Modelling nitrogen demand of cauliflower (*Brassica oleracea* L. *botrytis*) by using productivity-nitrogen relationships

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Kurzfassung

Um unproduktive und umweltschädliche Stickstoffverluste zu vermeiden, bedarf es einer vernünftigen Grundlage zur Bemessung der Düngermenge. Ein bedeutender Beitrag leistete die Einführung der heute weit verbreiteten N-Sollwerte im Gemüsebau, die einen empirischen Zusammenhang zwischen der Produktivität und den Stickstoffgehalten in Pflanzenbeständen herstellen. Die vorliegende Arbeit beruht auf der Hypothese, daß auf Grundlage der funktionalen Zusammenhänge zwischen Produktivität und Stickstoffangebot eine bedarfsgerechtere Düngung für standortspezifische und im Jahresverlauf veränderliche Klimabedingungen zu erzielen ist. Das Ziel dieser Arbeit war die Abschätzung der Unterschiede des individuellen N-Bedarfes am Beispiel von Blumenkohl (*Brassica oleracea* L. *botrytis*), indem die für die Produktivität entscheidenden Prozesse der Kohlenstoff- und Stickstoffassimilation und -verteilung innerhalb der Pflanze in Abhängigkeit von Stickstoffangebot und klimatischen Bedingungen quantifiziert wurden.

Dazu wurden in den Jahren 1996 bis 1998 zwei Freiland- und zwei Gewächshausversuche durchgeführt. Um eine Variation in den Stickstoffgehalten der Pflanze und ihrer Organe zu erhalten, wurden N-Angebot und Lichtumgebung variiert. In den Versuchen wurden der zeitliche Verlauf der Trockenmassen und N-Gehalte von Strunk, verschiedenen Blattfraktionen und Infloreszenz sowie der CO_2-Stoffwechsel auf Einzelblatt- und Ganzpflanzenebene bestimmt. Die Experimente dienten der Parameterisierung und Validierung funktionaler Zusammenhänge bei der Verteilung der Assimilate zwischen den Organen, der Photosynthese und Respiration einzelner Organe sowie der Stickstoffaufnahme und -verteilung innerhalb der Pflanze in Abhängigkeit des N-Angebotes und der Klimabedingungen.

Diese Teilaspekte wurden in einem Computermodell zusammenfügt, welches die gemessene Stoffproduktion und -verteilung in Blatt, Strunk und Infloreszenz in

einem unabhängigen Versuch mit einer Variation der Lichtumgebung und der N-Düngermenge von 0 bis 450 kg N ha^{-1} reproduzierte. Das Bestimmtheitsmaß für die Ausgleichsgerade zwischen gemessen und simulierten Trockenmassen lag zwischen r^2=0.91 und r^2=0.93. Neben der Kohlenstoff-Assimilation beschreibt das Modell die beobachteten Stickstoffgehalte von Blatt, Strunk und Infloreszenz (r^2=0.89, 0.66 und 0.86) sowie den Nitrat-Gehalt im Blatt (r^2=0.87). Trotz der Erhöhung der photosynthetischen Kapazität der Pflanze mit steigenden Proteingehalten im Blatt wird experimentell jedoch eine Sättigungsfunktion der Trockenmasse mit steigendem N-Angebot beobachtet. Dies erklärt das Modell durch die ebenfalls steigende Erhaltungsatmung der Pflanze infolge erhöhter Protein-N-Gehalte. Die maximal gebildete Trockenmasse ist eine Funktion der klimatischen Bedingungen.

Mit Hilfe von Simulationsläufen des Modells mit Klimawerten von 1997 für den Standort Ruthe bei Hannover wurde der minimal notwendige N-Bedarf zur Produktion einer Blumenkohlkultur von guter Qualität, inklusive eines Sicherheitsaufschlages von 40 kg N ha^{-1}, für verschiedene Pflanztermine berechnet. Während die Kulturdauer negativ mit der mittleren täglichen Strahlungssumme korrelierte, zeigte sich eine Abhängigkeit des minimalen N-Bedarfes von den klimatischen Bedingungen. Für die spezifischen Klimawerte dieses Standortes ergaben sich Unterschiede von 310 kg N ha^{-1} Anfang April zu 250 kg N ha^{-1} Anfang Juli bei der benötigten Stickstoffmenge der Kultur. Eine zutreffende Beschreibung des Modells vorausgesetzt, scheint damit die spezifische Bestimmung des N-Bedarfes für einzelne Standorte mit durchschnittlichen klimatischen Jahresverläufen zu einer weiteren Verbesserung in der Bemessung der benötigten Düngermenge zu führen.

Schlagwörter: Stoffverteilung, Photosynthese, Stickstoff

Abstract

The reduction of 'unproductive' and environmental harmful nitrogen losses from the production system requires to match nitrogen demand and supply. Considerable progress has been achieved by introducing N-target values as fertiliser recommendations for individual crops. These intensively used target values empirically relate crop productivity and available soil nitrate. However, it is hypothesised that a mechanistic understanding of the relationship between crop productivity and nitrogen supply predicts the needs of the crop under specific environmental conditions and provides growers with more specific fertiliser recommendations depending on season and location. This study is set up to assess the potential for individual N-fertiliser recommendations in cauliflower (*Brassica oleracea* L. *botrytis*) used as an example crop by exploring the functional relationships between carbon and nitrogen assimilation and distribution in the plant under specific environmental and agronomic conditions.

The experimental program consisted of two field and two greenhouse trials in the years 1996 to 1998. In order to provide a variation in the nitrogen contents of the plant and its organs, N-supply and light environment were varied. Dry matter and nitrogen contents of stem, several leaf groups and inflorescence were determined at intermediate harvests as well as the CO_2-exchange on single-leaf and whole-plant level. The experiments provided the data for the parameterisation and validation of physiological relationships between carbon and nitrogen assimilation and distribution in the plant as dependent on nitrogen supply and environmental conditions.

These different modules were combined to a simulation model. This computer program reproduced the observed dry matter production and distribution into leaf, stem and inflorescence under different light environments and N-fertiliser levels ranging from 0 up to 450 kg N ha^{-1}. The coefficient of determination of measured versus simulated dry matter for the various organs ranged between r^2=0.91 and

r^2=0.93. Besides carbon assimilation, the model described the observed nitrogen contents of leaf, stem and inflorescence (r^2=0.89, 0.66 and 0.86, respectively) as well as leaf nitrate content (r^2=0.87). Despite the increase in photosynthetic capacity of the canopy with increasing N-supply, experimental dry matter production was characterised by diminishing returns with increasing nitrogen availability and by an upper limit under specific environmental conditions. The model explained these empirical findings by enhanced maintenance respiration with increasing protein content of the plant. The maximum dry matter production under unlimited N-supply is determined by environmental conditions.

The minimum nitrogen demand for maximum cauliflower yield, including a surplus of 40 kg N ha^{-1}, was calculated by simulation runs for various planting dates in 1997 using climate data from the institute's experimental station, 15 km south of Hanover. Whereas the growth period correlated negatively with the average daily total of photosynthetically active radiation, the calculated minimum N-requirements varied with environmental conditions. The specific climate data led to differences in simulated N-demand ranging from 250 to 310 kg N ha^{-1} for planting dates in early July and early April, respectively. Presuming accurate model description, these results emphasise the importance of site-specific N-fertiliser recommendations to further match N-supply and N-demand in crop production.

Keywords: Dry matter partitioning, photosynthesis, nitrogen distribution

Contents

List of main symbols and parameters

Symbol	Description	Unit
a	Increase in stem dry matter per increase in leaf area	g m^{-2}
A_l	Leaf area	m^2 $plant^{-1}$
dat	Days after transplanting	d
f_{root}	Root partitioning coefficient	-
f_{soil}	Factor denoting source N-limitation	-
f_{stem}	Stem partitioning coefficient	-
K_{Nmin}	Curvature factor of the N_{min}-response curve	kg N ha^{-1}
l_c	Cumulative leaf area index	m^2 m^{-2}
LAI	Leaf area index	m^2 m^{-2}
m_g	Coefficient of growth respiration	mol CO_2 m^{-2}
m_m	Coefficient of maintenance respiration	µmol CO_2 s^{-1} g^{-1} N
m_R	Rate of decrease in respiration during the night per unit leaf area	mg CO_2 m^{-2} min^{-1} h^{-1}
n_a	Protein-N content per unit leaf area	g N m^{-2}
$n_{a,max}$	Maximum protein-N content per unit leaf area	g N m^{-2}
n_{area}	N-content per unit leaf area	g N m^{-2}
$n_{max,NO3-N}$	Maximum leaf NO_3-N-content	g NO_3-N g^{-1}
$n_{max,x}$*	Maximum N-content	g N g^{-1}
N_{min}	Available soil nitrate-N	kg N ha^{-1}
n_{NO3-N}	Leaf NO_3-N-content	g NO_3-N g^{-1}
no_{leaf}	Number of visible leaves	-
$N_{P,x}$*	Total of protein-N	g protein-N $plant^{-1}$
n_{red}	Coefficient of N-redistribution	g N g^{-1}
n_s	Structural leaf N-content per unit leaf area	g N m^{-2}
N_x*	Total of nitrogen	g N $plant^{-1}$
n_x*	N-content	g N g^{-1}
P_g	Rate of gross photosynthesis	µmol CO_2 m^{-2} s^{-1}
P_m	Rate of gross photosynthetic capacity	µmol CO_2 m^{-2} s^{-1}
P_{plant}	Rate of whole-plant net CO_2-uptake	mg CO_2 $plant^{-1}$ min^{-1}

Continued:

R	Rate of single-leaf respiration	µmol CO_2 m^{-2} s^{-1}
rgr	Relative growth rate	d^{-1}
rgr_{in}	Relative growth rate of inflorescence	d^{-1}
R_{plant}	Rate of whole-plant respiration	mg CO_2 $plant^{-1}$ min^{-1}
$R_{plant,a}$	Rate of whole-plant respiration per unit leaf area	mg CO_2 $plant^{-1}$ m^{-2} min^{-1}
R_x*	Respiration rate	mg CO_2 $plant^{-1}$ min^{-1}
sla	Specific leaf area	m^2 g^{-1}
T	Temperature	°C
W_g	Dry weight associated with generative growth	g $plant^{-1}$
$W_{in,cap}$	Potential sink capacity of the inflorescence	g $plant^{-1}$
W_p	Above-ground dry weight	g $plant^{-1}$
$W_{s,in}$	Stem dry weight associated with inflorescence growth	g $plant^{-1}$
$W_{s,l}$	Stem dry weight associated with leaf growth	g $plant^{-1}$
W_v	Vegetative dry weight	g $plant^{-1}$
W_x*	Dry weight	g $plant^{-1}$
I	Photosynthetically active photon flux density (PPFD)	µmol m^{-2} s^{-1}
I_0	PPFD above the canopy	µmol m^{-2} s^{-1}
I_{noon}	Maximum PPFD at solar noon	µmol m^{-2} s^{-1}
I_{ref}	Reference value of daily total of PPFD	MJ m^{-2} d^{-1}
$I_{tot,ave}$	Daily total of PPFD averaged over 14 days	MJ m^{-2} d^{-1}
θ	Curvature factor of the light-response curve	-
α	Initial slope of the light-response curve	µmol CO_2 μmol^{-1} PPFD

* index x:

in	inflorescence
leaf	leaf
root	root
stem	stem

1. Introduction

Nitrogen (N) is an essential element of many organic compounds such as nucleic acids, proteins, enzymes and chlorophyll that make plant life possible. The dependence of plant growth on these N-containing compounds indicates the quantitative significance of nitrogen availability for crop production. Nitrogen is absorbed by higher plants in the form of nitrate and ammonium from which nitrate is typically the dominant form in crop nutrition. It is supplied by micro-organisms breaking down soil organic matter from plant and animal residues and N_2-fixing symbiotic bacteria. However, the majority of nitrogen available to crops is transferred into agricultural systems by mineral N-fertilisers (Loomis and Connor, 1992).

The introduction of nitrogen fertilisers resulted in dramatic increases in crop yields (De Wit, 1972; Evans, 1996; Sinclair, 1990). However, the increased application of manufactured N-fertiliser and animal manure in the last decades go along with environmental risks of water and air pollution. The problem of nitrate leaching (Pang *et al.*, 1998; Voss, 1985) is especially pronounced in vegetables (Navarro Pedreno *et al.*, 1996) with relatively short cultivation periods. The crop is mostly harvested in full growth when the formation of the marketable yield is quantitatively and qualitatively very sensitive to the amount of available soil nitrate (Booij *et al.*, 1996). This results in considerable amounts of residual N_{min} and together with nitrogen in crop residues to large amounts of nitrogen left in the soil after harvest (Everaarts, 1993a). Both sources together accumulate in cauliflower to more than 50% of applied nitrogen that is left in the field (Everaarts *et al.*, 1996; Rahn *et al.*, 1992). These amounts are often not recovered by the succeeding crop partly due to the low rooting depth as a result of the short cultivation period.

Except for improved management practices on the cropping system level which comprises soil tillage (Davidoff *et al.*, 1992; Radke *et al.*, 1991) and crop rotations (Kunzmann, 1991) including catch crops (Thorup-Kristensen and Nielsen, 1998), a sound basis to match nitrogen demand and supply is required on the crop level.

Considerable progress has been achieved by introducing N-target values as fertiliser recommendations for individual crops (Lorenz *et al*., 1989; Scharpf, 1991). Since these target values empirically relate crop productivity with N-supply, they can only be adapted to specific locations and environmental conditions by considerable effort. However, it was hypothesised that the functional dependency between nutrient availability and crop growth as dependent on environmental conditions can be used to predict the needs of the crop and finally provides growers with more reliable and specific fertiliser recommendations (Greenwood, 1982; Van Keulen *et al*., 1989).

The aim of this study is to assess the potential for specific N-fertiliser recommendations in cauliflower by exploring the physiological relationships between N-supply, N-uptake and yield. The focus is here on the impacts of nitrogen availability on the primary processes determining productivity. The processes considered are N-uptake and distribution in the plant as well as resulting carbon assimilation and partitioning into the marketable part of the crop as outlined in Figure 1. The influence of nitrogen on quality aspects as well as on the development of pests and diseases and their effects on yield are classified as secondary nitrogen impacts and are therefore beyond the scope of this study. The complex interactions between nitrogen and water supply on productivity are circumvented for the same reason by providing sufficient irrigation in all experiments.

The most important processes determining yield are daily carbon assimilation and partitioning in the plant. Contrasting effects of nitrogen availability on the relative amount of dry matter distributed to the marketable product of vegetables have been observed. Whereas the harvest index of Brussels sprouts increases with N-supply it decreases for leeks, and in potatoes and spinach no influence was observed (Biemond, 1995). If generative plant parts are harvested as in cauliflower, assimilates distributed to the marketable product are lost for the photosynthetically active plant parts, which determine the assimilation capacity and therefore the yield of the plant. The mechanistic approach to yield requires

the understanding of dry matter partitioning into photosynthetically active, structural and generative plant parts as dependent on N-supply and environmental conditions (Brouwer, 1962b; Hirose, 1986; Marcelis, 1994) (Chapter 2).

Besides the indirect impact of nitrogen supply on assimilation capacity of the plant through dry matter partitioning, the photosynthetic performance is directly determined by leaf N-content which has been shown on the single-leaf level (Evans, 1983; Field and Mooney, 1986) as well as on the whole-plant level (Agren, 1985; Burns, 1994b; Greenwood *et al*., 1986). Not only the light-saturated photosynthesis increases with increasing leaf protein-N content (Del Pozo and Dennett, 1991; Muchow and Sinclair, 1994), but also the respiratory need of the plant due to enhanced protein-turnover of metabolic compounds (Penning de Vries, 1975) and additional costs for nitrogen uptake (Poorter *et al*., 1991; Van der Werf *et al*., 1988; Van der Werf *et al*., 1994). Benefits and costs of increased leaf N-contents occur on the leaf level. Therefore, a physiological approach to CO_2-assimilation has to quantify the photosynthesis-N relationship on single-leaf level and scale it up to whole-plant productivity (Chapter 3). The counteractive influence of increased leaf-N contents on productivity raises the question of the optimal N-content and distribution within the plant (Hilbert, 1990; Hirose and Werger, 1987b; Van der Werf *et al*., 1993). Does the plant follow certain criteria of optimisation or is there a potential for 'luxury N-consumption' stored in the plant ? These questions are also addressed in Chapter 3.

If the observed N-contents deviate from the optimum values, how else can nitrogen uptake and distribution into structural, photosynthetically active and storage nitrogen as well as remobilization within the N-pools be formulated ? The realistic prediction of dry matter assimilation and partitioning requires a framework to predict nitrogen content and distribution in the plant as dependent on nitrogen supply and plant physiology (Chapter 4). The combination of these functional relationships between carbon and nitrogen assimilation and distribution into a dynamic model allows to predict cauliflower yield for specific environmental and

agronomic conditions. The comparison of observed and simulated dry matter production and nitrogen distribution in field experiments with varying N-supply and under different light environments is also part of Chapter 4.

This intended model is supposed to provide a preliminary tool to evaluate the potential for site-specific N-fertilisation requirements in cauliflower by calculating the minimum N-requirements for maximum yield as dependent on environmental conditions (Chapter 5). The relevance of these scenario calculations is limited by the restriction to primary N-dependent processes determining yield. The applicability of the functional relationships derived in this study in situations deviating from the underlying assumptions and possible modifications are finally discussed in Chapter 5.

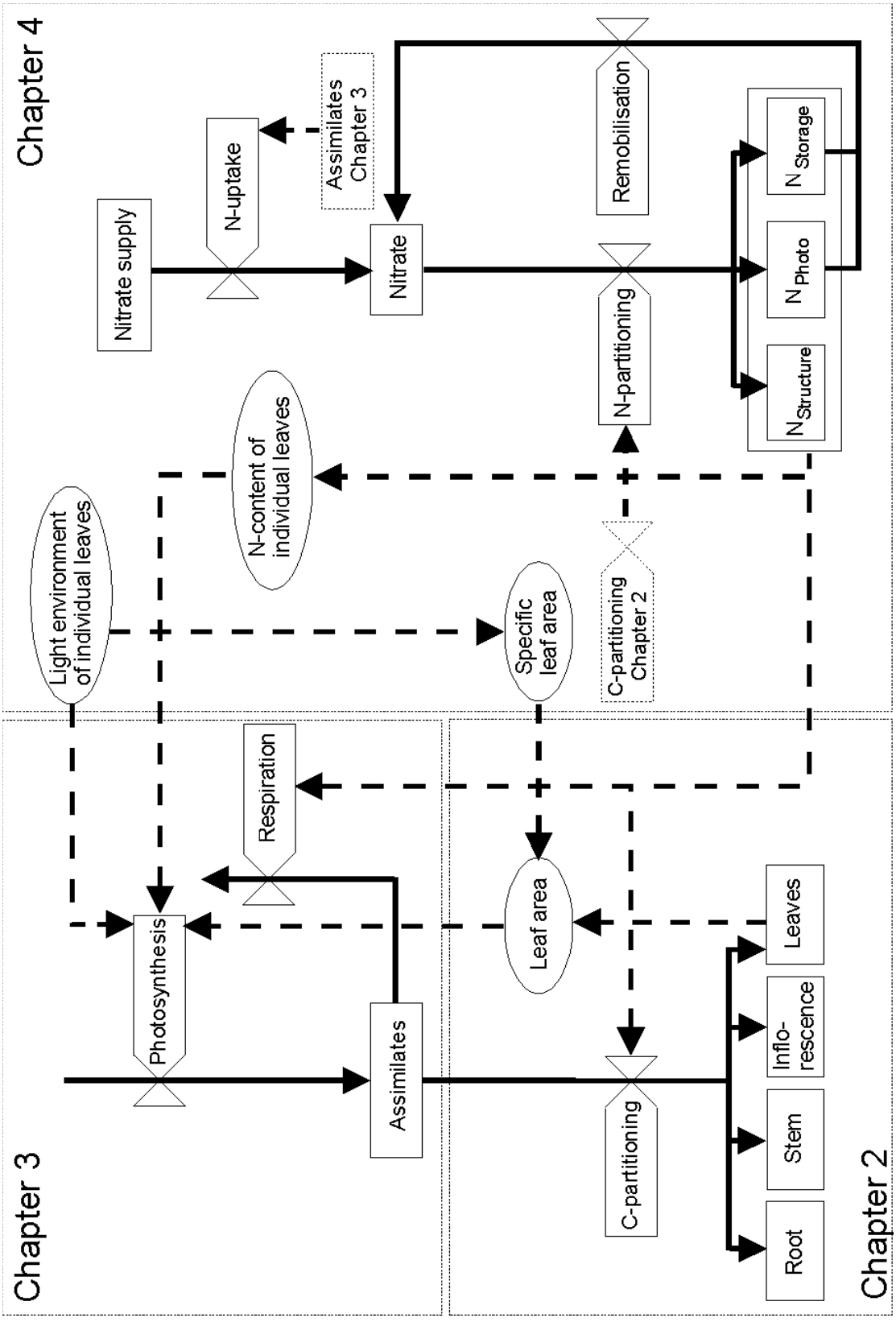

Figure 1: Schematic overview of main components and processes. Solid lines denote mass flows, broken lines denote information flows.

2. Influence of nitrogen status and light environment on dry matter partitioning

Abstract

Concepts of above-ground dry matter partitioning as dependent on nitrogen supply and light environment are presented. Dry matter partitioning between generative and vegetative compartments is based on a source-sink concept. Inflorescence growth rate is at the beginning sink limited (potential capacity) and later source limited (daily available assimilates). The intrinsic specific growth rate of the inflorescence is dependent on leaf nitrogen content. Leaf and stem partitioning is calculated according to a functional relationship between stem dry weight and leaf area independent of nitrogen status. The model is parameterised and validated with data from field experiments. Applied to an independent data set the model predicts proportions of inflorescence, leaf and stem on total dry matter (r^2 = 0.84, 0.92 and 0.22, respectively) for different nitrogen and light treatments.

2.1 Introduction

The partitioning of dry matter into photosynthetically active, structural and generative plant parts influences the amount of future accumulated assimilates and finally yield. The understanding of dry matter partitioning is therefore essential for a mechanistic approach to productivity. The dependence of environmental conditions and nitrogen supply on dry matter distribution has been shown in various species (Brouwer, 1962b; Hirose, 1986; Marcelis, 1994). The relative amount of dry matter distributed to the marketable product of vegetables is influenced in different ways by nitrogen availability (Biemond, 1995). The harvest index also determines the amount of crop residues which may contain considerable amounts of nitrogen (Rahn *et al.*, 1992). In cauliflower more than

50% of crop biomass remains in the field which results together with the residual N_{min} in more than 50% of applied nitrogen left in the field (Everaarts *et al.*, 1996). These amounts are often not taken properly into account for fertilisation of subsequent crops (Everaarts, 1993a,b). The determination of the exact amounts of crop residues can help to further reduce nitrogen losses and to increase nitrogen use efficiency in cropping systems.

Dry matter partitioning is characterised by a net flow of assimilates from source to sink organs. Although the mediating regulators of this flow (Munns and Cramer, 1996; Van der Werf and Nagel, 1996) as well as control strategies (Reynolds and Chen, 1996) are not fully understood several model approaches of biomass allocation have emerged: (1) Partitioning coefficients described by empirical constants, often as functions of developmental stage (Penning de Vries *et al.*, 1989); (2) allometric growth between different organs, i. e. fixed ratios between relative growth rates (Pearsall, 1927; Stützel and Aufhammer, 1991); (3) functional balance between root and shoot activity, first applied by (Brouwer, 1962a) and further developed to be regulated by C:N distribution (Johnson and Thornley, 1987) or nitrogen concentration in the plant (Agren, 1987; Levin *et al.*, 1989); (4) sink based models where dry matter distribution is regulated by the sink strength or by the sink strength including the transport path (Marcelis, 1993; Wien, 1997). The concept of sink strength is often applied to the assimilate accumulation of storage or reproductive organs as fruits (Chamont, 1993; Jones *et al.*, 1991). Although terms as (potential) sink strength and sink activity are widely used, they are neither uniquely defined nor is their usefulness generally accepted (Farrar, 1993). (Wolfswinkel, 1985) expressed sink strength as a potential capacity of the sink to accumulate assimilates, which may be related to the potential growth rate of the sink under non-limiting assimilate supply (Marcelis *et al.*, 1989).

Empirical and allometric models are usually more easily parameterised than sink strength based models but have only limited explanatory value and may have limited application under changing environmental conditions.

Although models on total dry matter production of cauliflower have been published (Olesen and Grevsen, 1995; 1997; Wheeler *et al*., 1995) only (Kage and Stützel, 1999) incorporate a model of dry matter partitioning based on allometric growth between leaf and stem. Inflorescence growth rate is calculated as a fraction of total growth rate depending on temperature sum. The empirical relations are derived for cauliflower crops under non-limiting nitrogen conditions. Dry matter distribution in cauliflower is related to crop development by the vernalisation process of the plant resulting in inflorescence initiation. Several models on cauliflower development distinguish juvenile, vernalisation and generative phase (Grevsen and Olesen, 1994; Wiebe, 1975; Wurr *et al*., 1990) except for (Pearson *et al*., 1994; Wheeler *et al*., 1995) who do not take a juvenile phase into account. All models cited above calculate the length of the generative phase by an empirical function of temperature sum after vernalisation is completed.

A mechanistic approach to dry matter partitioning in cauliflower under different environmental and agronomic conditions is still missing. This study formulates hypotheses for partitioning of above-ground dry matter as dependent on nitrogen status and light environment and evaluates them in independent field experiments. Root dry matter is neglected for reasons of simplicity since it stores the least amount of nitrogen due to a relatively small proportion on total dry weight and a N-concentration of about 2% (unpublished results).

2.2 Model

The total above-ground growth rate, dW_p/dt is the sum of the dry matter increases of vegetative and generative organs, dW_v/dt and dW_g/dt, respectively:

$$\frac{dW_p}{dt} = \frac{dW_v}{dt} + \frac{dW_g}{dt} \quad (1)$$

It is assumed that one fraction of stem dry matter, $W_{s,l}$, is associated with leaf growth, dW_{leaf}/dt, and that another fraction, $W_{s,in}$, is related to inflorescence growth. Thus:

$$\frac{dW_v}{dt} = \frac{dW_{s,l}}{dt} + \frac{dW_{leaf}}{dt}, \quad (2)$$

where $W_{s,l}$ is assumed to be proportional to leaf area, A_l:

$$W_{s,l} = a \cdot A_l \quad (3)$$

The parameter a can be interpreted as the increase in stem growth per increase in leaf area necessary to fulfil the stem's physiological and structural functions for the leaf. It is hypothesised that the plant's stability requirement is mainly determined by leaf area susceptible to wind.

If the specific leaf area, sla, is constant,

$$A_l = sla \cdot W_{leaf}, \quad (4)$$

then eqn. 2 can be rewritten to calculate dry matter increase of stem and leaf:

$$\frac{dW_{leaf}}{dt} = \frac{1}{1 + a \cdot sla} \cdot \frac{dW_v}{dt} \quad (5)$$

$$\frac{dW_{s,l}}{dt} = \frac{dW_v}{dt} - \frac{dW_{leaf}}{dt} \quad (6)$$

In case of varying specific leaf area during plant growth the same equations apply and sla in eqn. 5 refers to the relevant specific leaf area of the newly produced leaf dry matter.

When vernalisation is completed the inflorescence is initiated. From then, generative growth has priority over vegetative growth in order to satisfy the potential sink capacity of the inflorescence, $dW_{in,cap}/dt$, which is determined by its dry matter, W_{in}, and its specific growth rate, rgr_{in}:

$$\frac{dW_{in,cap}}{dt} = rgr_{in} \cdot W_{in} \qquad (7)$$

Following an original idea of Warren-Wilson (1967) rgr_{in} may be related to the sink activity, whereas W_{in} is a measure of sink size.

The initial dry matter of the inflorescence was set to $6.4 \cdot 10^{-6}$ g plant^{-1} estimated as 10% of a water filled sphere with a diameter of 0.6 mm which is the approximate diameter of the apical dome at the beginning of inflorescence growth (Wiebe, 1972b).

The specific growth rate is assumed to vary with the nitrogen content of the plant at the time of inflorescence initiation:

$$rgr_{in} = \text{function}(N - \text{content}) \qquad (8)$$

Accelerated inflorescence growth with better nitrogen supply may physiologically be explained by an increased number of initiated inflorescence cells or an up-regulated supply rate of available protein-N compounds during cell elongation. Both affect the sink capacity of the inflorescence positively.

With every increment in inflorescence dry weight stem growth is associated in order to meet the increased structural and physiological demands of the inflorescence:

$$\frac{dW_{s,in}}{dt} = f_{stem} \cdot \frac{dW_{in}}{dt}, \qquad (9)$$

where f_{stem} denotes the fraction of dW_{in}/dt associated with stem growth.

The total generative growth rate is the sum of inflorescence and associated stem growth:

$$\frac{dW_g}{dt} = \frac{dW_{in}}{dt} + \frac{dW_{s,in}}{dt} = (1 + f_{stem}) \cdot \frac{dW_{in}}{dt} \quad (10)$$

With increasing inflorescence weight the share of generative growth on total plant growth is continuously increasing until generative growth is limited by total growth rate imposing an upper limit to inflorescence growth rate. The dry matter increase of the inflorescence is at the beginning limited by its sink capacity (eqn. 7), and later on by total available assimilates:

$$\frac{dW_{in}}{dt} = \min\left(\frac{1}{1 + f_{stem}} \cdot \frac{dW_p}{dt}, \frac{dW_{in,cap}}{dt}\right) \quad (11)$$

Before the vernalisation process is completed dW_{in}/dt is set to zero. Given the inflorescence growth rate leaf and total stem growth rates can be calculated:

$$\frac{dW_{leaf}}{dt} = \frac{1}{1 + a \cdot sla} \cdot \left(\frac{dW_p}{dt} - (1 + f_{stem}) \cdot \frac{dW_{in}}{dt}\right) \quad (12)$$

$$\frac{dW_{stem}}{dt} = a \cdot sla \cdot \frac{dW_{leaf}}{dt} + f_{stem} \cdot \frac{dW_{in}}{dt} \quad (13)$$

2.3 Material and Methods

Field experiments

Two independent field experiments with cauliflower (*Brassica oleracea* L. convar. *botrytis* var. *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. The 1996 experiment was used for derivation of model parameters and the 1997 experiment served for model validation.

The seeds were sown in peat cubes with 4 cm edge length. 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 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 plant spacing was 0.60 m by 0.48 m giving the average density of 3.5 plants m^{-2}. Before planting Chlorfenvinphos (Birlane) and molybdenum sulphate were applied prophylactically. Weeds were controlled by hand. Metasystox (250 g l^{-1} Oxydemeton-methyl) and later E605 forte (500 g l^{-1} Parathion) were sprayed once for pest control in both years. Irrigation was given whenever needed.

Table 1: Dates of sowing, transplanting and harvesting of field experiments

Year	Sowing date	Transplanting date	Harvest dates (days after transplanting)
1996	23 May	18 June	28, 49, 69
1997	3 June	9 July	26, 47, 68*, 82

*Final harvest of N-fertilised treatments of non-shaded light environment (Table 2).

Experimental design

The experiments were laid out as split plots with two different light environments as main plots and four different nitrogen-fertiliser levels as sub-plots (Table 2). Main plots were covered in one meter height with a shading 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 150, 300 and 450 kg ha^{-1} target values.

Table 2: Light environments and nitrogen applications in both experiments

Factor	Level	Abbreviation
Light environment	non-shaded	I1
	shaded	I2
Nitrogen application	0	N0
(target values, kg N ha^{-1})	150	N1
	300	N2
	450	N3

Plant growth analysis

On several intermediate harvests in both years six plants per plot 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 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). The samples of all plant compartments were oven dried and weighed. After weighing total nitrogen and nitrate nitrogen was determined by the micro-Kjeldahl

method and a nitrate sensitive electrode, respectively. On all harvests also plant dimensions (height and width) and inflorescence diameter were measured.

Statistical analysis and model parameterisation

The statistical analyses of the experimental data were carried out using procedures NLIN and REG of the SAS-software package (SAS Institute, 1988). The level of significance was calculated with an error probability of 0.05. Above-ground plant growth rate served as an input variable for dry matter distribution (eqns. 11-13) and was calculated by interpolating the experimental data with an expo-linear function (Goudriaan and Monteith, 1990). The average specific leaf areas of the shaded and non-shaded light environments were also used as input parameters to calculate leaf area from simulated leaf dry weights.

The dynamic model of development and partitioning described above was programmed using the modelling environment ModelMaker (Walker, 1997). The integration was performed using the Euler algorithm (Thornley and Johnson, 1990) with a time step of one day. A non-linear least-squares regression analysis estimates the parameters f_{stem} (eqn. 9), and rgr_{in} (eqn. 7), using a Marquardt optimisation 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).

Cauliflower development

Cauliflower and leaf development were described analogous to Kage and Stützel (1999) where visible leaf number is expressed as an expo-linear function of the temperature sum with parameters k_1 and k_2. The values of the parameters were determined for the cultivar ‘Fremont’ from an independent experiment in 1998 to be k_1 = 0.0032 (±0.0001) $(d°C)^{-1}$ and k_2 = 0.0353 (±0.0036) $(d°C)^{-1}$ (unpublished results).

The vernalisation process is calculated according to (Wiebe, 1972a) using a daily vernalisation rate, dV/dt, which is a function of mean daily temperature, T:

$$\frac{dV}{dt} = \begin{cases} 0 & T \le T1 \\ v_{max} \cdot (1 - \frac{T2 - T}{T2 - T1}) & T1 < T \le T2 \\ v_{max} & T2 < T \le T3 \\ v_{max} \cdot (1 - \frac{T - T3}{T4 - T3}) & T3 < T \le T4 \\ 0 & T > T4 \end{cases} \qquad (14)$$

where v_{max} is the maximum vernalisation rate set to 0.11 d^{-1}. The four temperatures T1 to T4 are cultivar dependent and assumed to be 0°C, 10°C, 13°C and 28°C for the cultivar Fremont (Wiebe, personal communic.). The vernalisation phase is completed when the sum of daily vernalisation rates has reached a value of one.

2.4 Results

Parameterisation

Figure 2 shows measured and fitted total above-ground dry matter for the parameterisation data set in 1996 ($r^2 > 0.99$ for all treatments). The interpolated functions served as input for the dry matter distribution model.

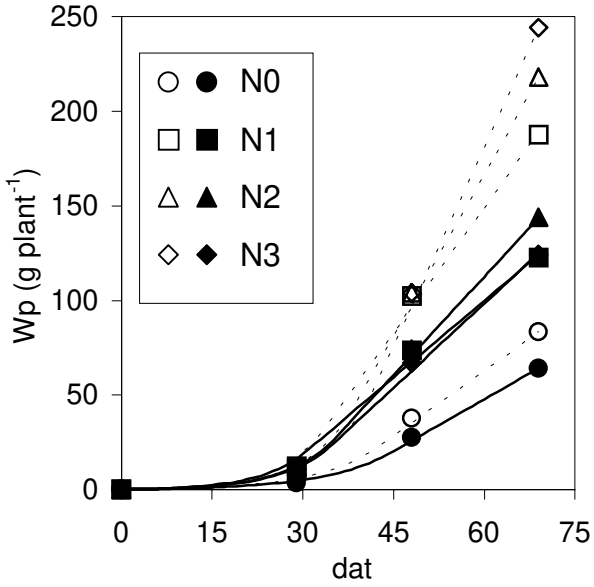

Figure 2: Total above-ground dry matter, W_p, vs. days after transplanting, dat; experiment 1996, open and closed symbols refer to measured values of non-shaded and shaded treatments, respectively; lines are fitted curves.

Linear relationships were found between stem and leaf dry matter during the vegetative phase, i. e. at harvests one and two (Figure 3A). There was no significant influence of the N-level on vegetative stem-leaf distribution within light environments but shaded plants had higher stem/leaf ratios than non-shaded. However, the average specific leaf areas of shaded and non-shaded plants also differed significantly with 145.4 (±3.9) and 93.0 (±8.1) $cm^2\ g^{-1}$ respectively (LSD = 12.8 $cm^2\ g^{-1}$). Thus, a common linear relationship between stem mass and leaf area existed for all nitrogen and light treatments (Figure 3B). The value of the

parameter a (eqn. 3) quantifying the increase in stem growth per increase in leaf area is determined by the slope of the regression line.

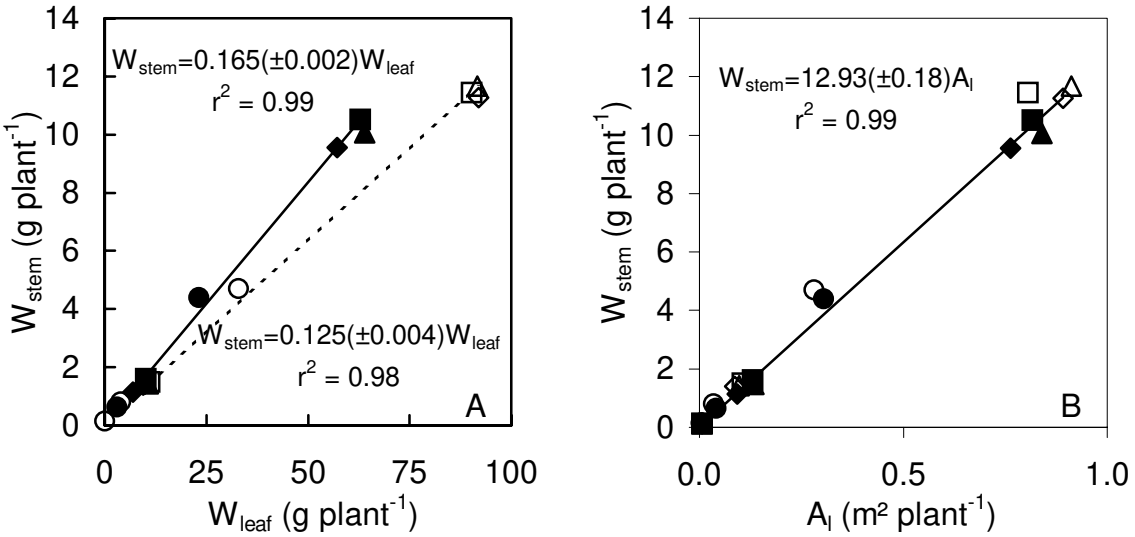

Figure 3: Measured stem, W_{stem}, vs. leaf dry weight, W_{leaf} (A), and vs. leaf area, A_l (B), for inflorescence dry weight <1g, i. e data from first two harvests where $W_{stem}=W_{s,l}$; experiment 1996, symbols as in Figure 2.

The different inflorescence dry weights between treatments at the final and second harvest of 1996 (Figure 4) were attributed to differences in specific inflorescence growth rates, rgr_{in} (eqn.7) and total available assimilates in the last period of inflorescence growth. rgr_{in} was estimated for each treatment separately by non-linear regression analyses of measured and simulated above-ground dry weights (Table 3). The simulation results of the inflorescence dry weights are shown in Figure 4. rgr_{in} was related to the nitrogen status of the plant expressed as leaf nitrogen content per unit leaf area at the time when the vernalisation phase was just completed, i. e. at harvest one (Figure 5). The slopes of the rgr_{in}-leaf nitrogen relationships obtained separately for the shaded and non-shaded treatments were not significantly different.

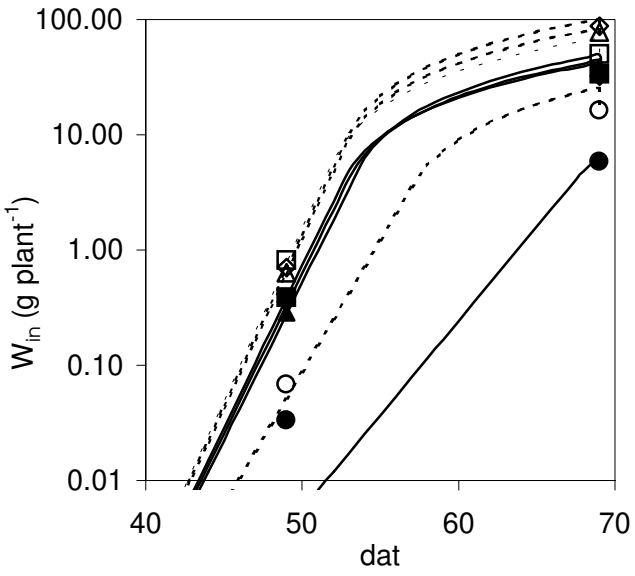

Figure 4: Accumulation of inflorescence dry weight, W_{in}; experiment 1996, symbols as in Figure 2; lines are simulations using eqns. 7 and 11 with parameters given in Table 3.

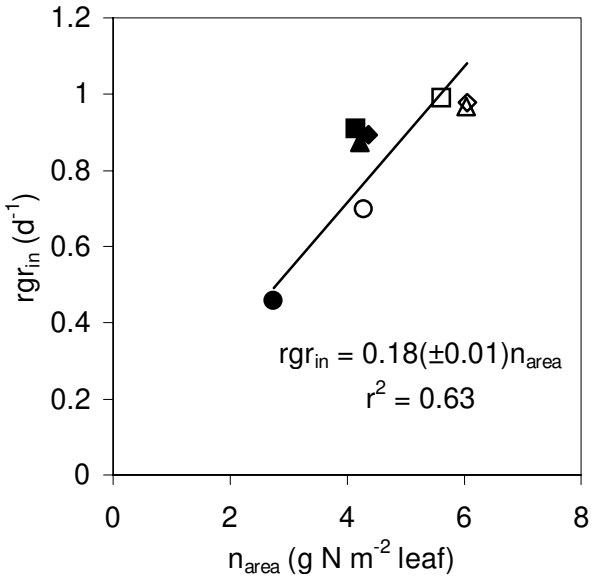

Figure 5: Estimated specific growth rates of inflorescence, rgr_{in} (Table 3), as dependent on leaf nitrogen content per unit leaf area, n_{area}, experiment 1996, symbols as in Figure 2.

The parameter f_{stem} describing the increase in stem growth with increasing inflorescence weight (eqn. 9) was determined by non-linear least-square regression analysis of measured and simulated above-ground dry weights. Its value was estimated to be 0.15 (± 0.01) and independent of treatment.

The agreement between simulated and measured fractions of individual organs on total dry matter for all harvests of the parameterisation data set is shown in Figure 6. Observed are only small variations in stem fractions for the different harvests and treatments. The fractions of inflorescence on total dry weight were underestimated for both light environments at the final harvest which results in an overestimation in leaf dry matter (Table 4).

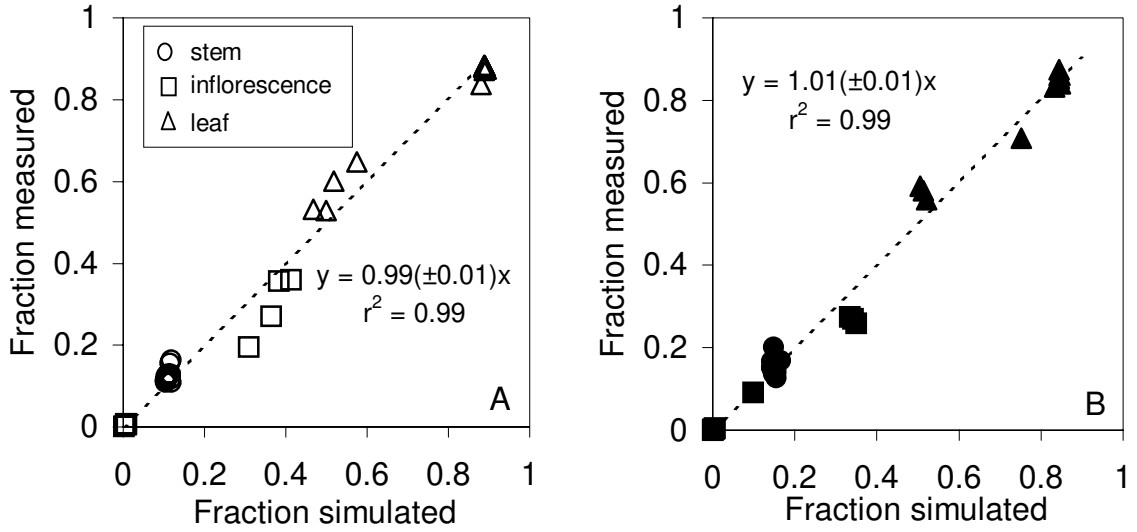

Figure 6 : Measured vs. simulated dry matter fractions (organ mass/total plant mass) of non-shaded (A) and shaded (B) treatments and all harvests; experiment 1996.

Validation

Figure 7 shows a very good agreement between calculated (Kage and Stützel, 1999) and measured leaf numbers for the validation experiment in 1997 suggesting a sufficiently accurate simulation of time of inflorescence initiation. Since daily average temperatures had differed only slightly there were no significant differences between light environments. The visible leaf numbers (diameter>1cm) of the N0-treatments at the first and second harvests lie significantly below the N-treatment means by one and two leaves, respectively.

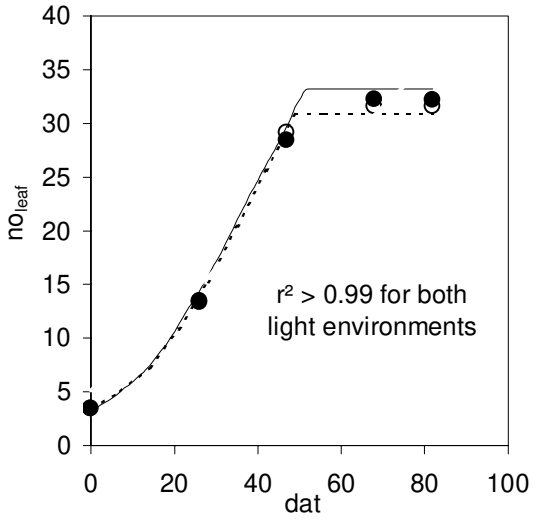

Figure 7: Calculated (lines) and measured (symbols) number of visible leaves per plant, no_{leaf}, means of shaded (closed symbols, solid line) and non-shaded N-treatments (open symbols, dashed line); experiment 1997.

Specific inflorescence growth rates, rgr_{in}, were calculated by the regression equation given in Figure 5 using leaf N-contents from the first harvest on day 26 after transplanting. This date was closest to the simulated day of inflorescence initiation, i. e. days 29 and 30 after transplanting for the non-shaded and shaded environment, respectively. Due to the lower N-contents in 1997 the specific inflorescence growth rates were below those of 1996 (Table 3).

Table 3: Specific inflorescence growth rates, rgr_{in} (d^{-1}), for the parameterisation and validation experiments; the latter were calculated by the regression equation given in Figure 5 using the leaf nitrogen contents, n_{area}, of the first harvest in 1997.

Treatment	Estimated rgr_{in} (±s.e.), parameterisation	Calculated rgr_{in}, validation	n_{area} (g N m^{-2})
I1-N0	0.70 (±0.05)	0.58	3.2
I1-N1	0.99 (±0.05)	0.72	4
I1-N2	0.97 (±0.05)	0.81	4.5
I1-N3	0.98 (±0.05)	0.81	4.5
I2-N0	0.46 (±0.03)	0.43	2.4
I2-N1	0.91 (±0.05)	0.52	2.9
I2-N2	0.87 (±0.05)	0.54	3
I2-N3	0.89 (±0.05)	0.58	3.2

These calculated values of rgr_{in} and the value of f_{stem}=0.15 derived from the parameterisation experiment were used to evaluate model predictions of dry matter distribution with experimental data of the validation experiment in 1997. The average specific leaf areas of the shaded and non-shaded light environments in 1997 were 168.9 (±5.8) and 116.0 (±8.4) cm^2 g^{-1}, respectively, and served as input parameters to calculate leaf area from simulated leaf dry weights. The agreement between simulated and measured fractions of individual organs on total dry matter is equally high for shaded and non-shaded light environments (Figure 8). Unfortunately, no data on leaf dry weights and thus, no data on dry matter partitioning, were obtained for the final harvest of the I1-N2- and I1-N3-treatments. Model predictions are comparably accurate for the different organs (Table 4). The stem fractions show the least amount of variation resulting in a lower coefficient of determination. The model performance is of similar quality for the validation experiment as it is for the parameterisation experiment.

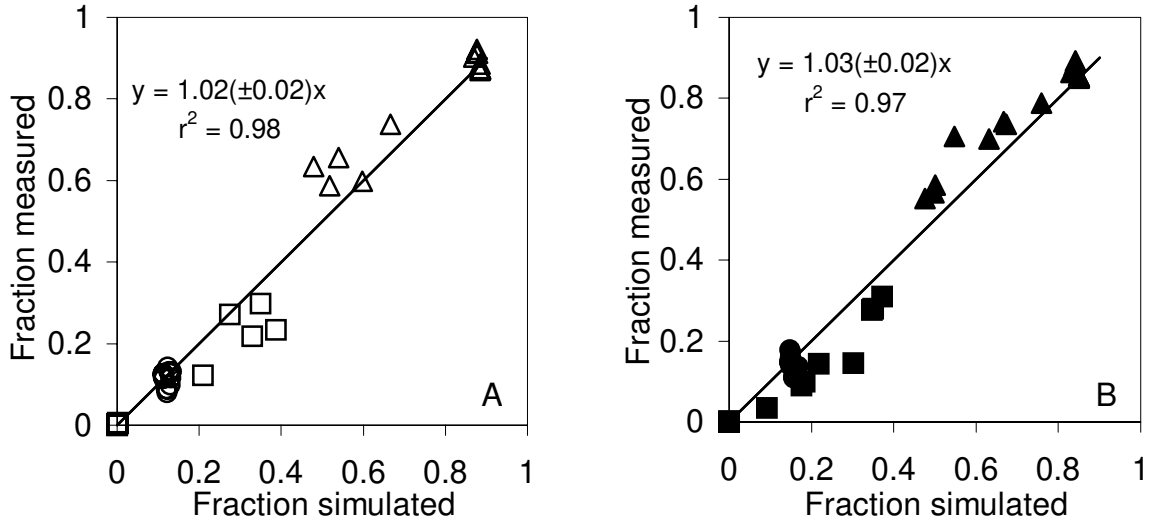

Figure 8: Measured vs. simulated dry matter fractions (organ mass/total plant mass) of non-shaded (A) and shaded (B) treatments for all harvests; experiment 1997, symbols as in Figure 6.

Table 4: Results of the linear regression analyses of measured vs. simulated dry matter fractions of cauliflower organs in both experiments*

Experiment	Organ	Slope (±s.e.)	r²
Parameterisation	Stem	1.04 (±0.03)	0.28
Parameterisation	Leaf	1.01 (±0.01)	0.92
Parameterisation	Inflorescence	0.80 (±0.02)	0.98
Validation	Stem	0.93 (±0.03)	0.22
Validation	Leaf	1.05 (±0.01)	0.82
Validation	Inflorescence	0.80 (±0.04)	0.92

*: Intercepts were in all cases not different from zero.

2.5 Discussion

This chapter explores dry matter partitioning in cauliflower as dependent on nitrogen status and light environment. The formulated hypotheses are evaluated in field experiments. In order to provide a variation in N-supply and radiation environment, four N-fertiliser levels and two light regimes were imposed in the experiments.

Allometric partitioning between stem and leaf has proven its usefulness under conditions of a relatively constant light environment (Kage and Stützel, 1999). The approach used in this paper is based on the stem's physiological and stability requirements imposed by the leaf and is able to describe stem-leaf distribution under variable light intensities. The quantitative relation between stem dry weight and leaf area in this model is independent of nitrogen supply but may change with wind environment that probably influences the stability requirements of the stem. The shading net may have acted to a certain extend also as a wind shield, thereby increasing the variation in wind speed over the experiment as a whole. The stem-leaf distribution seems therefore to be tested under a wide range of typical wind conditions. Since a single plant in a closed crop is protected by surrounding plants, the planting density may also be an important factor in a more comprehensive model.

Inflorescence growth is modelled using the concept of sink capacity as defined by the inflorescence' potential growth rate under non-limiting assimilate supply. Similar approaches, incorporating competition between different storage organs, have successfully been used in tomato (Jones *et al.*, 1991) and cucumber (Chamont, 1993). The relationship between sink capacity and leaf nitrogen status has been shown to explain the differences in inflorescence growth with nitrogen supply in cauliflower. The intrinsic relative growth rate, rgr_{in}, is dependent on the nitrogen status at the time of inflorescence initiation and considered fixed from then on because the number of initiated cells is already determined shortly after inflorescence initiation. A sensitivity analysis of rgr_{in} on the fraction of inflorescence on total above-ground dry weight at the final harvest was performed

for the experiment in 1997. Within ±10% around the calculated values an increase in rgr_{in} by 1% leads to an increase in the fractions of inflorescence on total above-ground dry weight between 1.0-1.7 %, average 1.2%, for the different treatments. Although rgr_{in} is the relevant parameter of the exponential growth phase of the inflorescence, sensitivity analysis revealed that the approach is of acceptable robustness. The observed dependence of the generative sink capacity on nitrogen supply during the initiation phase was also found for onions (Stuart and Griffin, 1945) and *Kalanchoe blossfeldiana* (Rünger, 1960).

The estimation of the parameter f_{stem} describing the increase in stem growth with increasing inflorescence weight (eqn. 9) to be 0.15 (± 0.01) implies a maximum fraction of inflorescence growth rate on total growth rate of 0.85. This value is similar to 0.82 found by Kage and Stützel (1999).

A comparison of visible leaf numbers (diameter > 1 cm) shows no significant differences between the N-treatments except for the N0-treatments at the first two harvests in 1997. Atherton *et al*. (1986), however, found that for cauliflower cv. Perfection the rate of leaf initiation was not affected by nitrogen shortage. Since final leaf numbers of all treatments do not differ significantly it was assumed for the simulations that the initiated leaf numbers were the same for all treatments within one light environment at all times. The number of initiated leaves is decisive for the end of the juvenile phase. The lesser numbers of visible leaves in the N0-treatments at the first two harvests are attributed to a decreased leaf expansion rate after initiation. This assumption implies a different correlation between initiated and visible leaf numbers in nitrogen deficient plants than found by Booij and Struik (1990) for well fertilised plants. Further research is needed on the interdependence of growth and developmental processes as may be indicated by this phenomenon.

The use of a growth function to determine daily growth rates and consequently smoothen actual growth rates due to daily changes in environmental conditions is not decisive for model performance since the presented model on dry matter

partitioning does not depend on daily changes in growth rates. Any model on dry matter partitioning that predicts daily growth rate can be used instead. Harvest prediction of time and quantity is then easily incorporated.

Conclusion

The formulated concept of above-ground dry matter partitioning as dependent on nitrogen supply and light environment was successfully evaluated in cauliflower using data from field experiments for parameterisation and validation. The model is based on a functional dependency between stem and leaf area as well as a correlation of generative sink capacity on the plant's nitrogen status. Further research is needed on the interrelation of developmental and growth processes.

3. Optimal nitrogen content and photosynthesis. Scaling up leaf to plant

Abstract

A simple model of photosynthesis is described as dependent on leaf area, protein-nitrogen content and distribution within the canopy as well as light and temperature environment. The model is parameterised for cauliflower used as an example crop. The optimised protein-N profile within the canopy is calculated with respect to daily growth rate. By comparison with measured protein-N contents the amount of 'luxury N-uptake' is assessed for two different nitrogen and light treatments. The amount of 'luxury N-consumption' depends on N-supply and can accumulate in cauliflower to more than 80 kg N ha^{-1}.

3.1 Introduction

The nitrogen management strategies in plant production today seek to match fertiliser N-supply with crop N-demand. Fertiliser recommendations for practical farming give target values for individual crop species (Lorenz *et al.*, 1989; Scharpf, 1991). However, they do not account for specific environmental and agronomic conditions. To further increase nitrogen-use efficiency more precise estimates of crop N-demand should be deduced from physiological principles, particularly the productivity-N relationship. The key question is how much nitrogen is necessary for a certain yield under certain environmental conditions.

A framework is needed to predict crop CO_2-uptake from physiological characteristics (leaf area, leaf-N content and distribution) and environmental conditions. Benefits and costs of increased leaf-N contents, e. g. increased photosynthetic capacity and higher rates of protein turnover, occur on the leaf

level, whereas the economic product is formed on the plant level. Therefore a physiological approach has to quantify the photosynthesis-N relationship on the leaf level and scale it up to plant productivity.

Leaf nitrogen and photosynthesis

Since more than 50% of leaf-N is photosynthetically active (Evans, 1989), close relationships were found for different species between photosynthetic capacity and leaf-N content, both either expressed in terms of leaf area or leaf dry matter. The coefficients of correlation for linear relationships were similar in both cases (Field and Mooney, 1986; Reich *et al.*, 1994). Since CO_2-exchange is an area-related phenomenon photosynthesis is preferably expressed on a leaf area basis. The conversion between both units is done by the specific leaf area. Besides linear relationships, which mean a constant increase of photosynthetic capacity per unit of leaf-N, hyperbolic dependencies have been found (Del Pozo and Dennett, 1991; Muchow and Sinclair, 1994) showing decreasing benefits with each additional unit of nitrogen. So far a unified mathematical description could not be found, neither experimentally nor theoretically. The experimental results have in common a minimal N-content, n_s, above which gross assimilation starts. Following the original idea of Caloin and Yu (1984) this photosynthetically inactive part can be regarded as a component of leaf structure (structural N-pool).

Following theoretical considerations positive effects of higher leaf-N contents on productivity are accompanied by increased respiration (Penning de Vries, 1975; Penning de Vries *et al.*, 1974). The dependency of maintenance respiration on protein-N content is mainly attributed to continuously ongoing processes of protein breakdown and synthesis. Protein turnover is eminent for the plant to maintain its cellular structures, ion gradients as well as the ability to adapt to a changing environment or pathogens (Penning de Vries, 1975; Penning de Vries *et al.*, 1974). A linear dependence of maintenance respiration on protein-N content was found in experiments with *Chenopodium album*, *Amaranthus retroflexus* (Byrd *et al.*, 1992) and *Lolium perenne* (Jones *et al.*, 1978). In both experiments maintenance respiration was determined as the respiration rate after 40 or 48

hours of consecutive darkness. Ryan (1995) found a corresponding linear relationship when measuring the respiration of fully expanded foliage of different subalpine and boreal trees and shrubs. The appropriate way to measure maintenance respiration (Amthor, 1984) or if it can be correctly determined at all (Shinano *et al*., 1996) is still discussed.

Growth respiration as the second major contribution to total CO_2-efflux is attributed to the construction of new dry matter. Specific growth respiration has first been empirically and theoretically proposed to be proportional to the organ's relative growth rate by McCree (1970) and Thornley (1970), respectively. This was confirmed in many species, e. g. herbaceous monocotyledonous plants (Van der Werf *et al*., 1994), Mediterranean shrubs (Merino *et al*., 1982) and trees (Will and Ceulemans, 1997; Wullschleger *et al*., 1992).

Nitrogen distribution within the canopy

Leaves have the ability to adapt their photosynthetic capacity to their light environment (Björkman, 1981; Evans, 1989; Fahl *et al*., 1994; Pons and Bergkotte, 1996; Pons and Pearcy, 1994). Due to the close correlation between photosynthetic capacity and nitrogen content also a close correlation between the light intensity incident on a leaf and its N-content is observed (Charles-Edwards *et al*., 1987; DeJong and Doyle, 1985; Yoshie *et al*., 1994). In dense crops with almost homogeneously distributed leaf area N-contents follow the decreasing light intensity within the canopy (Anten *et al*., 1995; Bange *et al*., 1997; Hirose and Werger, 1987a; Lemaire *et al*., 1991; Shiraiwa and Sinclair, 1993).

The adaptation of the N-distribution which is supported by N-remobilization from shaded to photosynthetically more active leaves leads to an increase in whole-plant assimilation capacity compared to a homogenous N-distribution within the canopy (Leuning *et al*., 1995; Sinclair and Horie, 1989; Sinclair and Shiraiwa, 1993). Following quantitative considerations this increase amounts to ca. 5-8% in *Cucumis sativus*, *Phaseolus vulgaris* (Evans, 1989) and *Medicago sativa* (Evans, 1993) and between 23-48% in *Solidago altissima* (Hirose and Werger, 1987b) and

Lysimachia vulgaris (Pons *et al.*, 1989). Field (1983), Field and Mooney (1986) and Hirose and Werger (1987b) derive the hypothesis, that plants distribute the available nitrogen in order to maximise net CO_2-uptake.

This hypothesis is evaluated here to quantify the minimal nitrogen content of a plant for maximal CO_2-uptake. Based on this knowledge it can be decided if plants restrict their uptake under non-limiting N-supply or show 'luxury consumption'. A simple framework is needed to predict the amount and distribution of nitrogen in the crop necessary for potential growth under different light environments. The first step in exploring the productivity-N relationship is the quantification of instantaneous crop CO_2-assimilation. The first part of this study presents a photosynthesis model to predict crop CO_2-uptake from leaf area, leaf N-content and distribution as well as light and temperature environment. The model is parameterised and validated for cauliflower used as an example crop. In the second part of this study measured leaf N-contents and distribution within the canopy are compared to the optimised values with respect to daily growth rate to assess 'luxury N-consumption' by the plant.

3.2 Model

Single-leaf and canopy photosynthesis

The photosynthesis-light response of a single leaf is described by a non-rectangular hyperbola (Johnson and Thornley, 1984; Marshall and Biscoe, 1980a,b; Rabinowitch, 1951):

$$P_g = \frac{\alpha I + P_m - \sqrt{(\alpha I + P_m)^2 - 4\Theta\alpha I P_m}}{2\Theta} \quad , \tag{15}$$

where P_g is the rate of gross photosynthesis on leaf area basis, α and Θ are two parameters describing the initial slope and curvature of the response curve, respectively. I is the incident photosynthetically active photon flux density, and P_m denotes the gross photosynthetic capacity which was shown to be a linear function of the protein-N content on leaf area basis, n_a, (Anten *et al.*, 1995; Jensen *et al.*, 1996):

$$P_m = m \cdot n_a + b \tag{16}$$

The respiration rate of a single leaf, R, has contributions from both maintenance and growth processes. Maintenance respiration is mainly attributed to protein turnover and therefore assumed proportional to leaf protein-N content, whereas growth respiration is assumed to be proportional to the leaf's relative growth rate, rgr:

$$R = m_m \cdot n_a + m_g \cdot rgr \quad , \tag{17}$$

with m_m and m_g denoting the proportionality coefficients of maintenance and growth respiration, respectively.

From single-leaf respiration instantaneous canopy respiration, R_{leaf}, can easily be calculated as the integral over total leaf area, A_l:

$$R_{leaf} = \int_0^{A_l} [m_m \cdot n_a(l) + m_g \cdot rgr(l)]dl = m_m \cdot N_{P,leaf} + m_g \cdot \frac{dA_l}{dt} \quad , \tag{18}$$

where $N_{P,leaf}$ is the total amount of leaf protein-nitrogen, and dA_l/dt is the increase in leaf area per plant. Similar expressions for canopy respiration were proposed by Hesketh *et al*. (1971), McCree (1970) and Thornley (1970), except that they associate maintenance with standing dry matter rather than with the amount of nitrogen. In case of a constant nitrogen concentration both expressions can be transformed into each other.

CO_2-efflux resulting from stem and root, R_{stem} and R_{root}, respectively, are treated similarly to canopy respiration. Maintenance respiration is proportional to the amount of protein-N in the compartment, $N_{P,stem}$, with the same coefficient m_m as in eqn. 18. Growth respiration of the compartments is calculated as a fraction of canopy growth respiration. This share is determined by the fraction of the compartment on leaf dry matter:

$$R_{stem} = m_m \cdot N_{P,stem} + m_g \cdot \frac{dA_l}{dt} \cdot \frac{W_{stem}}{W_{leaf}} \qquad (19)$$

where W_{stem} and W_{leaf} denote the dry weight of the different organs. R_{root} is calculated analogously using the fraction W_{root}/W_{leaf} determined by the final harvest.

The respiration of the inflorescence, R_{in}, is an increasing source of CO_2-loss in the last two weeks before harvest. R_{in}, has contributions proportional to its protein-N content, $N_{P,in}$, and increase in dry weight, dW_{in}/dt, analogous to canopy respiration (eqn. 18). In cauliflower exponential growth, i. e. $dW_{in}/dt = rgr_{in} \cdot W_{in}$, can be assumed during the exponential growth phase with relative growth rate rgr_{in} (Chapter 2). Thus,

$$R_{in} = m_m \cdot N_{P,in} + m_{1,in} \cdot \frac{dW_{in}}{dt} = (m_m + m_{1,in} \cdot \frac{rgr_{in}}{n_{in}}) \cdot N_{P,in} = m_{in} \cdot N_{P,in} \qquad (20)$$

where $m_{1,in}$ denotes the CO_2-production per increase in dry weight and n_{in} is the protein-nitrogen concentration. Total inflorescence respiration during the exponential growth phase is simplified in this way to be proportional to its protein-N content with m_{in} describing the rate of CO_2-production per unit protein-N.

The whole-plant respiration per unit of time is the sum of R_{leaf}, R_{stem}, R_{root} and R_{in}:

$$R_{plant} = R_{leaf} + R_{stem} + R_{root} + R_{in} \quad . \tag{21}$$

Instantaneous rate of whole-plant net CO_2-uptake for a certain light environment is the integral of single-leaf photosynthesis (eqn. 15) over the whole leaf area, A_l, subtracted by whole-plant respiration:

$$P_{plant} = \int_0^{A_l} dl\, P_g(I, P_m) - R_{plant} \tag{22}$$

The single-leaf gross photosynthetic capacity, P_m, varies within the canopy. It is calculated for the different leaf layers by eqn. 16 from the measured nitrogen profile.

Environmental influences

Since the radiation environment of the conducted greenhouse experiments was predominantly diffusive the distinction between direct and diffuse radiation was neglected for reasons of simplicity. Thus, the PPFD upon a leaf layer, $I(l_c)$, with cumulative leaf area index l_c and light extinction coefficient k is related to the light intensity above the canopy, I_0, by Monsi and Saeki (1953):

$$I(l_c) = k \cdot I_0 \cdot e^{-k \cdot l_c} \tag{23}$$

The light extinction coefficient for diffuse radiation and spherical leaf-angle distribution is approximately given by k=0.72 (Goudriaan, 1977).

The dependence of maintenance respiration and light-saturated photosynthetic capacity, P_m, on air temperature are incorporated. Maintenance respiration resulting from all compartments at temperature T is corrected for by the factor $2^{(T-20)/10}$ using a Q_{10}-value of 2 (Penning de Vries *et al.*, 1989) and a reference temperature of 20°C. The temperature dependence of P_m can be described by a plateau function for many species (Hikosaka, 1997; Penning de Vries *et al.*, 1989;

Walcroft *et al*., 1997). Independent measurements showed no reduction in P_m of cauliflower leaves between 15°C and 25°C (Kage *et al*., 1999). For every degree Celsius below 15°C or above 25°C a reduction in P_m of 1/15% is assumed. Thus, P_m was corrected for temperature by the factor f_P given by:

$$f_P = \begin{cases} 0 & T \le 0 \\ \frac{T}{15} & 0 < T \le 15 \\ 1 & 15 < T \le 25 \\ 1 - \frac{T-25}{15} & 25 < T \le 40 \\ 0 & T > 40 \end{cases} \qquad (24)$$

3.3 Material and Methods

Plant culture

In 1997 and 1998 cauliflower (*Brassica oleracea* L. convar. *botrytis* var. *botrytis* L. cv. Fremont) was grown in a glasshouse in Kick-Brauckmann pots, ca. 8 litre volume, filled with sand (particle size up to 2 mm). The seeds were sown for germination in planting plates filled with peat and transplanted by hand in cubes of rock wool (Grodan, Grodania A/S) with 4 cm edge length after about 7-9 days. When the plants had produced three visible leaves they were transplanted in the glasshouse (Table 5). Pots were arranged in rows with distances given in Table 5. The glasshouse minimum temperature was set to 14°C during daytime and 10°C during night.

Table 5: Planting dates and treatments of the greenhouse experiments

Year	Sowing date	Transplanting date	Row spacing (m × m)	Nitrogen levels (mg N l^{-1})	Light environment
1997	28 Jan	28 Feb	0.60 × 0.50	35, 145	shading net, suppl. light
1998	11 Feb	12 Mar	0.60 × 0.55	13, 45	no variation

Treatments

With transplanting two different light environments and nitrogen-fertiliser levels were imposed in 1997 (Table 5). Supplemental light was used in one half of the glasshouse and a shading net with an absorption of photosynthetically active radiation (PAR) of 14% in the other. The supplemental light consisted of 16 sodium high pressure lamps (SON-T 400, Philips) arranged evenly to ensure uniform light distribution of 200 μmol PAR m^{-1} s^{-1} at pot height. The lamps were operated approximately from one hour after sunrise till one hour before sunset. The average totals of daily PAR during the cultivation period were 2.6 and 4.6 MJ m^{-2} d^{-1} in the low-light and high-light treatments, respectively. The plants under one light environment were irrigated with one of two nutrient solutions differing only in nitrate-N content (Table 6). Irrigation was switched on 5-20 times per day during daytime depending on accumulated radiation and plant size. Each pot was irrigated with about 300 ml per interval.

In 1998 the experimental program concentrated on parameterisation and validation of the respiration part in the model (Table 7 and Table 8). The variation in light environment was sacrificed and replaced by a replication of the N-treatments due to the need of an increased number of plants of the same treatment to be used for destructive harvests. The N-concentrations of the nutrient solutions were reduced to 13 mg N l^{-1} and 45 mg N l^{-1} since the irrigation frequency was increased. Depending on plant size about 300 ml per interval were

given 2-5 times per hour during daytime to ensure an almost constant nitrogen concentration in the rooting zone.

Table 6: Composition of the nutrient solutions and their concentrations

Year	Final N-content (mg l^{-1})	N-free basic fertiliser* (g l^{-1})	$Ca(Cl)_2$ (g l^{-1})	$Ca(NO_3)_2$ (g l^{-1})	$NH_4(NO)_3$ (g l^{-1})
1997	35	0.7	0.3	0.3	-
	145	0.7	0.3	0.3	0.3
1998	13	0.7	0.5	0.1	-
	45	0.7	0.3	0.4	-

*: Flory Basisdünger 1, Euflor GmbH

Physiological measurements in 1997

On five intermediate harvests, on average every two weeks, single-leaf and whole-plant CO_2-uptake rates were determined. Single-leaf measurements (Table 7) were made using a mini cuvette with 2.5 cm^2 measuring area (Ciras-1, PP Systems, UK) on leaves 3, 5, 8, 11 and 14. All leaves were exposed to various photosynthetically active photon flux densities (PPFD) up to 2100 µmol m^{-2} s^{-1}. After measurements had been completed the leaf sections were collected and total and nitrate-nitrogen contents were determined by the micro-Kjeldahl method and a nitrate-sensitive electrode, respectively. For whole-plant measurements (Table 8) pots were transferred to a cuvette with a chamber volume of 1 m^3, which is described by Krug *et al.* (1977) and Lorenz (1981), around the middle of the day. The CO_2-uptake rates were recorded for various PPFD up to 1500 µmol m^{-2} s^{-1}. Two to four plants per treatment and harvest were chosen for gas-exchange analysis depending on plant size. Following CO_2-exchange measurements four plants per treatment and harvest were separated into stem, leaves including

petioles and inflorescence. At final harvest also root dry matter was determined by washing out a pie-quarter of the pot volume. Stems were cut 1 cm below sand level and at the onset of inflorescence. The foliage was further subdivided into groups of three consecutive leaves. Leaf area of every group was determined (Licor 3100, LI-COR Inc., Lincoln, NE, USA). After aliquots of all plant compartments had been oven dried until weight constancy dry matter was determined. Analysis of total and nitrate-N followed (see above).

Table 7: Physiological measurements on single-leaf level

Experiment	Leaf-chamber measurements of	Temp. (°C)	CO_2-conc. (ppm)	Rel. humidity (%)
glasshouse, 1997	photosynthesis	18-24	360 (±10)	70-90
field, 1997	photosynthesis	18-22	360 (±10)	70-90
glasshouse, 1998	respiration	18-24	360 (±10)	70-90

Physiological measurements in 1998

In 1998 gas-exchange measurements were conducted during the last six weeks before final harvest. Single-leaf CO_2-efflux was measured twice a week on leaves 3, 5, 8, 11, and 13, depending on plant size, of plants of both treatments under darkness. In order to calculate the relative growth rates length and width of the same leaves were determined on three consecutive days with gas exchange measurements in between. After measurements were completed the leaves were collected, leaf area, total nitrogen and nitrate-N was determined as above. Once a week plants of both treatments were transferred to the whole-plant cuvette and total plant respiration was measured under darkness in the evening and in the next morning. Since inert sand was used as substrate soil respiration was successfully prevented. Following the respiration measurements plants were separated into stem, leaves and inflorescence for dry matter determination and analysis of total and nitrate-N (see above). On four intermediate harvests three

plants per treatment and replication were collected and separated into stem, leaves and inflorescence as described above. Dry matter and nitrogen analysis followed.

Table 8: Physiological measurements on whole-plant level

Experiment	Whole-plant cuvette measurements of	Temp. (°C)	CO_2-conc. (ppm)	Rel. humidity (%)
glasshouse, 1997	photosynthesis,	20-22	340-380	80-90
	respiration	14-16	340-500	80-90
glasshouse, 1998	respiration	14-16	340-500	80-90
field, 1997	-			

Field experiment 1997

In addition to the glasshouse experiment in 1997 single-leaf photosynthesis was measured on plants of a field experiment to include data derived from the typical growth situation in practical farming. The same cauliflower cultivar 'Fremont' was grown on the institute's experimental farm located 15 km south of Hanover, Germany. Immediately after transplanting four different nitrogen-fertiliser levels were imposed. Nitrogen fertilisation was given as ammonium nitrate at the time of transplanting in quantities of 0, 150, 300 and 450 kg N ha^{-1}. Soil nitrate content of 15 kg N ha^{-1} in 0-60 cm were subtracted from the 150, 300 and 450 kg N ha^{-1} target values. For further details on this experiment see Chapter 2. On three intermediate harvests single-leaf measurements were conducted on leaves number 5, 8 and 11 of randomly chosen plants from different N-treatments under various PPFD up to 2100 µmol m^{-2} s^{-1}.

Calculating optimal nitrogen distribution

In order to calculate the optimal nitrogen distribution with respect to daily net CO_2-gain. i. e. maximising the daily integral of P_{plant} (eqn. 22), the model described above was programmed in Turbo Pascal implementing the downhill simplex optimisation method (Press *et al.*, 1986). The integration over time was performed using the Euler-algorithm (Thornley and Johnson, 1990) with a time step of one hour. The optimal N-contents of different leaf layers were calculated for every treatment and harvest in 1997. Input parameters were measured leaf area and daily increase in leaf area (eqn. 18) determined by interpolating the measured data by a logistic growth function. Variation in photosynthetically active photon flux density above the canopy, I_0, with time, t, was assumed to follow a sine-squared function:

$$I_0(t) = I_{noon} \cdot \sin^2(\pi \cdot \frac{t}{d}) \ , \qquad (25)$$

where d denotes the daylight period and I_{noon} is the maximum PPFD at solar noon calculated from the daily total, I_{tot}, by $I_{noon}=2\ I_{tot}\ d^{-1}$. I_{noon} was averaged over a period of two weeks before each harvest and ranged from 500 to 800 $\mu mol\ m^{-1}\ s^{-1}$, and from 700 to 1100 $\mu mol\ m^{-1}\ s^{-1}$ for the low and high light treatments in 1997, respectively. The assumed temperature regime was set to 18°C during the daylight period and 14°C during night. The average daylight period, d, varied for the different harvests according to the season from 12 to 14 hours.

Statistics

All statistical analyses were carried out using the procedures NLIN and REG of the SAS software package (SAS Institute, 1988). The level of significance was calculated with an error probability < 0.05.

3.4 Results

Parameterisation of the single-leaf photosynthesis model

Separate estimates of the parameters α and Θ of the non-rectangular hyperbola (eqn. 15) for every leaf showed no statistically significant relationship to light-saturated gross photosynthesis, P_m, (Figure 9).

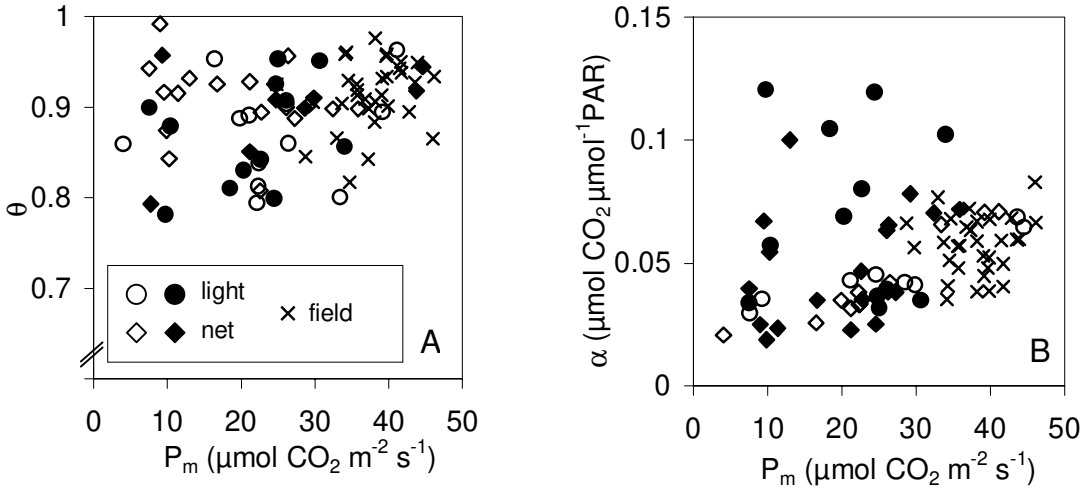

Figure 9: Curvature factor, θ (A), and initial slope, α (B), of the photosynthesis-light response curve vs. the gross photosynthetic capacity of single leaves, P_m; open and closed symbols refer to the N-treatments of 145gN l^{-1} and 35gN l^{-1}, respectively, in the glasshouse experiment 1997; field experiment 1997.

When the values of the parameters α and Θ were kept constant for all leaves the predictions of the non-rectangular hyperbola agreed well with the measured data of all leaves under different light intensities up to 2100 µmol PAR m^{-2} s^{-1} (Figure 10). The values were estimated to be α = 0.056(±0.002) µmol CO_2 µmol^{-1} PAR and Θ = 0.899(±0.012) by non-linear least-square regression analysis. For the calculation of photosynthesis the parameters α and Θ were kept at the estimated values and the gross photosynthetic capacity of a single leaf, P_m, was determined

as the sum of maximum net photosynthesis and respiration measured for each leaf. P_m varied from 2 to 50 µmol PAR m^{-2} s^{-1} within the canopy.

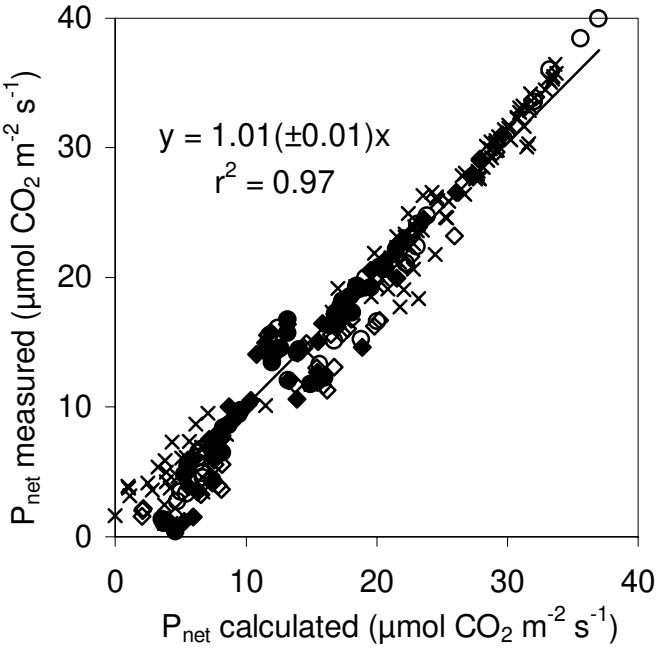

Figure 10: Measured and calculated net photosynthesis of single leaves; glasshouse experiment 1997; field experiment 1997; symbols as in Figure 9.

Seventy-five percent of the observed variation in P_m could be attributed to differences in leaf protein-N content on leaf area basis, n_a, (Figure 11). If P_m is related to total leaf N-content including nitrate the variability increases. The structural protein-N pool, n_s, defined as $P_m(n_s) = 0$, is calculated from the linear regression equation to be 0.40 g N m^{-2}.

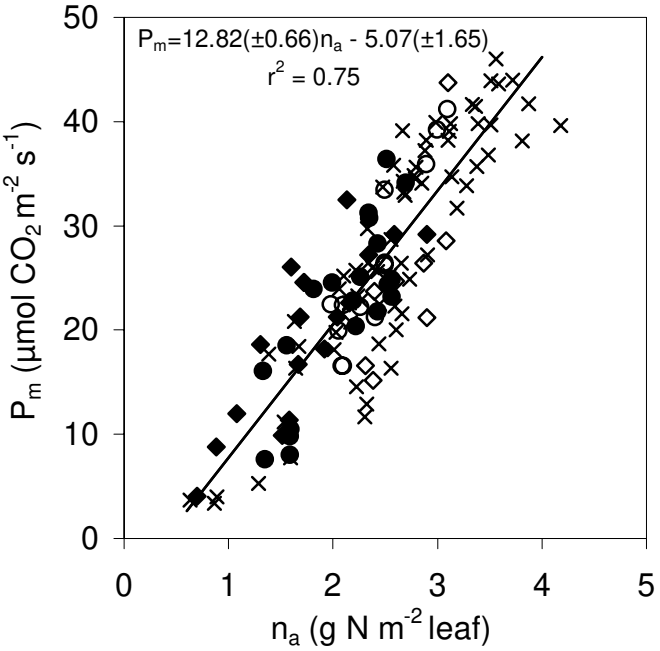

Figure 11: Relationship between gross photosynthetic capacity, P_m, and protein-N content per unit leaf area, n_a; glasshouse experiment 1997, field experiment 1997; symbols as in Figure 9.

The respiration rate of single leaves could well be described by eqn. 17 with growth respiration included (Figure 12). The leaves' relative growth rates, rgr, were estimated as the increase in leaf area within 24 hours per leaf area present.
The respiration rate of inflorescence measured immediately after cutting was linearly related to the inflorescence protein-N content, which was derived in eqn. 20 for the inflorescence during its exponential growth phase. The proportionality coefficient, m_{in} (eqn. 20) , was determined by the slope of the regression line (Figure 13) using all data, although some inflorescences having protein-nitrogen contents above 2-3 g probably have passed exponential growth phase already.

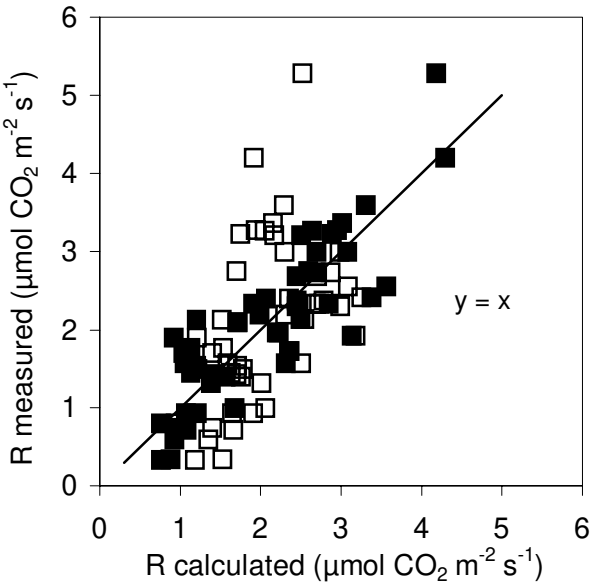

Figure 12: Single-leaf respiration, R, as dependent on protein-N content per unit leaf area, n_a, and relative growth rate, rgr: $R=0.68(\pm0.05)n_a+1.31(\pm0.17)rgr$, $r^2=0.74$, (closed symbols); neglecting rgr shows the importance of growth respiration, $R=0.99(\pm0.06)n_a$, $r^2=0.22$, (open symbols); experiment 1998.

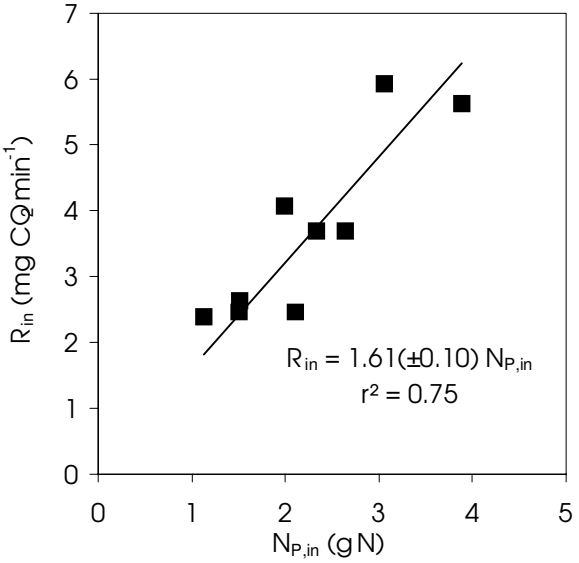

Figure 13: CO_2-loss of the inflorescence, R_{in}, vs. its protein-nitrogen content, $N_{P,in}$, shortly after cutting; experiment 1998.

Independent measurements showed a linear decrease in whole-plant respiration during the first 10 to 16 hours of darkness (data not shown). The exhaustion of carbohydrate stores may cause respiration to decline (Azcon-Bieto and Osmond, 1983). The decrease in respiration per unit leaf area was determined from canopy measurements at the beginning of the night and after about twelve hours in darkness. The decline progresses linearly with the duration of darkness, t_n:

$$R_{plant,a}(t_n) = R_{plant,a}(0) - m_R \cdot t_n \qquad (26)$$

where m_R denotes the rate of decrease in respiration per unit leaf area and $R_{plant,a}(0)$ is the initial whole-plant respiration per unit leaf area at the beginning of the night. In 1997 and 1998 the rate constant m_R was found to depend on $R_{plant,a}(0)$. The higher $R_{plant,a}(0)$ the faster the rate of decline (Figure 14).

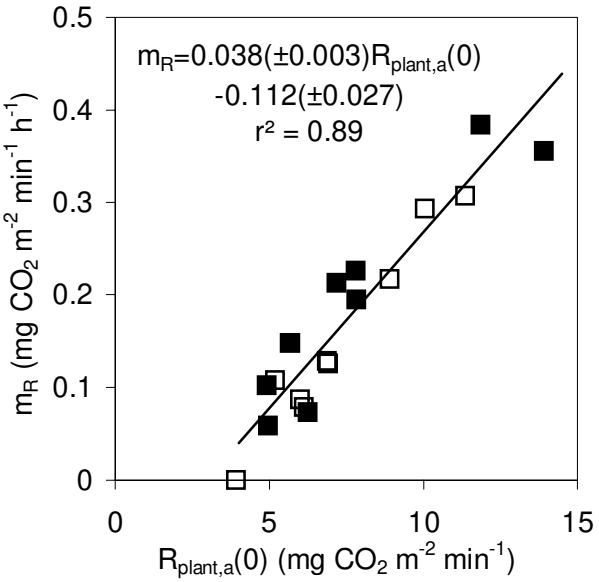

Figure 14: Dependency of the decrease in whole-plant respiration during the night, rate constant m_R, on whole-plant respiration during daytime, $R_{plant,a}(0)$; glasshouse experiments 1997 (open symbols) and 1998 (closed symbols).

Validation of the single-leaf photosynthesis model

There was good agreement between canopy photosynthesis measured with the whole-plant cuvette and the predicted values based on the single-leaf model described above (Figure 15). The model was validated with plants from all growth stages differing in leaf area, leaf growth rate and total and inflorescence dry weight as well as under different PPFD up to 1500 µmol m^{-2} s^{-1}.

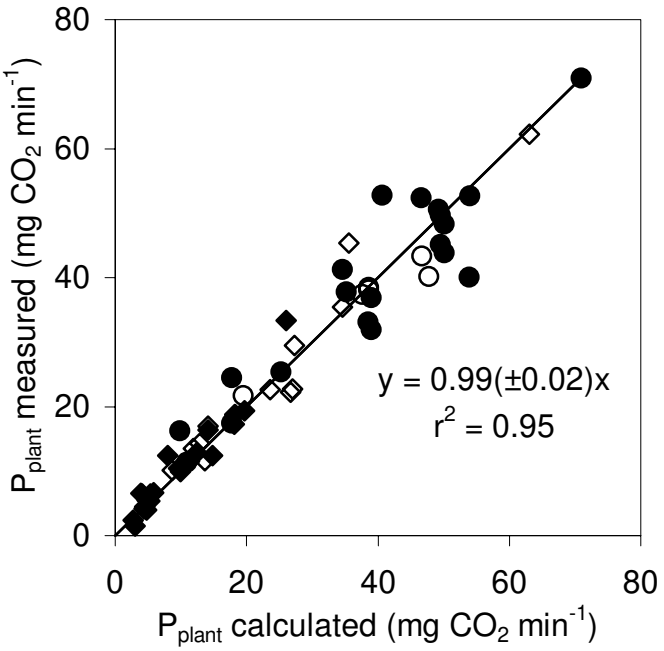

Figure 15: Measured vs. calculated whole-plant photosynthesis, P_{plant}, of plants from all harvests and treatments; glasshouse experiment 1997. The incident light intensity varied up to 1500 µmol PAR m^{-2} s^{-1}; symbols as in Figure 9.

The instantaneous whole-plant respiration was validated separately with plants from all growth stages (Figure 16). In both years the CO_2-efflux of randomly chosen plants differing in leaf area, leaf growth rate, nitrogen content and inflorescence dry weight was determined under darkness during the day.

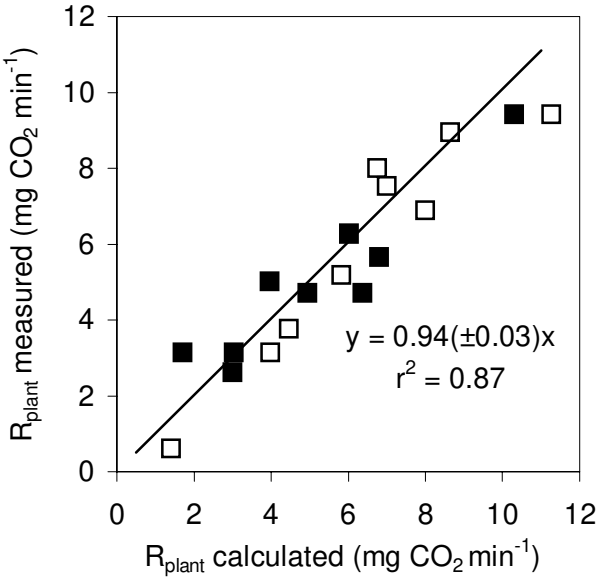

Figure 16: Measured vs. calculated daytime whole-plant respiration, R_{plant}, of plants from all harvests differing in leaf area, total and inflorescence dry weight; glasshouse experiments 1997 (open symbols) and 1998 (closed symbols).

Optimised nitrogen contents

The comparison between measured and optimised protein-N distributions within the canopy relative to the value at the top of the canopy, expressed per unit leaf area, shows different behaviours for the low and high N-treatments (Figure 17). Whereas the high N-treatments are well above the 1:1 line the low N-treatments lie closer to the calculated optima. The regression lines for the low and high nitrogen treatments are y=0.98(±0.03)x, r^2 = 0.68, and y=0.79(±0.12)x+0.23(±0.07), r^2 = 0.64, respectively. The comparison of the absolute protein-N contents per unit leaf area shows also different behaviours for both N-treatments (Figure 18). The measured N-contents of the high N-treatments lie always above the optimised values. Instead, the N-contents of the low N-treatments are below the predicted values in the upper leaf layers with higher N-contents. The regression lines for the low and high nitrogen treatments are y=0.71(±0.06)x+0.61(±0.14), r^2 = 0.77, and y=0.89(±0.09)x+0.86(±0.17), r^2=0.73, respectively.

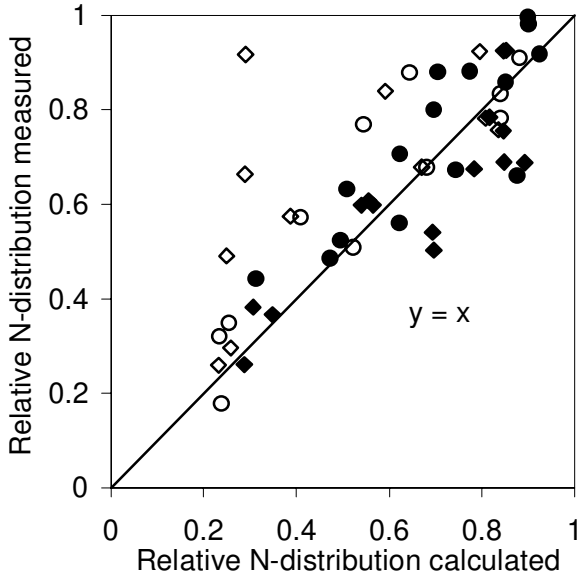

Figure 17: Measured vs. calculated protein-N contents per unit leaf area of leaf layers in different positions in the canopy relative to the value at the top of the canopy for all treatments and harvests; glasshouse experiment 1997; symbols as in Figure 9.

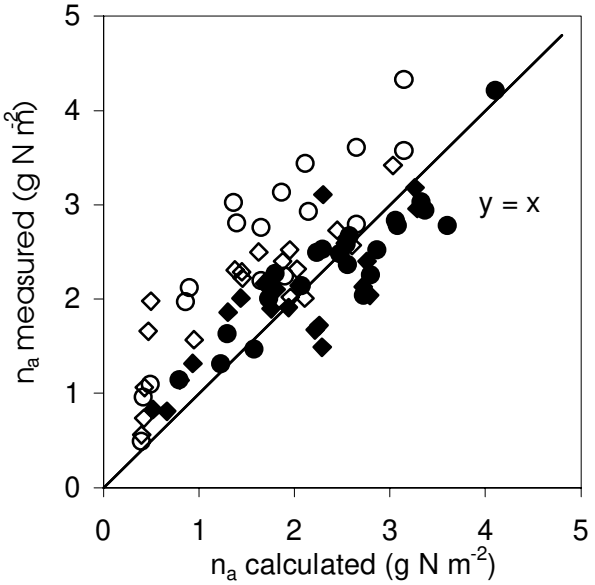

Figure 18: Measured vs. calculated protein-N contents per unit leaf area, n_a, of leaf layers in different positions in the canopy for all treatments and harvests; glasshouse experiment 1997; symbols as in Figure 9.

The total amount of protein-nitrogen taken up by the plant can accumulate in the canopy to more than 2.5 g N per plant during growth (Figure 19A). As before, both light treatments of the same N-supply show similar behaviour. The luxury N-uptake of the high N-treatments is accumulated almost from the time of transplanting. The low N-treatments first undergo a period of time up to a LAI between 0.5 and 1 where N-uptake does not follow demand. At the end of the growth phase they show luxury uptake to a smaller extend than the high N-treatments. The influence of luxury N-consumption on the assimilation capacity of a plant was the same for all treatments and harvests depending on the deviation from the optimised N-content (Figure 19B). A relative deviation from the optimised canopy N-content of about 10% has little consequences on CO_2-assimilation capacity.

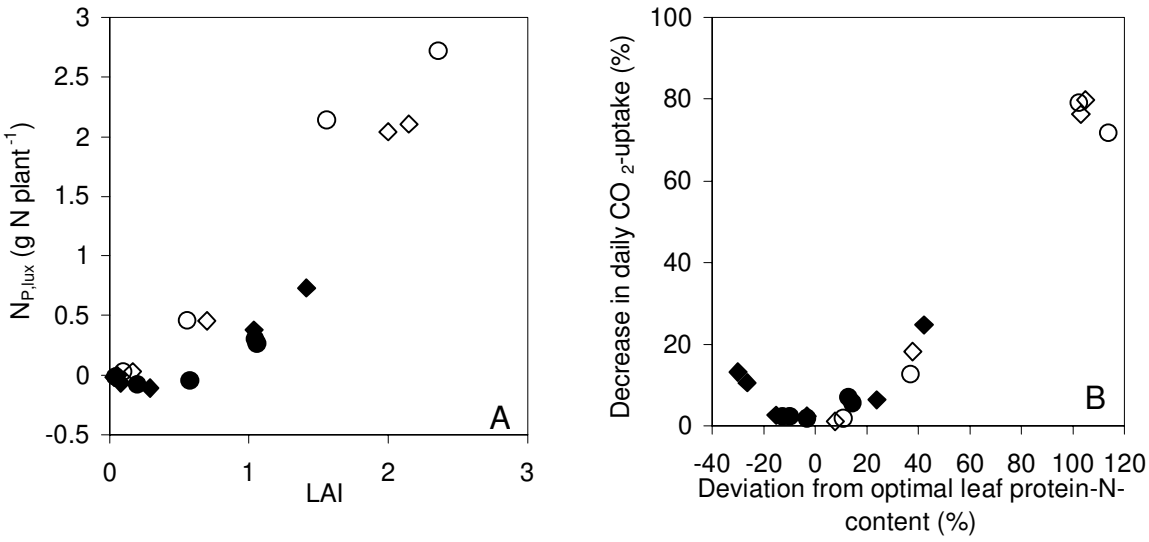

Figure 19: Amount of protein-N in the canopy above the predicted optimum, i. e. amount of luxury protein-N taken up, $N_{P,lux}$, vs. leaf area index, LAI (A). Decrease in daily net CO_2-uptake relative to the optimised value vs. relative deviation from the optimised canopy protein-N content (B); glasshouse experiment 1997; symbols as in Figure 9.

Nitrogen-use efficiency (NUE) on plant level is calculated for all treatments as the net CO_2-uptake by the canopy within 24 hours per unit of protein-nitrogen present in the leaves using the average environmental conditions during 14 days prior to harvest. The dependence of NUE on nitrogen status is described by the same behaviour for all treatments if compared relative to the optimised protein-N content and NUE calculated with the optimised protein-N profile (Figure 20). An increase in leaf protein-N content by 1% leads to a decrease in NUE by almost one percent irrespective of plant nitrogen status.

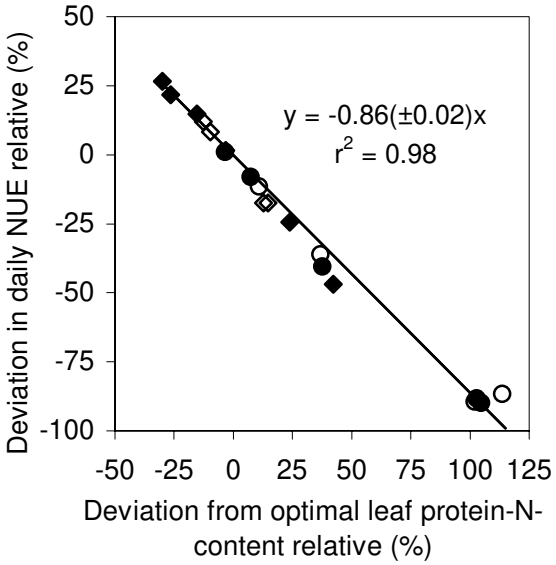

Figure 20: Deviation in daily NUE relative to the NUE calculated for the optimised canopy protein-N content vs. deviation from the optimised protein-N profile; glasshouse experiment 1997; symbols as in Figure 9.

3.5 Discussion

This study was set up to find out how cauliflower plants regulate their N-accumulation and distribution in the canopy. Specifically, the hypothesis was tested, whether plants control their N-accumulation and distribution such that they maximise net photosynthesis under the conditions given. In order to provide a variation in supply, two N-levels were offered by nutrient solution. A simple framework was developed to predict the amount and distribution of nitrogen in the crop necessary for potential growth. First the instantaneous crop CO_2-assimilation as dependent on leaf area, leaf protein-N content and distribution as well as light and temperature environment was quantified. Then measured leaf protein-N content and distribution within the canopy were compared to the optimised values with respect to daily growth rate to assess the plant's potential for 'luxury N-consumption'.

The non-rectangular hyperbola (eqn. 15) fitted the light response data of photosynthesis for all treatments well. The estimated values of the initial slope, α = 0.056(±0.002) μmol CO_2 μmol^{-1} PAR, and the curvature factor, Θ=0.899(±0.012), are similar to the values α = 0.056 μmol CO_2 μmol^{-1} PAR and Θ in the range of 0.7 to 0.9 cited by Boote and Loomis (1991) as a commonly observed among C_3 species. The same range of Θ and an almost constant value of α = 0.04 μmol CO_2 μmol^{-1} PAR was observed in maize (Stirling *et al.*, 1994). The single-leaf photosynthesis model showed good agreement with measured data from plants of all growth stages differing in leaf area, growth rate and protein-N content when scaling up to canopy photosynthesis. The linear relationship between P_m and leaf protein-N content also found for many other species, allowed to estimate the structural protein-N pool, n_s. The value of 0.40 g N m^{-2} lies in the range from 0.2 to 0.4 g N m^{-2} measured for *Oryza sativa*, *Glycine max*, *Sorghum bicolor*, *Amaranthus cruentus* and *Tetrorchidium rubrivenium* (Anten *et al.*, 1995).

The specific respiration of a single leaf during daytime was linearly related to its protein-N content and its relative growth rate. Maintenance respiration defined by the first term in eqn. 17 ranges in leaves with protein-N contents between 0.4 and

4 g N m^{-2} from 0.27 to 2.72 µmol CO_2 m^{-2} s^{-1}. Converting these values to a mass based unit using a specific leaf area of 0.01 m^2 g^{-1} for cauliflower leads to 0.01 to 0.10 g CO_2 g^{-1} dry weight d^{-1} which contains the range of 0.03 to 0.08 g g^{-1} d^{-1} cited by Penning de Vries *et al*. (1989) for field-grown leaves of different species at 20°C. If the coefficient of the growth contribution, i. e. the second term in eqn. 17, is converted using again a specific leaf area of 0.01 m^2 g^{-1} and corrected for the decrease in growth respiration during the night (eqn. 26), it predicts 0.48 g CO_2 efflux per g leaf dry matter produced. Penning de Vries *et al*. (1989) report a theoretical value of 0.46 g CO_2 g^{-1} for leaves of non-leguminous and non-rice crops. The same specific respiratory energy was assumed for all plant organs although it has been found to vary with the biochemical composition of the biomass (Penning de Vries *et al*., 1989; Poorter and Bergkotte, 1992). Following Penning de Vries *et al*. (1989) the specific respiratory energy for roots is less than for leaves by about 10-15%. If the fraction of root on total dry matter is assumed to lie in the range of 0.1 to 0.3 during most of the growth period and if growth respiration is assumed to contribute about 50% to the total respiration of the plant, the overestimation of root growth respiration is less than 3% to the total CO_2-efflux of the plant. The respiratory costs involved in ion uptake of roots (Van der Werf *et al*., 1988) were also neglected. Van der Werf *et al*. (1994) cite a value of 0.58 g C lost per g N taken up as the average for the species *Briza media* and *Dactylis glomerata*. Based on this value and a C/N ratio of 12 root respiration is underestimated by less than 5% of the plant's total C-gain. The underestimation of root respiration due to neglecting ion uptake may compensate the overestimation of root growth respiration. With the experimental set-up used the difference in respiratory costs for various organs or the energy involved in ion uptake could not be resolved.

The photosynthesis model was used to calculate the optimal N-distributions and N-contents for plants grown under different light environments and N-supply with respect to daily net CO_2-gain. In the high N-treatments nitrogen was more evenly distributed within the canopy than the model predicted to be optimal whereas the low N-treatments were close to the optimised distribution. Also, the absolute N-

contents of the high N-treatments were above the optimised values. It was therefore observed that the closer the total amount of nitrogen in the canopy is to its optimum the closer follows the relative N-distribution within the canopy the optimised distribution. The absolute N-contents of the lower leaf layers were in all treatments above the predicted values indicating insufficient N-translocation into upper layers. This may be due to a limited rate of N-remobilization within the canopy, probably due to the additional costs of N-translocation that are not taken into account by the model (Field, 1983). Incorporating the acclimation of single-leaf N-contents to changing light environment (Hikosaka and Terashima, 1995; Thornley, 1998) may explain the dynamical N-distribution within the canopy.

Luxury protein-N uptake by plant leaves can accumulate during growth to about 2.5 g N per plant, resulting in more than 80 kg N ha^{-1} with 33000 plants ha^{-1}. This does neither include nitrate-nitrogen nor contributions from stem or curd. The luxury N-consumption is mainly related to N-supply rather than light environment. During most of the growing period the N-contents of the low N-treatments were within ±15% relative to the optimised values. This is about the range within the assimilation capacity of the plant under average environmental conditions is little affected (Figure 19B). At the end of the growing period the high N-treatments deviate to more than 100% from the optimised N-content. Concerning the decline in relative growth rate luxury N-uptake is counter-productive. It could either not be sufficiently down-regulated by the plant or it was advantageous from a different perspective, e. g. inter-plant competition during evolution, or from an alternative concept of nitrogen distribution, e. g. the co-ordination theory (Chen *et al.*, 1993) or nitrogen-use efficiency on plant level defined as the net-CO_2-uptake by the canopy within 24 hours per unit of protein-N present in the leaves. NUE for these treatments proofed to continuously decrease with increasing leaf nitrogen content, even under conditions of sub-optimal growth. NUE on plant level is therefore no sensible criterion to use as an alternative to optimise nitrogen contents. Without further restriction this criterion would lead to highly N-deficient plants.

Using the concept of optimised N-contents with respect to productivity to compare different fertiliser strategies and to finally predict crop N-demand as discussed by Grindlay (1997) requires further the incorporation of N-uptake dynamics as dependent on N-supply.

Conclusion

The model presented was able to predict whole-plant assimilation from single-leaf photosynthesis in cauliflower under different environmental conditions. The nitrogen uptake of cauliflower is mainly dependent on N-supply and can exceed the optimal amount with respect to potential growth rate. This luxury consumption can amount to more than 100% of the leaf-nitrogen requirement or 80 kg N ha^{-1} in cauliflower. The closer the total amount of nitrogen in the canopy is to its calculated optimum the closer the relative N-distribution within the canopy follows the predicted distribution.

4. Nitrogen content and distribution in the plant

Abstract

A simple model of nitrogen uptake and distribution is described as dependent on the amount of available soil nitrate and plant growth rate. The model is parameterised for cauliflower used as an example crop. The nitrogen uptake is assumed as being 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 on single-leaf level. Applied to an independent data set the combined model predicted leaf, stem and inflorescence nitrogen concentrations (r^2 = 0.89, 0.66 and 0.86, respectively) as well as leaf nitrate-N concentrations (r^2 = 0.87) for different nitrogen and light treatments. Dry matter production based on the productivity-N relationship and the partitioning into leaf, stem and inflorescence was also reproduced (r^2 = 0.91, 0.93 and 0.92, respectively).

4.1 Introduction

Relationships between nutrient status and plant growth rate have long been observed, e. g. the productivity-nitrogen relationship on single-leaf (Evans, 1983; Field and Mooney, 1986) as well as on whole-plant level (Agren, 1985; Burns, 1994b). The combination of these physiological principles with N-uptake dynamics of the plant may be used to predict crop N-demand. A mechanistic understanding of the interrelations between plant nitrogen content, plant productivity and available nitrogen in the soil will help to match crop N-demand and fertiliser N-supply for specific environmental and agronomic conditions.

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; Justes *et al.*,

1994; 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). Theoretical considerations of Caloin and Yu (1984) explain the progressive decline by two plant compartments shifting their fraction on total plant weight during growth. One fraction is involved in photosynthesis whereas the other is associated with plant structure and storage having a smaller nitrogen content per unit dry weight. Bellert *et al.* (1998) parameterised this model for tomato plants. Greenwood *et al.* (1990) empirically quantified for many species a critical nitrogen concentration, n_{crit}, required for maximum growth rate. Comparing the nitrogen concentrations during crop growth with n_{crit} may be used for fertiliser recommendations (LeBot *et al.*, 1998). The concept of critical nitrogen concentrations was used by Greenwood *et al.* (1991) to predict crop growth under optimal and sub-optimal N-supply. This concept does not take account of specific environmental and agronomic conditions during growth and their possible influences on n_{crit} as well as negative effects of luxury N-consumption on crop productivity, e. g. increased maintenance respiration due to enhanced protein-turnover.

In Chapter 3 the physiological processes determining productivity, photosynthesis and respiration, were quantified in cauliflower with respect to nitrogen content. A simple model of photosynthesis was parameterised and validated depending on leaf area, growth rate, protein-nitrogen content and distribution within the canopy as well as light and temperature environment. Predicting the nitrogen demand for a specific yield under certain environmental and agronomic conditions requires the additional knowledge of the plant nitrogen content and distribution during growth. A simple framework is needed to predict nitrogen concentrations of different plant parts from plant physiology and soil nitrogen content.

4.2 Model

The nitrogen uptake by the plant may either be sink or source limited. Sink limitation is characterised by a maximum nitrogen concentration as a plant's physiological or genetically inherited upper limit. Source limited N-uptake due to restricted diffusion and mass flow to the roots is assumed to be related to the N_{min}-value as a determinant of the average NO_3-N concentration in the soil. This requires a root length density exceeding ca. 0.5 cm cm^{-3} in the relevant soil layers (De Willigen and Van Nordwijk, 1987a; Kage, 1997) which can be assumed in the present system during most of the growing period. The source limitation can be expressed by a factor f_{soil} ranging from one to zero as the available amount of nitrate in the soil decreases. Very high amounts of soil nitrate-nitrogen affecting plant growth negatively are not taken into account. Thus, the amount of leaf nitrogen taken up, N_{leaf}, is assumed to be the maximum N-content corrected for source limitation, i. e.

$$N_{leaf} = n_{max,leaf} \cdot W_{leaf} \cdot f_{soil}(N_{min}) \qquad (27)$$

where $n_{max,leaf}$ denotes the maximal N-concentration of the foliage under non-limiting N-supply. Nitrogen translocation and remobilization within the canopy due to senescence and self-shading lead to a decreasing leaf N-concentration with increasing leaf area index, LAI, even under optimal N-supply. Thus, $n_{max,leaf}$ may be expressed as a function of LAI:

$$n_{max,leaf} = -m_1 \cdot LAI + b_1 \qquad (28)$$

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 well fertilised transplants.

The amount of nitrogen taken up per unit of time, dN_{leaf}/dt, is derived from eqn.27:

$$\frac{dN_{leaf}}{dt} = n_{max,leaf} \cdot f_{soil}(N_{min}) \cdot \frac{dW_{leaf}}{dt} + n_{max,leaf} \cdot W_{leaf} \cdot \frac{df_{soil}(N_{min})}{dt} \qquad (29a)$$

where dW_{leaf}/dt denotes the increase in leaf dry matter. Since f_{soil} is assumed to be a continuous function depending smoothly on N_{min} the last term in eqn. 29a is

of major importance whenever nitrogen supply in the soil changes very rapidly with time, e. g. when splitting N-fertiliser applications. Since this is not the case in the present study the term will be neglected in the following.

The N-uptake of stem, root and inflorescence have the same form as the first term in eqn. 29a with stem, root and inflorescence N-concentrations $n_{max,stem}$, $n_{max,root}$ and $n_{max,in}$, respectively:

$$\frac{dN_{stem}}{dt} = n_{max,stem} \cdot f_{soil}(N_{min}) \cdot \frac{dW_{stem}}{dt} \tag{29b}$$

$$\frac{dN_{root}}{dt} = n_{max,root} \cdot f_{soil}(N_{min}) \cdot \frac{dW_{root}}{dt} \tag{29c}$$

$$\frac{dN_{in}}{dt} = (n_{max,in} \cdot f_{soil}(N_{min}) + n_{red}) \cdot \frac{dW_{in}}{dt} \tag{29d}$$

The additional parameter n_{red} in eqn. 29d represents nitrogen redistribution from vegetative into generative organs as observed for many field crops (Booij *et al.*, 1997; Sinclair and de Wit, 1975). All vegetative organs are supposed to contribute to the rate of nitrogen translocation, i. e. $n_{red} \cdot dW_{in}/dt$ (eqn. 29d), according to their fraction on the total amount of nitrogen stored in leaves, stem and root. The fraction translocated e. g. from leaves is given by $n_{red} \cdot dW_{in}/dt \cdot N_{leaf}/(N_{leaf}+N_{stem}+N_{root})$. 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 g N g^{-1}.

The profile of protein-nitrogen in the canopy was examined in detail in the previous chapter 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 optimised distribution which follows closely the light profile in the canopy. It was therefore assumed here that a linear relationship existed between nitrogen content per unit leaf area, n_a, and cumulative leaf area index, l_c, as determined

from the top of the canopy which was also found in sunflower (Bange *et al.*, 1997) and soybean (Shiraiwa and Sinclair, 1993). Thus,

$$n_a = -m_2 \cdot l_c + n_{a,max}\,, \tag{30}$$

where $n_{a,max}$ is the maximum N-content at the top of the canopy and $-m_2$ denotes the decline with l_c.

Dry weight and leaf area based nitrogen contents are converted into each other by using the specific leaf area, sla, which depends on the light environment at time of leaf growth (Björkman, 1981). The sla of growing leaves is assumed to be a function of the daily total of photosynthetically active radiation (PAR) averaged over a period of previous days, $I_{tot,ave}$:

$$sla = function(I_{tot,ave}) \tag{31}$$

The nitrate-N concentrations in leaves depend on light environment (Marschner, 1984; Wheeler *et al.*, 1998). Therefore, the maximum nitrate-N concentration of the compartment leaf, $n_{max,NO3\text{-}N}$, is assumed to increase with increasing leaf area index due to decreasing average light intensity in the canopy. Thus, under non-limiting N-supply

$$n_{max,NO3-N} = \frac{I_{ref}}{I_{ave}} \cdot function(LAI) \tag{32a}$$

where the quotient I_{ref}/I_{ave} relates the average light intensity above the canopy to a reference value. To account for a decrease in leaf nitrate concentrations, $n_{NO3\text{-}N}$, due to limiting N-supply (Gardner and Roth, 1990; Marschner, 1984) it is assumed that the change in the nitrate buffer of the plant with nitrogen availability progresses proportional to N-supply itself (Bellaloui and Pilbeam, 1991; Burns, 1994a; Gardner and Roth, 1990). This assumption predicts that $n_{NO3\text{-}N}$, is proportional to $(f_{soil})^2$ rather than f_{soil}:

$$n_{NO3-N} = n_{max,NO3-N} \cdot f_{soil}^2(N_{min}) \tag{32b}$$

4.3 Material and Methods

Two independent field experiments with cauliflower (*Brassica oleracea* L. convar. *botrytis* var. *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. The 1996 experiment was used for derivation of model parameters and the 1997 experiment served for model validation. The seeds were sown in peat cubes with 4 cm edge length. 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 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 plant spacing was 0.60 m by 0.48 m giving the average density of 3.5 plants m^{-2}. Before planting Chlorfenvinphos (Birlane) and molybdenum sulphate were applied prophylactically. Weeds were controlled by hand. Metasystox (250 g l^{-1} Oxydemeton-methyl) and later E605 forte (500 g l^{-1} Parathion) were sprayed once for pest control in both years. Irrigation was given whenever needed.

Experimental design

The experiments were laid out as split plots with two different light environments as main plots and four different nitrogen-fertiliser levels as sub-plots (Table 2). Main plots were covered in one meter height with a shading net absorbing 40% of the photosynthetically active radiation (PAR) either immediately after the 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 ha^{-1} in both years in 0-60 cm were subtracted from the 150, 300 and 450 kg ha^{-1} target values.

Plant growth analysis

On three and four harvests in 1996 and 1997, respectively, six 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. 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). The samples of all plant compartments were oven dried and weighed. After weighing total nitrogen and nitrate nitrogen was determined by the micro-Kjeldahl method and a nitrate sensitive electrode, respectively. On all harvests also plant dimensions (height and width) and curd diameter were measured.

Cauliflower development

Leaf development was described analogous to Kage and Stützel (1999) where visible leaf number is expressed as an expo-linear function of the temperature sum having the two parameters k_1 and k_2. The values of the parameters were determined for the cultivar 'Fremont' from an independent experiment in 1997 to be $k_1 = 0.0032$ $(d°C)^{-1}$ and $k_2 = 0.0350$ $(d°C)^{-1}$ (unpublished results). The vernalisation process was calculated according to (Wiebe, 1972b) using a daily vernalisation rate as a function of mean daily temperature (eqn. 14).

Photosynthesis

Photosynthesis was calculated depending on leaf area, protein-nitrogen content and distribution within the canopy as well as light and temperature environment as described in Chapter 3. The instantaneous rate of whole-plant net CO_2-uptake, P_{plant}, for a certain light environment, I, is the integral of single-leaf photosynthesis on a leaf area basis, P_g, over the leaf area, A_l, subtracted by whole-plant respiration, R_{plant}:

$$P_{plant} = \int_0^{A_l} dl\, P_g(I,P_m) - R_{plant} \qquad (33)$$

P_g is given by the non-rectangular hyperbola,

$$P_g = \frac{\alpha I + P_m - \sqrt{(\alpha I + P_m)^2 - 4\Theta\alpha I P_m}}{2\Theta}, \quad (34)$$

where α and Θ are two parameters describing the initial slope and curvature of the response curve, respectively. Their values are determined to be α=0.056 µmolCO_2 µmol^{-1}PAR and Θ=0.899. The single-leaf gross photosynthetic capacity, P_m (µmol CO_2 m^{-2} s^{-1}), varies within the canopy according to the N-content per unit leaf area, n_a,(gN m^{-2})

$$P_m = 12.82 \cdot n_a - 5.07 \quad (35)$$

R_{plant} (mg CO_2 plant^{-1} min^{-1}) has contributions from maintenance associated with the amount of protein-N in plant dry weight, $N_{P,plant}$ (g protein-N plant^{-1}), and growth respiration depending on the increase in dry weight per day, dW_{plant}/dt (g dry weight plant^{-1} d^{-1}):

$$R_{plant} = 1.80 \cdot N_{P,plant} + 0.40 \cdot \frac{dW_{plant}}{dt} \quad (36)$$

The decrease in respiration per unit leaf area, $R_{plant,a}$= R_{plant}/A_l, during the night progresses linearly with the duration in darkness, t_n (h):

$$R_{plant,a}(t_n) = R_{plant,a}(0) - (0.038 \cdot R_{plant,a}(0) - 0.042) \cdot t_n, \quad (37)$$

where the rate of decline depends on the initial respiration at beginning of the night, $R_{plant,a}(0)$, which is determined by eqn. 36 divided by A_l..

For the derivation of the photosynthesis model and model parameters see Chapter 3.

Light environment

The variation in photosynthetically active photon flux density (PPFD) above the canopy, I_0, with time, t, is assumed to follow a sine-squared function:

$$I_0(t) = I_{noon} \cdot \sin^2(\pi \cdot \frac{t}{d}) \quad (38)$$

where d denotes the daylight period and I_{noon} is the maximum PPFD at solar noon calculated from the daily total PPFD, I_{tot}, by I_{noon}=2 I_{tot} d^{-1}. I_{tot} is determined from the daily global radiation using a factor of 0.5 (Szeicz, 1974). The light profile within the canopy is calculated by separating I_0 into diffuse, $I_{0,dif}$, and direct, $I_{0,dr}$, components [Γουδριααν, 1994 #372]. The attenuation of the different components into the canopy is 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 :

$$I_{df}(l_c) = I_{0,df} \cdot e^{-k_{df} \cdot l_c} \quad (39a)$$

$$I_{dr}(l_c) = I_{0,dr} \cdot e^{-\sqrt{(1-\sigma)} \cdot k_{bl} \cdot l_c}) \quad (39b)$$

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

$$I_{dr,df}(l_c) = I_{dr}(l_c) - I_{dr,dr}(l_c) \quad (40)$$

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

$$I_{dr,dr}(l_c) = I_{0,dr} \cdot e^{-k_{bl} \cdot l_c} \quad (41)$$

The separation of incoming radiation implies a distinction of shaded and sunlit leaf area receiving different radiation components. Incident on the shaded leaf area is the diffuse component, I_{df}, and the diffused component of the direct flux, $I_{dr,df}$. The

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

$$I_{sh}(l_c) = k_{df} \cdot I_{df}(l_c) + k_{bl} \cdot I_{dr,df}(l_c) \quad (42)$$

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

$$I_{sl}(l_c) = I_{sh}(l_c) + (1-\sigma) \cdot k_{bl} \cdot I_{0,dr} \quad (43)$$

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

$$f_{sl}(l_c) = e^{-k_{bl} \cdot l_c} \quad (44a)$$

$$f_{sh}(l_c) = 1 - f_{sl}(l_c) \quad (44b)$$

The photosynthetic rate at canopy height l_c, $P_g(l_c)$ (eqn. 34), is the weighted sum of shaded and sunlit contributions:

$$P_g(l_c) = f_{sl}(l_c) \cdot P(I_{sl}(l_c)) + f_{sh}(l_c) \cdot P(I_{sh}(l_c)) \quad (45)$$

Dry matter partitioning

The increase in plant dry matter, dW_{plant}/dt, i. e. the net CO_2-uptake P_{plant} (eqn. 33) multiplied by the CO_2-CH_2O-conversion factor of 30/44, is partitioned between stem, leaf and inflorescence according to Chapter 2. After vernalisation has been completed generative growth has priority over vegetative growth 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, rgr_{in}. The dry matter increase of the inflorescence is at the beginning limited by its sink capacity and later on by total available assimilates:

$$\frac{dW_{in}}{dt} = \min\left(\frac{1}{1+f_{stem}} \cdot \frac{dW_{plant}}{dt}, rgr_{in} \cdot W_{in}\right) \quad (46)$$

where f_{stem} has the value of 0.15 describing the fraction of stem on inflorescence growth rate. rgr_{in} (d^{-1}) is a function of the nitrogen content per unit leaf area, n_{area}, at the time of inflorescence initiation:

$$rgr_{in} = 0.18 \cdot n_{area} \quad (47)$$

The growth rate of leaf dry matter is given by:

$$\frac{dW_{leaf}}{dt} = \frac{1}{1 + a \cdot sla + f_{root}} \cdot \left(\frac{dW_{plant}}{dt} - (1 + f_{stem}) \cdot \frac{dW_{in}}{dt}\right) \quad (48)$$

where a = 12.93 g stem dry weight 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 on leaf growth rate. Thus, stem and root growth rate are given by:

$$\frac{dW_{stem}}{dt} = a \cdot sla \cdot \frac{dW_{leaf}}{dt} + f_{stem} \cdot \frac{dW_{in}}{dt} \quad (49)$$

$$\frac{dW_{root}}{dt} = f_{root} \cdot \frac{dW_{leaf}}{dt} \quad (50)$$

where 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 the greenhouse experiment in 1997 (Chapter 3) where cauliflower was cultivated in nutrient solution containing 145 mg N l^{-1}. A similar dependency was found for seedlings of different rice cultivars (Cock and Evans, 1983).
For a detailed derivation of eqns. 46 to 49 see Chapter 2.

Net mineralisation

The amount of nitrogen mineralised during 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_{min} from 0-120 cm at final harvest subtracted by N_{min} at transplanting. The average daily mineralisation 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 present conditions, neglects temperature effects on mineralisation 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 (Thornley and Johnson, 1990) with a time step of one hour. A non-linear least squares regression analysis is implemented in ModelMaker using a Marquardt optimisation 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_{Nmin}. All statistical analyses if not stated otherwise were carried out using the procedures NLIN and REG of the SAS software package (SAS Institute, 1988).

4.4 Results

Parameterisation experiment 1996

The leaf nitrogen concentration declined during growth independent of light environment even under non-limiting N-supply determined from the first two harvests of the N3-treatments of both light environments (Figure 21A). These data were chosen to parameterise eqn. 28 since they best reflected non-limiting N-supply unaffected by N-translocation into the inflorescence.

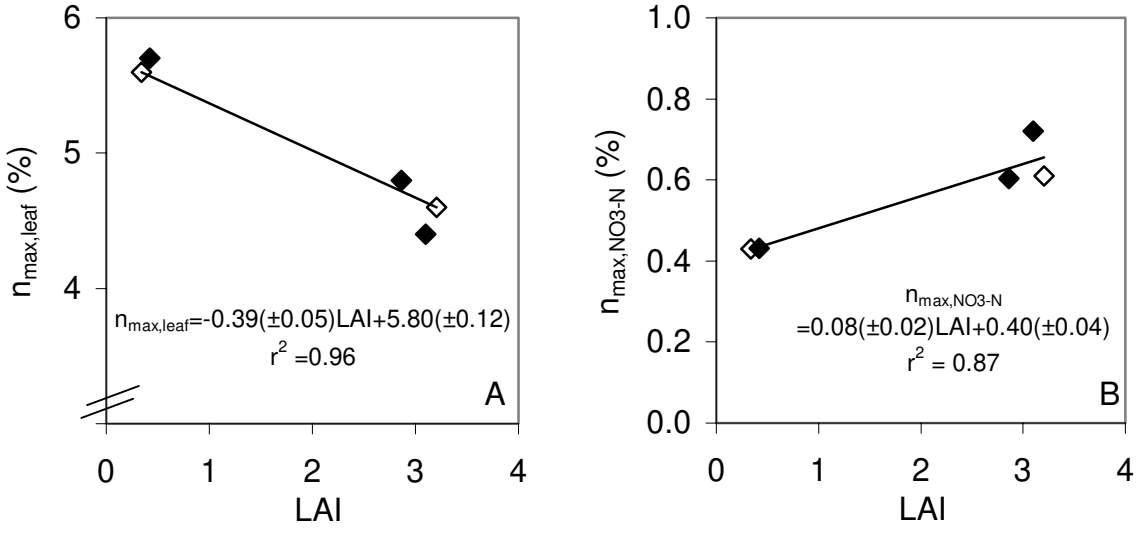

Figure 21: Maximum leaf N-concentration, $n_{max,leaf}$ (A), and nitrate-N concentration, $n_{max,NO3-N}$ (B), under non-limiting N-supply vs. leaf area index, LAI; experiment 1996, I2-N3-treatment (solid symbols) and first two harvests of I1-N3-treatment (open symbols).

The same variants show an increase in nitrate-N concentration during growth attributed to the declining average light intensity in the canopy with increasing leaf area index (Figure 21B). The average daily total of PAR of the non-shaded light environment during crop growth was used as the reference value, I_{ref}, in eqn. 32, i. e. I_{ref} = 7.8 MJ m^{-2} d^{-1}. The nitrate-N contents of the shaded treatment were

corrected for light environment by multiplying with a factor of 0.6, i. e. the transmission of the shading net. The linear regression equation was used to parameterise eqn. 32b.

The profile of protein-nitrogen per unit leaf area, n_a, decreased linearly with increasing depth in the canopy, proportionality coefficient m_{na}, for all treatments, e. g. final harvest (Figure 22A), This suggests a protein-nitrogen profile in the canopy according to:

$$n_a(l_c) = n_{a,max} \cdot (1 - m_{na} \cdot \frac{l_c}{LAI}) \qquad (51a)$$

where l_c is the cumulative leaf area index as determined from the top of the canopy and LAI denotes the leaf area index of the crop. The maximum value of n_a at the top of the canopy, $n_{a,max}$, is then given by the total amount of leaf protein-N, $N_{P,leaf}$, by integrating eqn. 51a over LAI:

$$n_{a.max} = \frac{N_{P,leaf}}{LAI \cdot (1 - \frac{m_{na}}{2})} \qquad (51b)$$

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. Its value was estimated to be m_{na}=0.53 (±0.02). The observed N-profiles for all treatments and harvests could well be described by the same parameter value of m_{na} (Figure 22B).

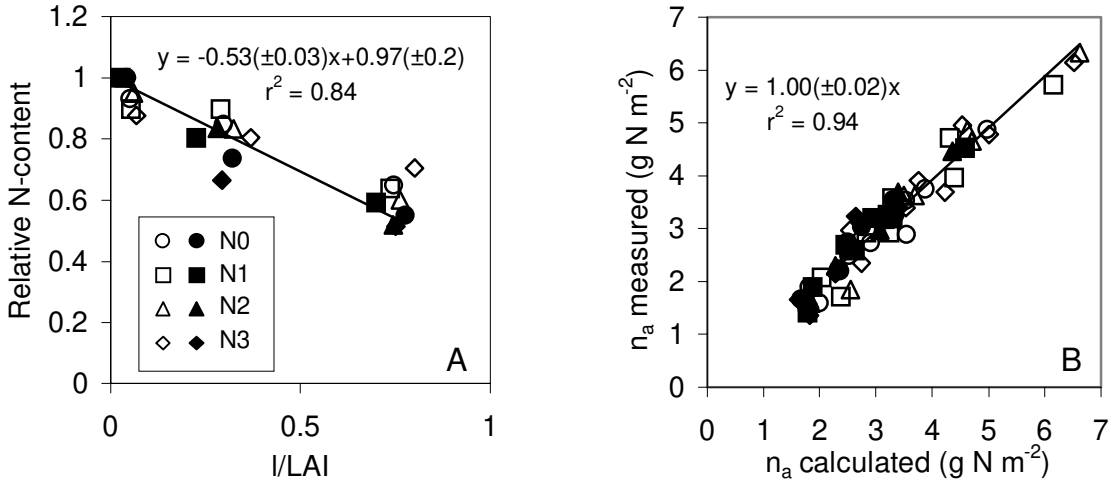

Figure 22: Protein-nitrogen contents per unit leaf area, n_a, relative to the maximum value at the top of the canopy vs. fraction of leaf area above, l/L, for the third harvest (A). Measured vs. calculated profile of leaf protein-nitrogen contents per unit leaf area for all harvests (B); experiment 1996, open and closed symbols refer to non-shaded and shaded treatments, respectively.

The maximum stem nitrogen-concentrations, $n_{max,stem}$ 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% (unpublished results). The maximum inflorescence N-concentration, $n_{max,in}$, was found to be a function of the inflorescence dry weight, W_{in}, (Figure 23).

The specific leaf area, sla, was related to the daily amount of PAR incident on the canopy and averaged over the time during leaf growth for all treatments (Figure 24). There were no significant statistical differences between the specific leaf areas of the N-treatments for the same light environment at the first two harvests.

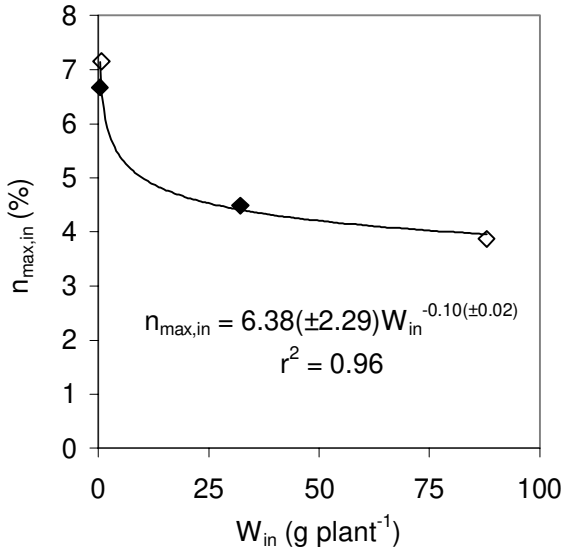

Figure 23: Maximum nitrogen concentration of the inflorescence, $n_{max,in}$, vs. dry weigth, W_{in}; data from the first two harvests of the I1-N3- (open symbols) and I2-N3-treatments (closed symbols); experiment 1996.

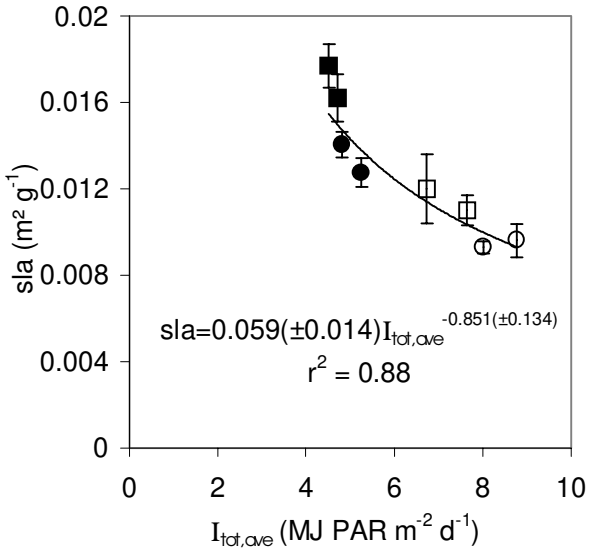

Figure 24: Relationship between specific leaf area, sla, of youngest leaf group, and daily total of PAR averaged over 14 days prior to harvests, $I_{tot,ave}$; data from leaves 1-5 (first harvest) and leaves 11-15 (second harvest) in 1996 (circles) and 1997 (squares), open and closed symbols refer to non-shaded and shaded treatments, respectively. Vertical bars denote ± standard deviation of N-treatment means.

So far model parameters characterising sink limitations on N-uptake were quantified. The model parameter associated with source limiting processes is f_{soil} (eqns. 29 and 32). Since the general behaviour of the dependency of f_{soil} on N_{min} is assumed to be smooth it can be studied by comparing the 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 (Figure 25). Since the data of each harvest can be described well by a non-rectangular hyperbola, it is chosen as the mathematical relationship between f_{soil} and N_{min}:

$$f_{soil} = \frac{N_{min}}{K_{Nmin} + N_{min}} \tag{52}$$

where K_{Nmin} is the parameter influencing the curvature of the curve and $f_{soil}(K_{Nmin})=0.5$. 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. Its value was estimated to be $K_{Nmin}=38.5$ (±3.0) kg N ha^{-1}.

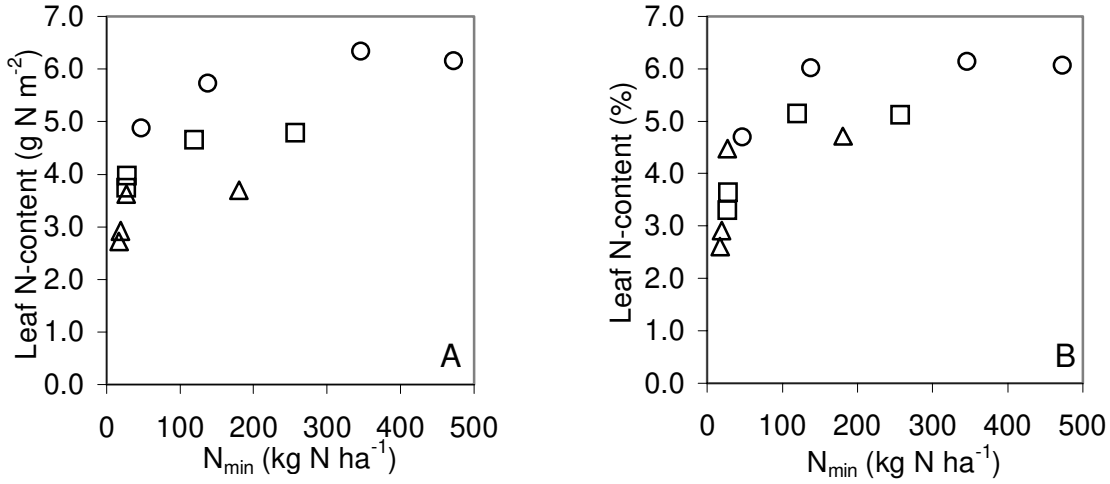

Figure 25: Leaf area based (A) and mass based leaf nitrogen contents (B) of youngest leaf group vs. N_{min} from 0-120 cm for first (circles), second (squares) and final (triangles) harvests of non-shaded treatments; experiment 1996.

The above-ground dry matter assimilation of all treatments could well be simulated by the model for both years (Figure 26). 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 fertilised N-treatments of the same light environment showed similar dry matter production a differentiation in leaf nitrogen contents as well as nitrate-N concentrations were observed at an early growth stage (Figure 27).

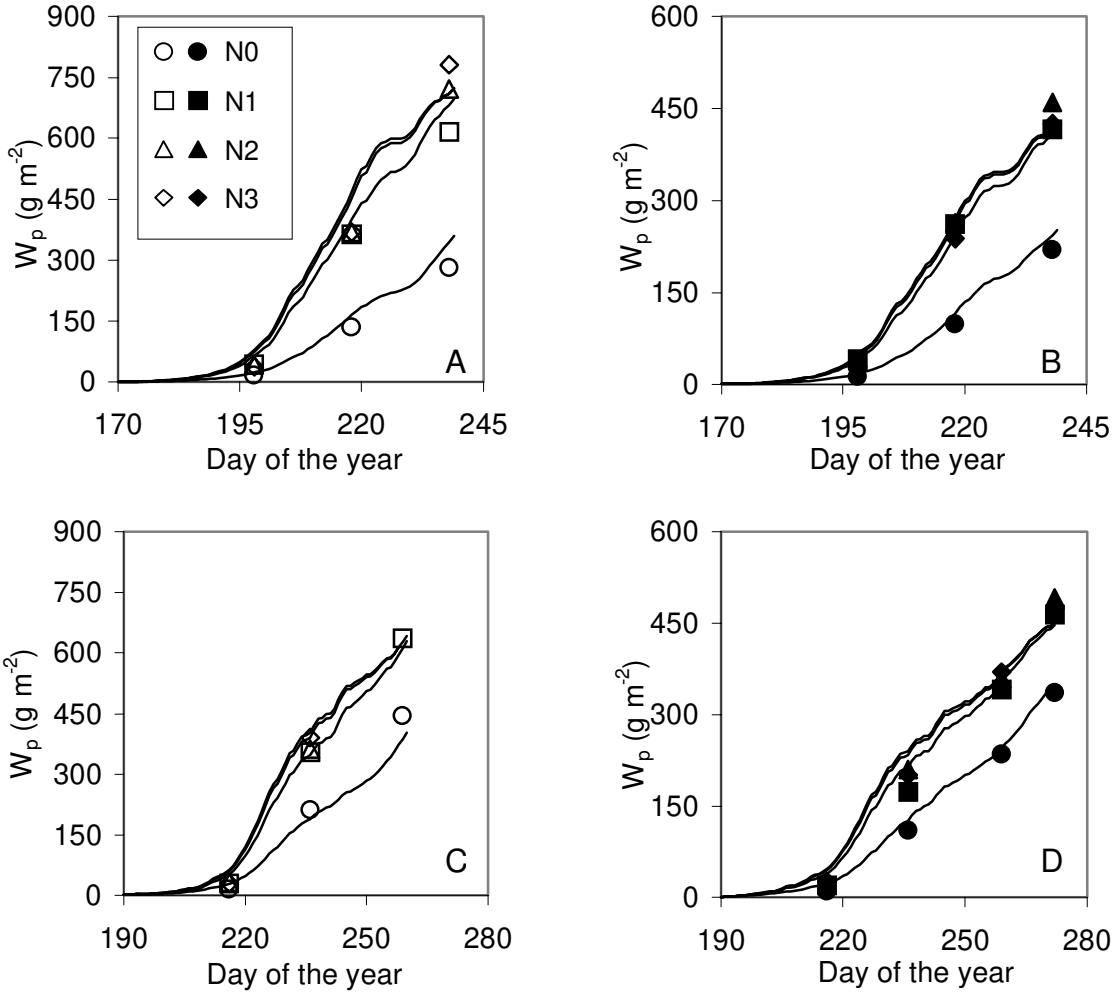

Figure 26: Measured vs. simulated above-ground dry weight, W_p, for all harvests; experiments 1996 (A,B) and 1997 (C,D), open and closed symbols for non-shaded and shaded treatments, respectively.

The leaf nitrate-nitrogen concentrations increased during growth for most of the N-fertilised treatments due to the decreasing average light intensity within the canopy. Limiting N-supply caused NO_3-N-concentrations to decline earlier and faster in time than leaf-N concentrations were effected as was also found for cabbage (Burns, 1994a). The linear regressions between simulated and measured leaf N- and nitrate-N concentrations for all treatments and harvest were $y=1.04(\pm0.02)x$, $r^2=0.89$ and $y=1.09(\pm0.04)x$, $r^2=0.91$, respectively. Nitrogen concentrations of stem and inflorescence differed similarly between treatments (Figure 28) and declined also for all treatments during growth.

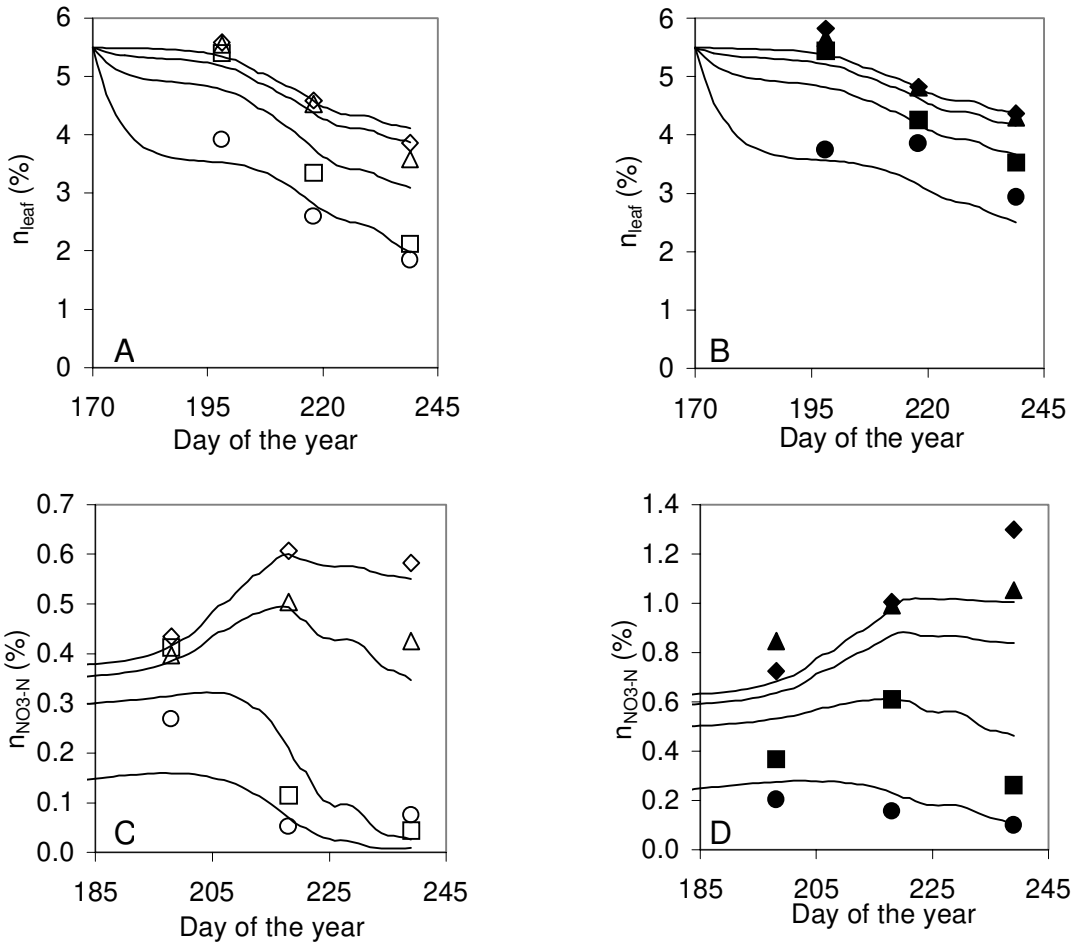

Figure 27: Measured vs. simulated leaf-N content, n_{leaf} (A, B), and leaf nitrate-nitrogen content, n_{NO3-N} (C, D), for all harvests of non-shaded and shaded treatments; experiment 1996, symbols as in Figure 26.

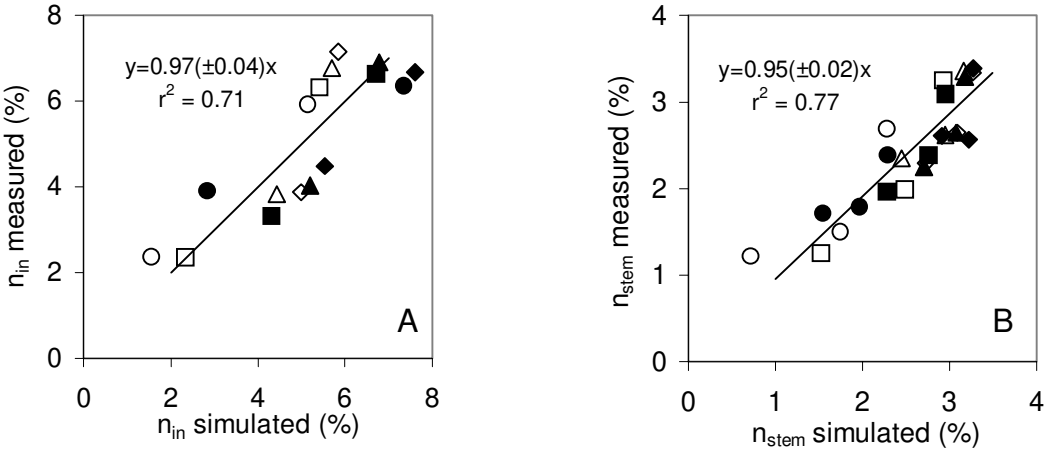

Figure 28: Measured vs. simulated inflorescence (A) and stem (B) nitrogen content, n_{in} and n_{stem}, respectively, for all harvests; experiment 1996, symbols as in Figure 26.

Validation experiment 1997

The model including model parameters derived above from the experiment in 1996 were validated with data from an independent field experiment in 1997. The leaf nitrogen-contents showed again a differentiation between treatments soon after transplanting (Figure 29). The leaf nitrate-nitrogen contents of the validation experiment were higher due to a reduction in average daily PAR 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 validation experiment as for the parameterisation experiment.

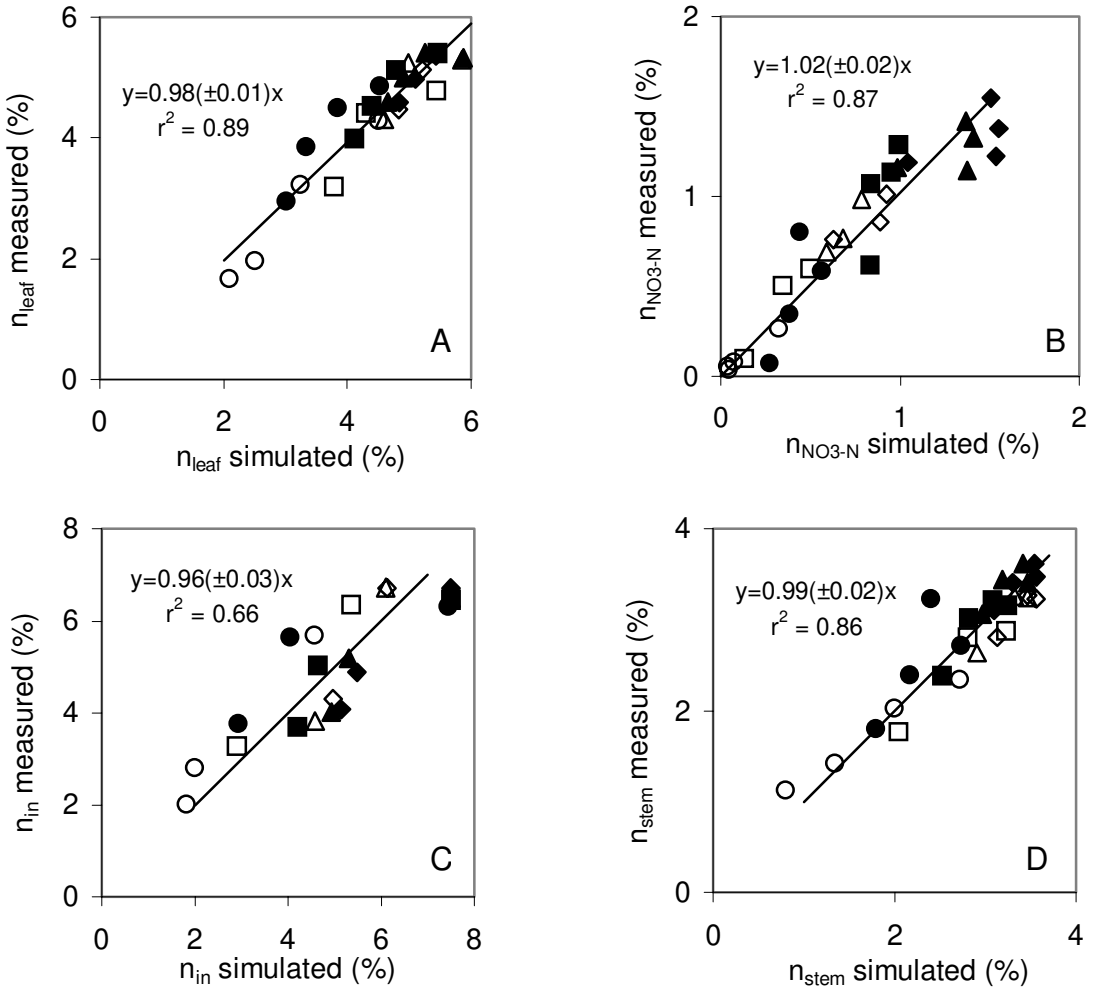

Figure 29: Measured vs. simulated leaf, n_{leaf} (A), leaf nitrate-, n_{NO3-N} (B), inflorescence, n_{in} (C), and stem, n_{stem} (D), nitrogen content for all harvests; experiment 1997, symbols as in Figure 26.

Nitrogen concentrations of inflorescence and stem were similar to the data from 1996 (Figure 29). A decline in N-concentrations was observed for all treatments and plant compartments during growth. The simulated N_{min}-values showed good agreement with the measured data suggesting a sufficiently accurate simulation of source limitation (Figure 30). The goodness of the above-ground dry matter production and partitioning is compared for both experiments in Table 9.

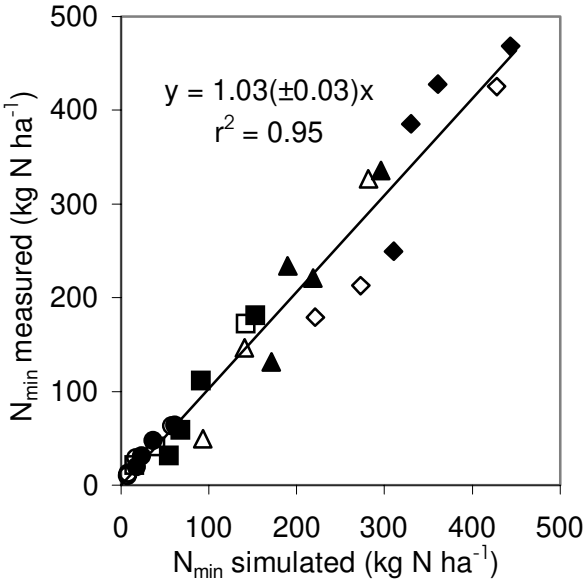

Figure 30: Measured vs. simulated N_{min}-contents in 0-120 cm soil layer for all treatments and harvests; experiment 1997, symbols as in Figure 26.

Table 9: Results of the regression analyses of measured vs. simulated dry matter of cauliflower organs and leaf area in both experiments*

Experiment	Organ	Slope (± s. e.)	r^2
Parameterisation	Above-ground total	1.05 (±0.03)	0.96
Parameterisation	Leaf	0.90 (±0.02)	0.98
Parameterisation	Stem	0.93 (±0.03)	0.94
Parameterisation	Inflorescence	1.11 (±0.05)	0.95
Parameterisation	Leaf area	0.82 (±0.03)	0.91
Validation	Above-ground total	1.03 (±0.02)	0.96
Validation	Leaf	1.05 (±0.04)	0.91
Validation	Stem	1.05 (±0.03)	0.93
Validation	Inflorescence	1.01 (±0.05)	0.92
Validation	Leaf area	1.02 (±0.03)	0.94

*Intercepts were in all cases not significantly different from zero.

4.5 Discussion

This study was set up to find out how nitrogen uptake by cauliflower and distribution in the plant are influenced by light environment and soil nitrogen content. In order to provide a variation in supply, four N-fertiliser levels were imposed in each of two field experiments together with a variation in light intensity in both years. The experiments in 1996 and 1997 served as model parameterisation and validation, respectively. A simple framework was developed to predict nitrogen uptake and distribution in the plant as dependent on plant growth rate, available soil nitrogen content and environmental conditions. N-uptake dynamics were combined with a photosynthesis model as dependent on leaf nitrogen. This combined model predicts carbon and nitrogen assimilation and distribution based on the productivity-nitrogen relationship from transplanting to harvest.

The average leaf nitrogen concentration under conditions close to non-limiting N-supply was independent of light environment and declined during growth. This was attributed to a maximum leaf N-concentration as a physiological upper limit that was not maintained during leaf area growth, maybe due to senescence and self-shading both increasing with increasing leaf area index. The decline in N-concentration during growth was found in many species and termed the 'law of progressive decline' (LeBot *et al.*, 1998).

The protein-nitrogen per unit leaf area declined linearly with increasing depth in the canopy which was also found for soybean (Shiraiwa and Sinclair, 1993) and sunflower (Bange *et al.*, 1997). Theoretical considerations predict a N-distribution close to the light profile (Charles-Edwards *et al.*, 1987; Hirose and Werger, 1987b). This discrepancy, also found for soybean (Sinclair and Shiraiwa, 1993), lucerne (Evans, 1993) and two monocotyledons (Pons *et al.*, 1993) may partly result from an insufficient low rate of N-remobilization due to additional costs (Field, 1983).

The specific leaf area of the newly produced leaf dry matter was related to the average light intensity above the canopy, which is close to the PPFD incident on growing leaves at the top of the canopy. Although water vapour deficit and wind environment, which may have contributed to the observed differences in sla between shaded and non-shaded light environments, have not been taken into account, the dependence of sla on PPFD successfully described the experimental data of leaf area development for all treatments.

The reduction in N-uptake and consequently in leaf, stem and inflorescence nitrogen content due to limiting N-supply could well be described by the factor f_{soil}, i. e. a hyperbolic dependency between the reduction in N-uptake with decreasing 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 also described by Michaelis-Menten kinetics (Epstein and Hagen, 1952; Peuke and Kaiser, 1996). The value of K_{Nmin} found in this study exceeds the corresponding single-root values obtained from nutrient solution experiments by one to two orders of magnitude (Kage, 1995; Peuke and Kaiser, 1996). This suggests the assumption that nitrate uptake of cauliflower is limited by the transport of nitrate from the bulk soil to the root surface which was also 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-fertilised treatments of the same light environment in both years their differentiation in nitrogen-concentrations was more pronounced and observed early after transplanting. Both of these experimental findings, also found for many field corps (Booij *et al*., 1996; Greenwood *et al*., 1980; Van den Boogaard and Thorup-Kristensen, 1997), were simulated by the model. The increased photosynthetic capacity of a plant due to increased leaf protein-nitrogen content was mainly offset by increased

maintenance respiration due to enhanced protein-turnover under the given light environments.

Conclusions

The model presented was able to predict nitrogen uptake and distribution in cauliflower from plant growth rate, available soil nitrate-nitrogen content and environmental conditions. The observed nitrogen concentrations declined in all plant compartments 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 are observed soon after transplanting dry matter production is affected later and less intense. The increased photosynthetic capacity of plants due to increased leaf protein-nitrogen contents is mainly offset by increased maintenance respiration due to enhanced protein-turnover.

5. Final discussion

The reduction of 'unproductive' and environmental harmful N-losses from the production system requires to match nitrogen demand and supply. N-target values as fertiliser recommendations for individual crops (Lorenz *et al.*, 1989; Scharpf, 1991) empirically relate crop productivity to available soil nitrate. However, it was hypothesised that a mechanistic understanding of the relationship between crop productivity and nitrogen supply predicts the needs of the crop under specific environmental conditions and provides growers with more specific fertiliser recommendations (Greenwood, 1982; Van Keulen *et al.*, 1989). This study was set up to assess the potential for individual N-fertiliser recommendations in cauliflower used as an example crop by exploring the functional relationships between carbon and nitrogen assimilation and distribution in the plant under specific environmental and agronomic conditions.

The productivity-nitrogen relationship confirmed and physiologically explained the empirical findings of diminishing returns with increasing N-supply and upper limits to dry matter production under specific environmental conditions (Booij *et al.*, 1996; Everaarts, 1993a; Greenwood *et al.*, 1980; Van den Boogaard and Thorup-Kristensen, 1997). The physiological principles propose the dependence of the optimal leaf protein-N content with respect to potential growth on temperature and light environment. Therefore, the minimum amount of nitrogen required for maximum yield is dependent on environmental conditions. This clearly suggests the modification of the N-target values given as fertiliser recommendation (Lorenz *et al.*, 1989; Scharpf, 1991) depending on season and location. The modified target value may be obtained by scenario calculations of the simulation model derived in this study using long term averages of environmental conditions for specific locations.

The potential for specific N-fertiliser recommendations was exemplary estimated by simulation runs of the model using environmental data of 1997 from the institute's experimental farm located 15 km south of Hanover. An average daily

net mineralisation of 0.7 kg N ha^{-1} as observed in the field experiments in 1996 and 1997 and ample water supply were assumed. The imposed quality criteria were an inflorescence diameter of 20 cm corresponding to 67.5 g dry weight (Kage and Stützel, 1999) and an inflorescence N-concentration ≥ 2% as the minimum value observed in the field experiment in 1996, which were accompanied by inferior quality. These standards are supposed to represent a marketable product of high quality. The minimum N-demand to fulfil these criteria including a surplus of 40 kg N ha^{-1} is calculated by the model. Whereas the estimated growth period depends rather on the average daily total of PAR, the N-demand correlates with average daily temperature and with the fraction of temperature and radiation (Table 10). The difference in N-requirements during the season amounts to 60 kg N ha^{-1} for this specific location.

Table 10: Calculated minimum N-demand, N_{demand}, of cauliflower for assumed transplanting dates in 1997

Transplanting date	Growth period (days)	N_{demand} (kg N ha^{-1})	T_{ave}*1 (°C)	I_{ave}*2 (MJ m^{-2} d^{-1})	T_{ave}/I_{ave} (°C MJ^{-1} m^2 d)
April 1	72	310	10.8	8.5	1.3
May 1	59	300	14.3	9.7	1.5
June 1	64	285	16.7	9.1	1.8
July 1	72	250	18.7	7.5	2.5

*1: average daily temperature during growth period

*2: average daily total of PAR during growth period

Observed is the tendency of declining N-requirements with increasing temperature, which can partly be explained by the growing share of CO_2-loss on CO_2-uptake due to increasing maintenance respiration under the observed radiation environment. This general tendency is accompanied by the combined effect of dry matter partitioning and vernalisation on N-demand. Both of these

processes determine the fraction of structural, photosynthetically active and generative on total dry weight as dependent on nitrogen content and environmental conditions. An increased fraction of leaf dry matter containing higher N-concentrations compared to the inflorescence enlarges the nitrogen needs of the crop which was the case for the early planting dates. These simulation results reflect the importance of both dry matter assimilation and distribution as dependent on N-supply and environmental conditions in determining the N-demand of the crop which was proposed in this study. An interesting simplification in site-specific adjustment of N-target values may be obtained using the ratio of average temperature and radiation as suggested by the model simulations. Although the model was validated with data from an independent field experiment, its predictions as well as possible simplifications need to be verified by further experimental data.

Besides yield and required N-supply, the model predicts the amount of nitrogen in crop residues and nitrate left in the soil which accumulates in cauliflower often to more than 50% of the amount of applied N-fertiliser (Everaarts, 1993a; Everaarts *et al.*, 1996; Rahn *et al.*, 1992). Additional work is needed on the N-dynamics of mineralisation and immobilisation to further match N-demand and N-supply of the subsequent crop and to increase nitrogen use efficiency in cropping systems.

Nitrogen accumulation is described in this study as taken up by one big root in a homogenous soil neglecting mass flow and diffusion in the soil. Although the factor f_{soil} (eqns. 27 and 29) expressed successfully the reduction in whole-plant N-uptake due to limiting N-supply under the given conditions, a more comprehensive approach may be required for soils with low water holding capacity or insufficient and heterogeneous water distribution. Several models on the solute movement in the soil-root system are available (De Willigen and Van Nordwijk, 1987b; Hansen *et al.*, 1991; Kage, 1997; Nye and Tinker, 1977) but only few data exist on temporal and spatial root development in vegetables (Greenwood *et al.*, 1982; Smit *et al.*, 1996; Thorup-Kristensen and van den Boogaard, 1998). More detailed approaches may physiologically explain the

comparably high K_{Nmin} -value (eqn. 52) derived by the aggregated approach used in this study. They are also necessary for describing the effects of temporal or spatial N-availability on N-uptake and yield, e. g. as observed after split N-fertiliser applications (Everaarts, 1993b; Van den Boogaard and Thorup-Kristensen, 1997) or band placement of fertiliser (Everaarts and de Moel, 1995; Everaarts *et al.*, 1996).

The incorporation of solute movement in the soil seems also suitable to address the reduction in productivity due to limiting water availability. The functional relationships between carbon and nitrogen assimilation and distribution were derived under conditions of ample water supply during crop growth. However, a realistic prediction of yield and quality under practical field conditions requires the incorporation of physiological mechanisms influenced by drought stress such as the regulation of stomata and osmotic potential (Clarke and McCaig, 1982; Kumar *et al.*, 1984), a reduced leaf area expansion (Jefferies, 1989; Lecoeur *et al.*, 1996) and an intensified root growth (Hoogenboom *et al.*, 1987; Smucker and Aiken, 1992). The direct impact of stomatal closure on internal CO_2-partial pressure affects photosynthesis (Heitholt *et al.*, 1991; Jensen *et al.*, 1996), which may be incorporated in the model by either an empirical relationship between stomata resistance and photosynthetic capacity, P_m (eqns. 15 and 16), or a more detailed description of photosynthesis including explicitly CO_2-diffusion (Farquhar *et al.*, 1980; Friend, 1995; Leuning *et al.*, 1995; Von Caemmerer *et al.*, 1981). The reduction of leaf area expansion seems already implemented in the existing framework. A reduction in total carbon assimilation, e. g. as a consequence of stomata closure, affects the absolute amount of assimilates distributed to leaves. An increased root-shoot ratio due to intensified root growth (Cruz *et al.*, 1986; Huck *et al.*, 1986) further results in a decline of assimilates available to leaves. Both adaptations lead to a reduced area of light interception and in turn have again a negative feedback on leaf area expansion. The conversion between leaf mass and leaf area, i. e. the specific leaf area, may also be altered (Ashraf and Mehmood, 1990; Jensen *et al.*, 1996) resulting in a further reduction of light intercepting area. This mechanistic concept of attributing the reduction in leaf area

expansion to a decrease in assimilates available to leaves was successful with nitrogen shortage. The reduction in leaf area development with decreasing N-supply, observed for many species (Palmer, 1996; Stadenberg *et al*., 1994; Vos and Biemond, 1992), was explained in this study by a reduced photosynthetic performance of the canopy due to decreased leaf N-contents and a reduced area of light interception itself. There was no need for an empirical correlation between N-supply and leaf area expansion.

Besides the aspect of water supply, also the impact of nitrogen on the quality of the marketable product is a relevant extension in a more comprehensive approach. Quality aspects are size, colour and looseness of the inflorescence as well as riceyness, i. e. the premature development of small flower buds on the surface, and green bracts which are small leaves penetrating through the surface. These criteria are important for the economic outcome, especially in weeks of abundant supply, which occur in cauliflower due to the temperature dependence of the vernalisation process (Wiebe and Krug, 1974). Whereas riceyness and green bracts have been found to result from either high or low temperatures during different periods of crop development (Fujime, 1983; Grevsen and Olesen, 1994; Wiebe, 1973a,b), colour and looseness are related to the self-shading capacity of the canopy, duration of inflorescence formation and its nitrogen content (Wiebe, pers. communic.). Further research is needed to evaluate the influence of nitrogen supply on these criteria, which were also apparent in the field experiments of this study as already mentioned above.

The enumeration of model limitations and aspects of further research to extend this study and the presented physiological processes determining the productivity-nitrogen relationship in cauliflower is far from being complete. For instance, in the field experiments also an effect of nitrogen supply on the infestation of plants with cabbage aphid, flea beetle and cabbage butterfly has been observed. Although not statistically evaluated, these insects seemed to prefer the plots of low N-fertilisation. This suggests the examination of the influence of nitrogen availability on pests and diseases as well as non-biotic disorders.

Obviously, the realistic prediction of productivity and yield as dependent on nitrogen supply in plant production is a highly complex and ambitious aim. The contribution of this study is the quantification of the nitrogen impact on the primary processes determining productivity, i. e. carbon and nitrogen assimilation and partitioning in cauliflower which was used as an example crop. As has been shown above, intensive research remains to describe the presented processes in more detail and to include other relevant aspects.

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