry weight at transplanting was 0.34 g in 1996 and 0.39 g per plant in 1997. Plant spacing was 0.60 m by 0.48 m giving an average density of an average of 3.25 and 3.5 visible leaves on June 18 and July 9 in 1996 and 1997, respectively, they were transplanted into the field. The initial dry weight at transplanting was 0.34 g in 1996 and 0.39 g per plant in 1997. Plant spacing was 0.60 m by 0.48 m giving an average density of 3-5 plants m$^{-2}$. Before planting, chlorofenviphos (Birlane) and molybdenum sulphate were applied prophylactically. Weeds were controlled by hand. Oxydemeton-methyl (250 g l$^{-1}$ Metasystox) and later parathion (500 g l$^{-1}$ E605 forte) were sprayed for pest control once in both years.
Experimental design

Experiments were laid out as split plots with two different light environments (unshaded, I1 and shaded, I2) as main plots and four different nitrogen-fertilizer levels as sub-plots in four replications. Shaded main plots were covered with a shading net absorbing 40% of the photosynthetic photon-flux (PPF) placed 1 m above the ground, either immediately after transplanting (1996) or 2 weeks after transplanting (1997). Nitrogen fertilizer was given as ammonium nitrate at the time of transplanting to achieve 0, 150, 300 and 450 kg N ha$^{-1}$. In both years, soil nitrate content was 10–15 kg ha$^{-1}$ at a depth of 0–60 cm and was allowed for in the applications: N0–N3 denote the 0–450 kg N ha$^{-1}$ fertilizer applications.

Plant growth analysis

At three harvests in 1996, 28, 49 and 69 d after transplanting, and at four harvests in 1997, 26, 47, 68 and 82 d after transplanting, six adjacent plants per plot were collected and separated into stem, leaves (including petioles) and inflorescence. Stems were cut 1 cm below field level and at the onset of inflorescence development. The foliage was further subdivided into groups of five consecutive leaves (1–5, 6–10, etc.). The leaf number corresponded to leaf appearance. Leaf area of every leaf group was measured with a LICOR 3100 leaf area meter (LI-COR Inc., Lincoln, NE, USA). Samples of all plant fractions were oven dried and weighed. Total nitrogen and nitrate nitrogen concentration in dry matter were determined by the micro-Kjeldahl method and a nitrate sensitive electrode, respectively. Plant dimensions (height and width) and curd diameter were measured at all harvests.

Net mineralization

The amount of nitrogen mineralized during the growth period was determined from the N-budget of the N0-treatments as the sum of the measured amount of nitrogen in the above-ground plant parts and $N_{\text{min}}$ from 0–120 cm depth at final harvest after subtracting $N_{\text{min}}$ at transplanting. The average daily mineralization rate was calculated to be 0.72 kg N ha$^{-1}$ d$^{-1}$ and 0.67 kg N ha$^{-1}$ d$^{-1}$ in 1996 and 1997, respectively. This simplification, which was assumed to be sufficiently accurate under the conditions of the experiments, neglects temperature effects on mineralization during the rest of the season as well as the solute nitrate movement in the soil layers.

Model implementation and statistics

The dynamic model of development, dry matter production and partitioning as well as nitrogen uptake and distribution described above was programmed using the modelling environment ModelMaker (Walker, 1997). The integration was performed by the Euler-algorithm with a time step of 1 h. A non-linear least squares regression analysis is implemented in ModelMaker using a Marquardt optimization algorithm (Marquardt, 1963). Together with the estimate of the parameter value, the software gives the value of the square root of the diagonal elements of the covariance matrix. Multiplying this value with the square root of the mean square of the residual yields the asymptotic standard error of the coefficient (Gallant, 1987). The non-linear least squares regression analysis implemented in ModelMaker was used to estimate the parameter $K_{\text{cmin}}$ [eqn (1)]. All statistical analyses, if not stated otherwise, were carried out using the procedures NLIN and REG of the SAS software package (SAS Institute, 1988).

RESULTS

Parameterization experiment, 1996

When N-supply was non-limiting, as could be assumed for the N3-treatments at harvests 1 and 2, the leaf nitrogen concentration declined during growth independent of light environment (Table 1). The same treatments caused an increase in nitrate-N concentration with increasing leaf area index during growth. The average daily total PAR of the non-shaded treatment during the entire period of crop growth, $I_{\text{ref}} = 7.8$ MJ m$^{-2}$ d$^{-1}$, was used as the reference value in eqn (8). The nitrate-N contents of the shaded treatment were corrected for light environment by multiplying by a factor of 0.6, characterizing the transmission of the shading net. The linear regression equations were used to parameterize eqns (3) and (8B).

Protein-nitrogen per unit leaf area, $n_a$, decreased linearly with increasing depth in the canopy for all treatments as shown for the final harvest in Fig. 1A. Thus, the protein-nitrogen profile can be described by:

$$n_a(l_c) = n_{a,\text{max}} \left(1 - m_n a \frac{l_c}{LAI}\right) \quad (28A)$$

where $m_n$ describes the slope of the linear decline and $l_c$ is the cumulative leaf area index as determined from the top of the canopy. The maximum value of $n_a$ at the top of the canopy, $n_{a,\text{max}}$, is then given by the total amount of leaf protein-N, $N_{\text{P,leaf}}$, by integrating eqn (28A) over LAI:

$$n_{a,\text{max}} = \frac{N_{\text{P,leaf}}}{\text{LAI}\left(1 - \frac{m_n a}{2}\right)} \quad (28B)$$

<table>
<thead>
<tr>
<th>Organ</th>
<th>$n_{\text{max,organ}}$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf-N</td>
<td>$-0.39(\pm 0.05)\text{LAI} + 5.80(\pm 0.12)$</td>
<td>0.96</td>
</tr>
<tr>
<td>Leaf-NO$_3$-N</td>
<td>$0.08(\pm 0.02)\text{LAI} + 4.40(\pm 0.04)$</td>
<td>0.87</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>$-6.38(\pm 2.29)W_n - 0.10(\pm 0.02)$</td>
<td>0.96</td>
</tr>
</tbody>
</table>

TABLE 1. Regression equations fitted to the experimental data for maximum leaf N-concentration, $n_{\text{max,leaf}}$, and nitrate-N concentration, $n_{\text{max,NO3-N}}$, vs. leaf area index, LAI, and maximum inflorescence N-concentration vs. dry mass, $W_n$, under non-limiting N-supply in the I2-N3 (450 kg N ha$^{-1}$) treatment and first two harvests of I1-N3-treatment; experiment 1996.
The parameter $m_{na}$ was determined by non-linear least-squares regression analysis of measured and calculated protein-nitrogen profiles for all harvests and treatments in 1996. Its value was estimated to be $m_{na} = 0.53 \pm 0.02$. The observed N-profiles for all treatments and harvests were well described by the same parameter value of $m_{na}$ (Fig. 1B), which was used to parameterize eqn (5).

The maximum stem nitrogen-concentration, $n_{max,stem}$, was determined from the first harvest of the I2-N3-treatment to be 3.4%. The maximum root N-concentration was taken from an independent cauliflower experiment to be $n_{max,root} = 2.5\%$ (unpubl. res.). The maximum inflorescence N-concentration, $n_{max,in}$, was found to be a function of the inflorescence dry mass $W_{in}$ (Table 1), parameterizing eqns (4B)–(4D). Specific leaf area was related to the daily amount of PPF incident on the canopy and averaged over the period between harvests for all treatments (Fig. 2). The regression line was used to parameterize eqn (6). There were no statistically significant differences between the specific leaf areas of the N-treatments for the same light environment at the first two harvests.

The model parameter associated with source limiting processes is $f_{soil}$ [eqns (5) and (8)]. Since the general behaviour of the dependency of $f_{soil}$ on $N_{min}$ is assumed to be smooth, it can be studied by comparing leaf-N contents for the different N-treatments. Maximum nitrogen contents per unit leaf mass as well as per unit leaf area declined with decreasing N-supply for all harvests (Fig. 3). The relationship between $f_{soil}$ and $N_{min}$ for each harvest is described well by a non-rectangular hyperbola [eqn (1)]. The parameter $K_{Nmin}$ was determined by non-linear least-squares regression analysis of measured and simulated leaf, stem and inflorescence N-concentrations of all harvests and treatments in 1996. Its value was estimated to be $K_{Nmin} = 38.5 \pm 3.0$ kg N ha$^{-1}$, parameterizing eqn (1).

The above-ground dry matter assimilation of all treatments was well simulated by the model for both years (Fig. 4). Unfortunately, no data on leaf dry weights and leaf area were obtained for the final harvest of the I1-N2- and I1-N3-treatments. Although the fertilized N-treatments at the same light environment showed similar dry matter production, leaf nitrogen contents as well as nitrate-N concentrations differed in early growth (Fig. 5). The leaf nitrate-nitrogen concentrations increased during growth for most of the N-fertilized treatments due to the decreasing average light intensity within the canopy. Limiting N-supply caused NO$_3$-N-concentrations to decline earlier and faster than leaf-N concentrations as found in cabbage (Burns, 1994). Nitrogen concentrations of stem and inflorescence differed similarly between treatments (Table 2) and also declined for all treatments during growth.
The model including model parameters derived above from the experiment in 1996 was evaluated with data from an independent field experiment in 1997 (Table 2). The leaf nitrogen-contents again showed differences between treatments soon after transplanting. The leaf nitrate-nitrogen contents of the evaluation experiment were higher due to a reduction in average daily PPF of 15% in 1997. The agreement of simulated and measured N-contents is equally high for shaded and non-shaded treatments. The model performance is of similar quality for the evaluation experiment as for the parameterization experiment. Nitrogen

**Fig. 3.** Leaf area based (A) and mass based leaf nitrogen contents (B) of youngest leaf group vs. $N_{\text{min}}$ from 0–120 cm for first (○), second (□) and final (△) harvests of non-shaded treatments; experiment 1996.

**Fig. 4.** Measured (symbols) vs. simulated (lines) above-ground dry weight, $W_p$, for all harvests; experiments 1996 (A,B) and 1997 (C,D); symbols as in Fig. 1.
concentrations of inflorescence and stem were similar to the data from 1996. A decline in N-concentrations was observed for all treatments and plant compartments during growth. The model predictability of the above-ground dry matter production and partitioning is compared for both experiments in Table 3.

### Table 2. Results of the regression analyses* of measured vs. simulated N-concentrations of cauliflower organs in both experiments

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Organ</th>
<th>Slope (±s.e.)</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td>Leaf-N</td>
<td>1.04 (±0.02)</td>
<td>0.89</td>
</tr>
<tr>
<td>1996</td>
<td>Leaf-NO$_3$-N</td>
<td>1.09 (±0.04)</td>
<td>0.91</td>
</tr>
<tr>
<td>1996</td>
<td>Inflorescence</td>
<td>0.97 (±0.04)</td>
<td>0.71</td>
</tr>
<tr>
<td>1996</td>
<td>Stem</td>
<td>0.95 (±0.02)</td>
<td>0.77</td>
</tr>
<tr>
<td>1997</td>
<td>Leaf-N</td>
<td>0.98 (±0.01)</td>
<td>0.89</td>
</tr>
<tr>
<td>1997</td>
<td>Leaf-NO$_3$-N</td>
<td>1.02 (±0.02)</td>
<td>0.87</td>
</tr>
<tr>
<td>1997</td>
<td>Inflorescence</td>
<td>0.96 (±0.01)</td>
<td>0.66</td>
</tr>
<tr>
<td>1997</td>
<td>Stem</td>
<td>0.99 (±0.02)</td>
<td>0.86</td>
</tr>
</tbody>
</table>

* In all cases intercepts were not significantly different from zero.

### Table 3. Results of the regression analyses* of measured vs. simulated dry matter of cauliflower organs and leaf area in both experiments

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Organ</th>
<th>Slope (±s.e.)</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td>Above-ground total</td>
<td>1.05 (±0.03)</td>
<td>0.96</td>
</tr>
<tr>
<td>1996</td>
<td>Leaf</td>
<td>0.90 (±0.02)</td>
<td>0.98</td>
</tr>
<tr>
<td>1996</td>
<td>Stem</td>
<td>0.93 (±0.03)</td>
<td>0.94</td>
</tr>
<tr>
<td>1996</td>
<td>Inflorescence</td>
<td>1.11 (±0.05)</td>
<td>0.95</td>
</tr>
<tr>
<td>1996</td>
<td>Leaf area</td>
<td>0.82 (±0.03)</td>
<td>0.91</td>
</tr>
<tr>
<td>1997</td>
<td>Above-ground total</td>
<td>1.03 (±0.02)</td>
<td>0.96</td>
</tr>
<tr>
<td>1997</td>
<td>Leaf</td>
<td>1.05 (±0.04)</td>
<td>0.91</td>
</tr>
<tr>
<td>1997</td>
<td>Stem</td>
<td>1.05 (±0.03)</td>
<td>0.93</td>
</tr>
<tr>
<td>1997</td>
<td>Inflorescence</td>
<td>1.01 (±0.05)</td>
<td>0.92</td>
</tr>
<tr>
<td>1997</td>
<td>Leaf area</td>
<td>1.02 (±0.03)</td>
<td>0.94</td>
</tr>
</tbody>
</table>

* In all cases intercepts were not significantly different from zero.

**DISCUSSION**

The average leaf nitrogen concentration under conditions close to non-limiting N-supply was independent of light environment (Fig. 1) and declined during growth (Fig. 5). This was attributed to a maximum leaf N-concentration as a physiological upper limit that was not maintained during...
leaf area growth, possibly due to senescence and self-shading, both increasing with increasing leaf area index. The decline in N-concentration during growth has been found in many species and has been termed the ‘law of progressive decline’ (LeBot et al., 1998). Such a decline of N concentrations during growth of plants has also been explained by an increasing proportion of structural components with lower N content (Caloin and Yu, 1984). The small effect of shading on relative protein contents (Fig. 1) indicates that this was possibly one of the factors causing the observed decrease of nitrogen contents over time in our experiments.

The ratio of protein to nitrogen per unit leaf area declined linearly with increasing depth in the canopy, as also found for sunflower (Bange et al., 1997). Theoretical considerations predict a N-distribution close to the light profile (Charles-Edwards et al., 1987). This discrepancy, also found for soybean (Sinclair and Shiraishi, 1993) and lucerne (Evans, 1993), may be partly due to additional energy consumption required for N-remobilization, which offset possible benefits of N-translocation (Field, 1983). However, the observed decline of N content within the canopy may again be the consequence of increasing proportions of structural leaf components of older leaves situated deeper in the canopy.

The specific leaf area of newly produced tissue was related to the average light intensity above the canopy (Fig. 2), which is closely related to the PPF incident on growing leaves at the top of the canopy. Although the changed wind conditions may have contributed to the observed differences in sla between shaded and non-shaded light environments (Retuerto and Woodward, 1992), they have not been taken into account. Their influence may be regarded to be of minor importance because the dependence of sla on PPF successfully described leaf area development for all treatments.

The reduction in N-uptake was well described by the factor $f_{soil}$, which is hyperbolically dependent on the amount of soil nitrate. The factor $f_{soil}$ associated with N-uptake by the total root system can be compared to single-root influx rates which are widely accepted to be described by Michaelis–Menten kinetics (Peuke and Kaiser, 1996). The value of $K_{\text{Nmin}}$ found in this study exceeds the values of the Michaelis–Menten constants obtained from nutrient solution experiments by one or two orders of magnitude (Peuke and Kaiser, 1996). This suggests that $K_{\text{Nmin}}$ depicts mainly effects of a limited nitrate transport from the bulk soil to the root surface which was found for faba bean (Kage, 1997).

The nitrate-nitrogen contents in leaves were related to light environment and nitrogen supply. They were affected first by limiting N-supply and declined earlier than leaf protein-N contents. Although dry matter production was similar for the N-fertilized treatments in the same light environment in both years (Fig. 4), nitrogen-concentrations differed substantially soon after transplanting (1996 data: Fig. 5A and B). Both of these experimental findings, also found for many field crops (Booij et al., 1996; Van den Boogaard and Thorup-Kristensen, 1997), were simulated from the model. This was achieved by increased photosynthetic capacity of the plant due to increased leaf protein-nitrogen content, which was offset by increased maintenance respiration due to enhanced protein-turnover under the given light environments.

In conclusion, the model presented was able to predict nitrogen uptake and distribution in cauliflower from plant growth rate, available soil nitrate-nitrogen content and radiation environment. The observed nitrogen concentrations declined in all plant organs during growth. The maximum leaf nitrogen content under non-limiting N-supply was independent of light environment. Although decreased leaf nitrogen concentrations due to limiting N-supply were observed soon after transplanting, dry matter production was affected later and the effect of N was smaller than on N-concentration. The increased photosynthetic capacity of plants due to increased leaf protein-nitrogen contents was mainly offset by increased maintenance respiration due to enhanced protein-turnover.

ACKNOWLEDGEMENTS

We thank Dr A. van der Werf for helpful comments on an earlier version of the manuscript. The technical assistance of I. Lippert and E. Diedrich is gratefully acknowledged.

LITERATURE CITED


<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Unit</th>
</tr>
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<tbody>
<tr>
<td>(a)</td>
<td>Increase in stem dry matter per increase in leaf area</td>
<td>g m(^{-2})</td>
</tr>
<tr>
<td>(A_i)</td>
<td>Leaf area</td>
<td>m(^2) per plant</td>
</tr>
<tr>
<td>(d)</td>
<td>Period between sunrise and sunset</td>
<td>h</td>
</tr>
<tr>
<td>(\text{dV/dt})</td>
<td>Daily rate of vernalization</td>
<td>d(^{-1})</td>
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<tr>
<td>(f_{\text{root}})</td>
<td>Root partitioning coefficient</td>
<td>–</td>
</tr>
<tr>
<td>(f_{\text{sh}, \text{slh}})</td>
<td>Fraction of sunlit and of shaded leaf area</td>
<td>–</td>
</tr>
<tr>
<td>(f_{\text{stem}})</td>
<td>Stem partitioning coefficient</td>
<td>–</td>
</tr>
<tr>
<td>(k_{\text{Bol,kdf}})</td>
<td>Light extinction coefficient of direct, diffuse radiation</td>
<td>m(^2) m(^{-2})</td>
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<tr>
<td>(K_{\text{Nmin}})</td>
<td>Curvature factor of the (N_{\text{min}})-response curve</td>
<td>kg N ha(^{-1})</td>
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<td>(\text{LAI})</td>
<td>Leaf area index</td>
<td>m(^2) m(^{-2})</td>
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<td>(I_{\text{c}})</td>
<td>Cumulative leaf area index</td>
<td>m(^2) m(^{-2})</td>
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<td>(m_{\text{na}})</td>
<td>Protein-N content per unit leaf area</td>
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<tr>
<td>(n_{\text{na}})</td>
<td>Maximum protein-N content per unit leaf area</td>
<td>g N m(^{-2})</td>
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<td>(n_{\text{N, \text{NO3-N}}})</td>
<td>Maximum N-content</td>
<td>g N g(^{-1})</td>
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<td>Leaf NO(_3)-N-content</td>
<td>g NO(_3)-N g(^{-1})</td>
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<td>g protein-N per plant</td>
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<td>(n_{\text{red}})</td>
<td>Coefficient of N-redistribution</td>
<td>g N g(^{-1})</td>
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<td>(n_{\text{s}})</td>
<td>Structural leaf N-content per unit leaf area</td>
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<td>g N per plant</td>
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<td>g N g(^{-1})</td>
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<td>Rate of gross photosynthesis</td>
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<td>Specific leaf area</td>
<td>m(^2) g(^{-1})</td>
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<tr>
<td>(T)</td>
<td>Temperature</td>
<td>°C</td>
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<tr>
<td>(V)</td>
<td>Vernalization</td>
<td>d(^{-1})</td>
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<td>(W_{\text{*}})</td>
<td>Dry weight</td>
<td>g per plant</td>
</tr>
<tr>
<td>(I)</td>
<td>Photosynthetic photon flux (PPF)</td>
<td>(\mu)mol m(^{-2}) s(^{-1})</td>
</tr>
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<td>PPF above the canopy</td>
<td>(\mu)mol m(^{-2}) s(^{-1})</td>
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<tr>
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<td>Daily total of PPF averaged over 14 d</td>
<td>MJ m(^{-2}) d(^{-1})</td>
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<tr>
<td>(I_{\text{noon}})</td>
<td>Reference value of daily total of PPF</td>
<td>(\mu)mol m(^{-2}) s(^{-1})</td>
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<td>(I_{\text{ref}})</td>
<td>Direct, diffuse PPF above canopy</td>
<td>(\mu)mol m(^{-2}) s(^{-1})</td>
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<tr>
<td>(I_{\text{dr}, I_{\text{df}}})</td>
<td>Direct, diffuse component of PPF</td>
<td>(\mu)mol m(^{-2}) s(^{-1})</td>
</tr>
<tr>
<td>(I_{\text{sl}, I_{\text{sh}}})</td>
<td>PPF of sunlit, shaded leaves</td>
<td>(\mu)mol m(^{-2}) s(^{-1})</td>
</tr>
<tr>
<td>(\sigma)</td>
<td>Scattering coefficient</td>
<td>–</td>
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<tr>
<td>(\Theta)</td>
<td>Curvature factor of the light-response curve</td>
<td>–</td>
</tr>
<tr>
<td>(\alpha)</td>
<td>Initial slope of the light-response curve</td>
<td>(\mu)mol CO(_2) (\mu)mol(^{-1}) PPF</td>
</tr>
</tbody>
</table>

* index \(x\): in, inflorescence; leaf, leaf; plant, whole-plant; root, root; stem, stem.