



Nitrogen concentration of cauliflower organs as determined by organ size, N supply, and radiation environment

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Key words: *Brassica oleracea* L. botrytis, cauliflower, nitrogen concentration, N_{min}, organ size, radiation intensity, shading

Abstract

Data from field experiments carried out in three consecutive years under contrasting N supply and radiation environment altered by artificial shading were used to identify (a) the relationship between N concentration and organ size under conditions of unrestricted N supply and (b) critical levels of soil nitrate (N_{min,crit}), where nitrogen concentration of cauliflower organs begin to decline because of N limitations. The decline of N concentrations in cauliflower was analysed at different levels of morphological aggregation, i.e., the whole shoot level, the organ level (leaves, stem, and curd), and within different leaf groups within the canopy. N_{min,crit} values (0–60 cm soil depth) for total nitrogen concentration of cauliflower organs leaves, stem and curd were estimated at 85, 93 and 28 kg N ha⁻¹, respectively. Within the canopy, N_{min,crit} values for total N of leaves increased from the top to the bottom from 44 to 188 kg N ha⁻¹. N_{min,crit} values for protein N in leaves from different layers of the canopy were much lower at around 30 kg N ha⁻¹, without a gradient within the canopy. It is discussed that these differences in N_{min,crit} values are most likely a consequence of N redistribution associated with nitrogen deficiency. The decline of average shoot nitrogen concentrations, [Nm] (%N DM), with shoot dry matter, W_{sh}, (t ha⁻¹) under conditions of optimal N supply was [Nm] = 4.84 (±0.071) W_{sh}^{-0.089(±0.011)}, r² = 0.67 (±S.E.). The reduction of radiation intensity by artificial shading (60% of control) had no significant influence on total nitrogen concentrations of leaves and only a small influence on protein nitrogen concentrations in lower layers of the canopy. The leaf nitrate nitrogen fraction of nitrogen, f_{nitr} (-), within the canopy decreased linearly with increased average incident irradiance in different canopy layers (I_{av}, W PAR m⁻²) (f_{nitr} = 0.2456(±0.0188) - 0.0023(±0.0004)I_{av}, r² = 0.67).

Introduction

Nitrogen concentrations of plant organs usually declines during growth even under sufficient N supply. This decrease is caused by an increasing portion of assimilated carbon being allocated to structural organs or to structural parts of organs with a low N concentration (Cabin and Yu, 1984) and because of self shading effects within the canopy (Lemaire et al., 1991). Whereas the first factor may be more closely related to the leaf dry matter, the latter factor should

be more closely related to the leaf area. In order to identify N deficiency of crops ‘critical N dilution curves’ as well as ‘maximum dilution curves’ have been derived, which relate average shoot N concentration with shoot dry matter either under conditions of maximum dry matter productivity or under unrestricted N supply (Colenne et al., 1998; Greenwood et al., 1990, 1991; Justes et al., 1994; Plenet and Lemaire, 2000; Sheehy et al., 1998). Such ‘dilution curves’ may not only facilitate the analysis of experimental data but may also be used to derive fertilisation recommendations (Lemaire and Gastal, 1997) and for the calculation of N demand in crop growth models

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(Jamieson and Semenov, 2000; Stockle and Debaeke, 1997).

The whole shoot level, however, may not always be the most appropriate level of morphological aggregation at which useful weight/N concentration relationships should be obtained. Stress responses may change the partitioning of dry matter between different plant parts and thereby the shape of the dilution curves. Additionally, modern rapid field methods (Vouillot et al., 1998) usually determine N concentration at the single leaf level or at the top of the canopy and not at the whole shoot level. Rather than using shoot N concentration, information about the N concentration of organs may be better suited for certain applications. It further remains open, if different N pools (e.g., nitrate N, protein-N) are sensible diagnostic parameters.

Under N-limiting conditions, N concentrations of plant shoot and of plant organs are lower rather than predicted by dilution curves (Deviene-Barret et al., 2000). Therefore, certain soil nitrate levels are needed to ensure an appropriate N uptake rate (Barraclough, 1986) and to sustain maximum or critical N concentrations.

The aim of the presented paper, therefore, is to derive maximum N dilution curves for cauliflower at different levels of morphological aggregation, ranging from the whole shoot to specific leaf groups within the canopy under conditions of unrestricted N supply. These dilution curves then are used to identify critical soil nitrate levels, at which initial decline of N concentrations of cauliflower is expected. For this purpose data from field experiments with cauliflower from three years were used covering a wide range of N supply and a variation of the light environment due to artificial net shading in two of three years.

Material and methods

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

Field experiments with cauliflower (*Brassica oleracea* L. var. *botrytis* cv. Fremont) were conducted on an experimental farm located 15 km south of Hannover, Germany, on a typical loess derived hapludalf soil. Transplanting dates, harvest dates, initial leaf number and initial plant dry weight are summarised in Table 1. Due to severe bird attacks in 1998, the experiment was replanted with left over oversized transplant

Table 1. Dates of sowing, transplanting and harvesting of field experiments average visible leaf number (n_{L0}) and dry weight (DW) of transplants

Year	Sowing date	Transplanting date	Harvests (days after transplanting)	n_{L0}	DW (g plant ⁻¹)
1996	23 May	18 June	28, 49, 69	3.25	0.34
1997	3 June	9 July	26,47, 68*, 82	3.5	0.39
1998	18 May	18 June	21 ^S , 33,48,71	5.2	0.63

*Final harvest of N-fertilised treatments of non-shaded light environment.

^SOmitted from analysis.

material. This resulted in high initial leaf number and also caused some problems in crop establishment. Therefore, the first intermediate harvest in 1998 was omitted from the analysis. The average plant density in all experiments was 3.5 plants m⁻². Irrigation was given whenever needed to ensure optimal growth.

The experiments were laid out as split plots with two different light environments, i.e., shaded and unshaded, as main plots in 1996 and 1997 and irrigated and non-irrigated plots in 1998 and four different N-fertiliser levels as sub-plots. In the analysis presented here, only the irrigated treatments from the 1998 experiment are used. Shaded main plots were covered in one meter height with a net absorbing 40% of the photosynthetically active radiation (PAR) either immediately after transplanting (1996) or 2 weeks after transplanting (1997). Nitrogen fertilisation was given as calcium ammonium nitrate at the time of transplanting. Soil nitrate content of 10–15 kg N ha⁻¹ in 1996, 1997 and 1998 in 0–60 cm were subtracted from 150 (N1), 300 (N2) and 450 kg ha⁻¹ (N3) target values. Furthermore a N0 treatment was included, which received no fertilizer N.

On several intermediate harvest dates (Table 1) six plants per plot were collected and separated into stem, leaves including petioles, and inflorescence. Leaves were considered and counted down to a size of approximately 1 cm². Stems were cut 1 cm below soil surface level and at the onset of the inflorescence. Leaf area was measured with a LICOR 3100 leaf area meter (LI-COR Inc., Lincoln, NE, USA). The samples of all plant compartments were oven dried and weighed at 70 °C until weight constancy. Total N and nitrate N was determined by the micro-Kjeldahl method and a nitrate specific electrode, respectively. The protein N concentrations are computed from the difference of total and nitrate N concentrations. At every harvest

date soil samples were collected down to a depth of 120 cm and analysed for nitrate N with the exception of the shaded treatments in 1996.

Weather data were recorded using an automated weather station (Campbell Sci. Ltd., Shephed, UK) located on the experimental station within 500 m of the experimental plots. Average values of PAR for the last 10 day before each intermediate harvest were calculated from recorded values of global radiation intensity taking account of the transmissivity of the shading net and using a conversion factor of 0.5 between global radiation and PAR. These values were used to relate nitrate concentrations in different leaf groups of cauliflower to light intensity. Thereby, radiation intensity incident in different leaf groups was calculated from a negative exponential extinction equation using an extinction coefficient of 0.75 (Kage et al., 2001).

Regression analysis

It was hypothesised that 100 kg soil nitrate N from 0 to 60 cm is sufficient for optimal N supply on a bess loam soil under irrigation. Therefore, a sub-set was extracted from the experimental data of the N2 and N3 treatments for regression analysis where the soil nitrate content from 0 to 60 cm soil depth was higher than 100 kg N ha⁻¹. For the 1996 shaded treatments, where no soil nitrate samples were taken, the corresponding N_{min} values of the unshaded plots with the same N treatment were used as the criterion of data inclusion. Also, leaf N concentration data for the leaf group 6–10 were included only for the first two harvests because leaf senescence may have influenced N concentrations at later stages of plant development. The resulting data were used to derive organ size dependent reference N concentration under optimal N supply, [N_m]. We related N concentrations of leaves alternatively to leaf area or to leaf dry weight throughout this paper. For the leaf group level, the leaf area based equations were used to calculate reference N concentrations.

Differences between [N_m] to the actual measured N concentration ([N_{dif}]) was calculated and related to soil nitrogen content. For this purpose a linear response-plateau model was applied which assumes that [N_{dif}] is zero above a certain threshold soil nitrate content, N_{min,crit}, and decreases linearly with decreasing log transformed soil nitrate contents, N_{min}:

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

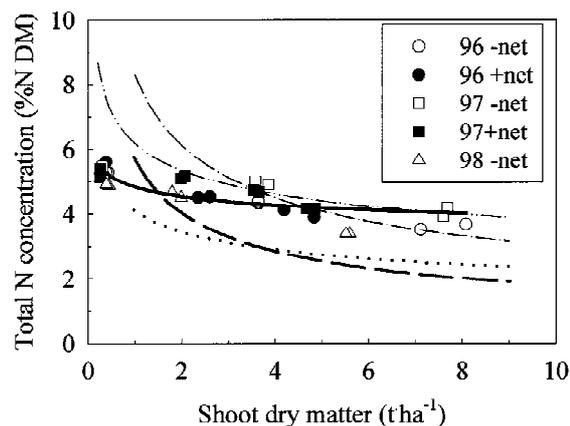


Figure 1. Relationship between shoot N concentration [N_{sh}] and shoot dry matter (W_{sh}) of cauliflower plants grown under optimal N supply in three different years (1996, 1997, 1998) either with (+net) or without net shading (-net) in comparison with maximum ([N_m]) and critical ([N_c]) dilution curves for different crops. The lines shown are: (—) fit to the data [N_{sh}] = 4.84 (+0.071) W_{sh}^{-0.089(±0.011)}, r² = 0.67, n = 32; (- · - ·) [N_m] = 8.3 W_{sh}^{-0.44}, wheat (Justes et al., 1994); (- · · -) [N_m] = 6.18 W_{sh}^{-0.21}, canola (Colnenne et al., 1998); (····) [N_c] = 4.48 W_{sh}^{-0.25}, canola after (Colnenne et al., 1998); and (- - - -) [N_c] = 5.7 W_{sh}^{-0.5}, general for C3-crops after (Greenwood et al., 1990).

The analysis was performed using the procedure IN-LIN from the SAS statistical package (SAS Institute, 1988)

Results

At the shoot level, the [N_m] values of cauliflower are decreasing with increasing shoot dry matter (Figure 1). This decrease is lower than predicted by [N_c] dilution curves for winter rape (Colnenne et al., 1998) and for C3 plants in general (Greenwood et al., 1990). Our data but correspond, at least for shoot dry matter values higher than 2 t ha⁻¹, quite well with [N_m] curves proposed by Justes et al. (1994) for wheat and by Colnenne et al. (1998) for winter oilseed rape.

The [N_m] values of the whole leaf fraction are decreasing with organ size, expressed either on a leaf weight (Figure 2) or leaf area index (m² m⁻²) basis ([N_m] = 5.66 (+0.12) - 0.271 (±0.0017) LAI, r² = 0.63, n = 29). Similarly, curd and stem [N_m] values

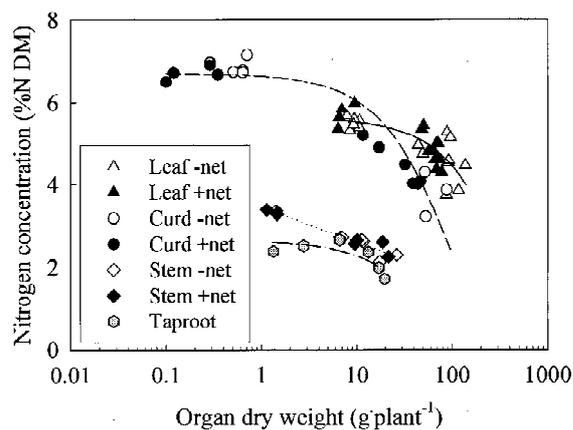


Figure 2. Average N concentration ($[N]$, % DW) of cauliflower organs under optimal N supply as a function of organ weight (DW, g plant^{-1}). The regression lines are: leaf, $[N] = 5.63 (\pm 0.11) - 0.0118 (\pm 0.0017) \text{ DW}$, $r^2 = 0.63$, $n = 29$; curd, $[N] = 6.70 (\pm 0.147) \exp(-0.0106 (+0.001) \text{ DW})$, $r^2 = 0.89$, $n = 19$, stem, $[N] = 3.45 (+0.063) - 0.366 (+0.029) \ln(\text{DW})$, $r^2 = 0.93$, $n = 14$ (1997 data omitted); tap root, $[N] = 2.65 (+0.1595) - 0.0381 (\pm 0.0130) \text{ DW}$, $r^2 = 0.68$, $n = 6$.

are strongly decreasing with organ size (Figure 2), without any significant differences between shading treatments.

The $[N_{\text{dif}}]$ values of leaves, stem and curd could successfully be described using the approach outlined in Equation (1) (Figure 3). This supports the validity of our hypothesis that there is no significant response of total plant N concentration to soil nitrate levels higher than 100 kg N ha^{-1} . The estimated parameter values (Figure 3) indicate that vegetative organs such as leaves and stem have much greater $N_{\text{min,crit}}$ values compared to the curd. The response of leaves, stem and curd to N shortage is similar for the different experimental years and the shading treatments. However, the $[N_{\text{dif}}]$ values for the curd from the shaded treatments lie somewhat below the values of the unshaded treatments (Figure 3).

Likewise, at the level of single leaf groups there is a clear trend of decreasing $[N_{\text{m}}]$ values with increasing organ size either expressed on a leaf area or leaf dry matter basis (Table 2). The values of the intercepts and the absolute values of the slopes of the regression equations between total N concentrations and leaf dry weight or leaf area are almost linearly decreasing with increasing leaf number (Table 2). It was therefore possible to construct simple multiple linear regression models which explain N concentrations of the single leaf groups as a function of the organs size expressed either as leaf dry matter or leaf area,

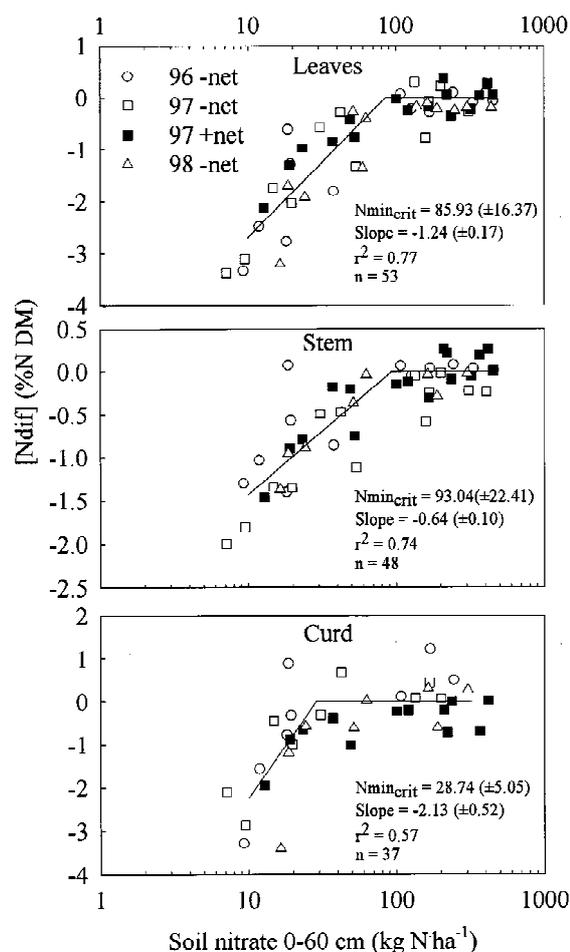


Figure 3. Deviations from reference N concentration $[N_{\text{dif}}]$ as a function of the soil mineral nitrate content (0–60 cm) for leaves, stem and curd of cauliflower plants. Parameters given: critical soil nitrogen content (kg N ha^{-1} 0–60 cm) ($N_{\text{min,crit}}$) and slope of a linear response-plateau model ($\%N \ln(\text{kg N ha}^{-1})$). Symbols: (○) 1996, –net shading; (□) 1997, –net shading; (■) 1997, +net shading; (△) 1998, –net shading.

the average leaf number of the group and the interaction between leaf size and average leaf number (Table 3). Again, there was no significant difference in the estimated parameter values between the shaded and unshaded treatments (data not shown). There was a slight advantage for leaf dry matter compared to leaf area as explaining variability of $[N_{\text{m}}]$ values of leaf groups (Table 3).

Also for the leaf groups $[N_{\text{dif}}]$ values could successfully be described using Equation (1) (Figure 4). The critical soil nitrate amount is decreasing with increasing leaf number from a value above 100 kg N ha^{-1} for the group of leaves 6–10 down to a value of about 45

Table 2. Parameter estimates (\pm SE) for the intercept, slope, r^2 and number of observations (n) of linear regressions between the logarithms of leaf dry matter (g pl^{-1}) or leaf area ($\text{cm}^2 \text{pl}^{-1}$) of different leaf number groups consisting of five leaves each and leaf N concentration (%N DM)

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

Table 3. Parameter estimates (\pm SE), r^2 and number of observations (n) of multiple regression equations expressing total N concentration of cauliflower leaf groups (%N DM) as a function of leaf size expressed as (a) leaf dry matter (DM) (g per five leaves) or (b) leaf area (cm^2 per five leaves). Leaf size, average leaf number per group and leaf size \times number interaction term were used as independent variables

Ind. var.	Intercept	Leaf size	Leaf number	Number \times size	r^2	n
DM	7.58 ± 0.28	-0.81 ± 0.11	-0.074 ± 0.02	0.021 ± 0.007	0.78	76
Area	11.03 ± 0.95	-0.76 ± 0.13	-0.158 ± 0.05	0.020 ± 0.007	0.75	66

kg N ha^{-1} for the youngest leaf group under consideration (Figure 4). There are no obvious differences in the response of total leaf N concentrations to limiting amounts of soil nitrate nitrogen between years and shaded and un-shaded treatments (Figure 4).

The leaf protein concentrations of the leaf groups are also declining with increasing leaf size (Figure 5), but here there is an indication that for the leaf group 6–10 and especially for the group 11–15 the decline of leaf protein concentration with leaf size is higher for the shaded plants. Therefore, distinct equations for shaded and unshaded treatments for these two leaf groups were used to compute [Nm] values (Table 4). The [Ndif] values are again described using the linear response – plateau model of Equation (1) with the exception of the leaf group 6–10 (Figure 6). In contrast to the response of the total leaf N concentrations (Figure 4), protein N declines at similar soil nitrate levels for most groups. Response of leaf pro-

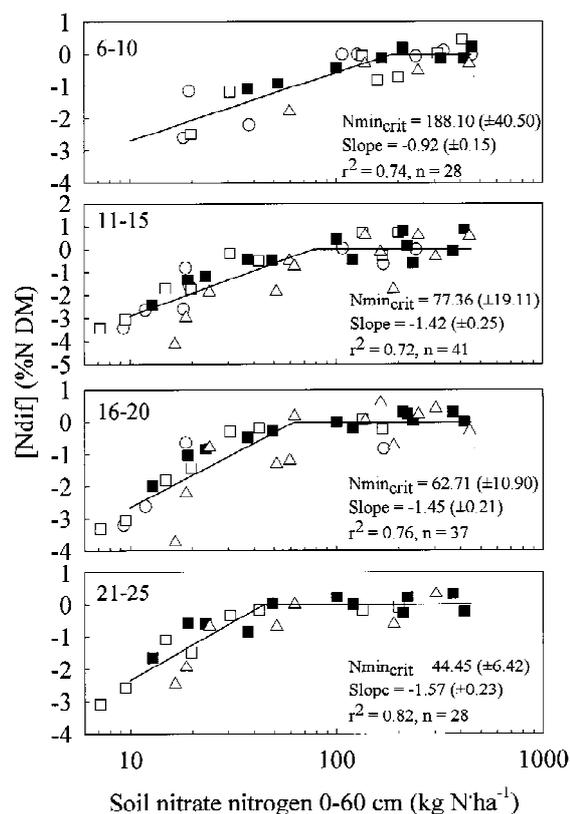


Figure 4. Deviation from reference N concentration [Ndif] as a function of the soil mineral nitrate content (0–60 cm) for different leaf groups of cauliflower plants. Parameters given are critical soil nitrate nitrogen content (kg N ha^{-1} 0–60 cm) ($N_{\text{min,crit}}$) and slope of a linear response-plateau model. Symbols: (○) 1996, –net shading; (□) 1997, –net shading; (■) 1997, +net shading; (△) 1998, –net shading.

Table 4. Parameters slope, intercept, r^2 and number of observations (n) of linear regressions between the logarithms of leaf dry matter (g pl^{-1}) or leaf area ($\text{cm}^2 \text{pl}^{-1}$) of different leaf number groups and leaf protein N concentration (%N DM)

Ind. var.	Leaf group	Shading treatment	Intercept	Slope	r^2	n
DM	6–10	Both	6.34 ± 0.45	-0.81 ± 0.17	0.62	16
DM	6–10	Shaded	6.05 ± 0.61	-0.81 ± 0.24	0.65	8
DM	6–10	Unshaded	6.85 ± 0.63	-0.89 ± 0.22	0.73	8
DM	11–15	Both	6.09 ± 0.21	-0.63 ± 0.07	0.84	19
DM	11–15	Shaded	5.94 ± 0.28	-0.69 ± 0.09	0.87	11
DM	11–15	Unshaded	6.37 ± 0.22	-0.58 ± 0.06	0.93	8
DM	16–20	Both	5.67 ± 0.16	-0.48 ± 0.07	0.79	15
DM	21–25	Both	5.27 ± 0.14	-0.39 ± 0.08	0.72	11
LA	6–10	Both	10.97 ± 1.01	-0.90 ± 0.14	0.76	16
LA	11–15	Both	12.98 ± 3.52	-1.09 ± 0.42	0.34	15
LA	16–20	Both	8.66 ± 0.92	-0.57 ± 0.12	0.71	11
LA	21–25	Both	7.16 ± 0.11	-0.38 ± 0.02	0.98	9

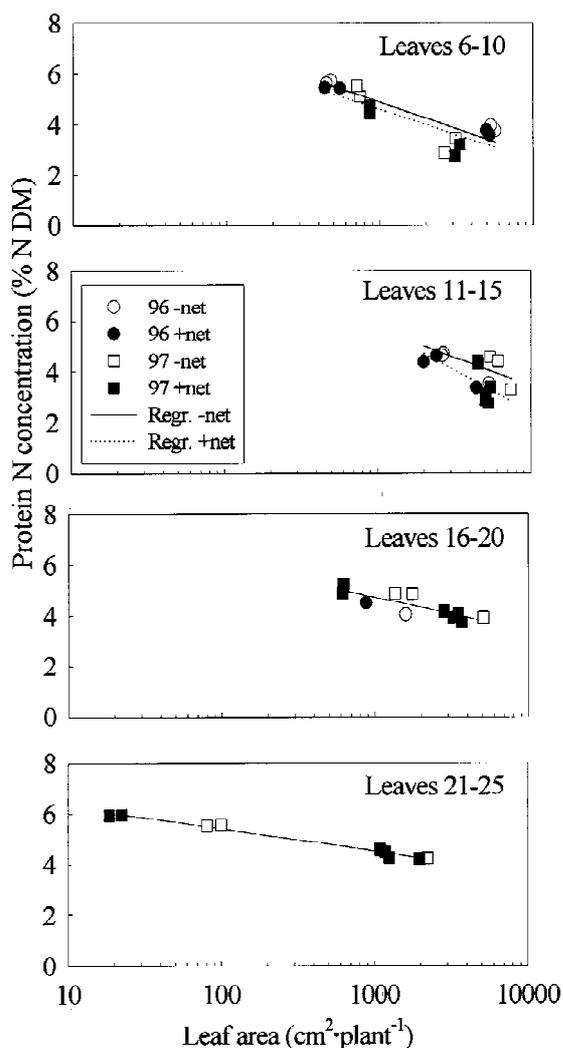


Figure 5. Protein N concentration (% DM) of cauliflower leaf groups under optimal N supply as dependent on the leaf area of the particular leaf group. Parameters of linear regressions are outlined in Table 4.

tein N concentrations to a limited N supply were not affected by shading and was similar for the different experimental years.

The leaf nitrate N/total leaf N ratio from the 1996 experiment show a significant negative correlation with the average radiation incident on the different leaf groups of shaded and unshaded plants (Figure 7).

Discussion

The aim of this study was to establish functional relationships between plant/organ size and N concen-

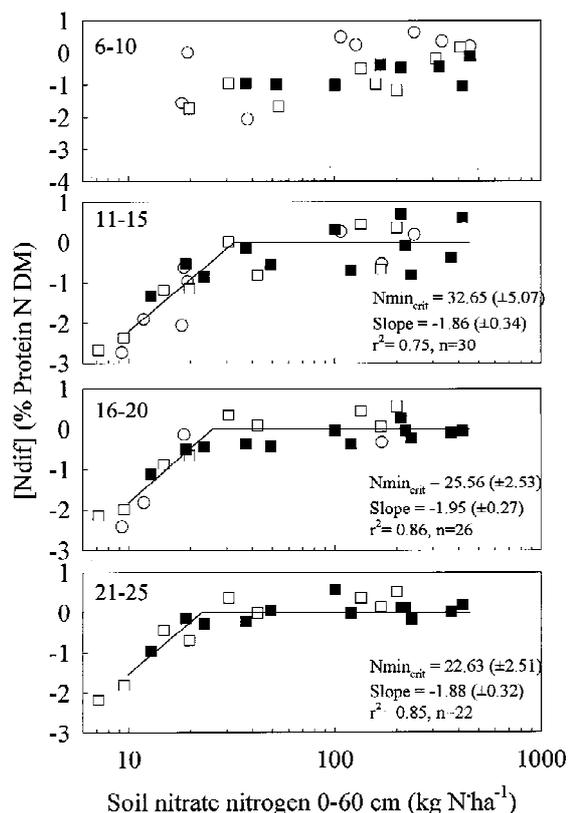


Figure 6. Deviation from reference protein N concentration [Ndif] as a function of the soil mineral nitrate content (0–60 cm) for different leaf groups of cauliflower plants. Parameters given: critical soil nitrogen content (kg N ha⁻¹ 0–60 cm) ($N_{min,crit}$) and slope of a linear response-plateau model (%N ln (kg N ha⁻¹)). Symbols: (○) 1996, -net shading; (□) 1997, -net shading; (■) 1997, +net shading; (△) 1998, -net shading.

trations under optimal N supply ([Nm] values) for cauliflower and to obtain estimates of critical soil nitrogen levels required to attain these [Nm] values.

The methodology to distinguish between N limited and non-limited growth conditions used in this study was related more closely to the concept of the 'maximum N dilution curves' than to 'critical N dilution curves' (Colnenne et al., 1998; Justes et al., 1994). In the latter case the N concentration is sought which, if maintained, gives no significant reduction of the standing biomass at any given time during the growth period. Following our approach, however, any plant N concentration measured in plants which were grown at nitrogen contents of the soil above 100 kg N ha⁻¹ were assumed not to be influenced by limited N supply. This may imply the inclusion of effects of 'luxury' N consumption. However, there was no signi-

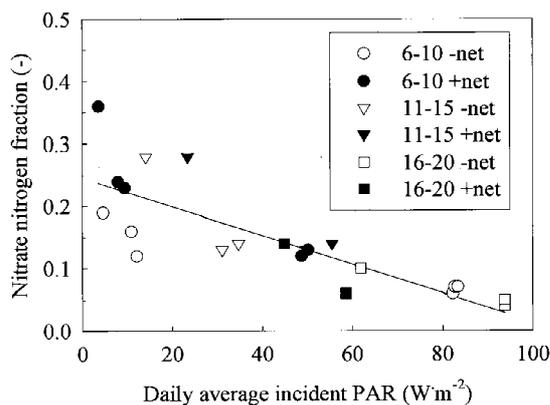


Figure 7. Leaf nitrate N/total N ratio as a function of daily average photosynthetic active radiation (PAR) for different leaf groups as well as shaded and unshaded plants. Data are from the 1996 field experiment and were selected for soil nitrate nitrogen $0-60 \text{ cm} > 100 \text{ kg N ha}^{-1}$. The regression line shown is: $y = 0.2456(+0.0188) - 0.0023(\pm 0.0004)x$, $r^2 = 0.67$, $n = 23$.

ficant increase of plant N concentrations, neither total N nor protein-N concentrations above our hypothesized threshold value of 100 kg N ha^{-1} (Figures 5, 7 and 9), suggesting a well controlled N uptake even under these high soil N levels.

Generally, we found no significant influence of shading on relationships between leaf size expressed either as leaf area or leaf dry weight and total N concentration (Table 2). Only for protein N in the oldest leaf groups, a differentiation between shaded and unshaded plants could be found (Figure 5). It seems that quite substantial reductions in incident PAR are needed to increase nitrate fractions in cauliflower leaves (Figure 7) and that total N concentrations are even less influenced by the radiation regime. Such a limited impact of irradiance levels on leaf N concentration was also reported for vine (Hikosaka et al., 1994) and rice (Makino et al., 1997). Hikosaka et al. (1994) found that leaf age was of similar importance for leaf N concentration of vine (*Ipomoea tricolor* Cav.) than irradiance. The almost missing adaptation of the N concentration of cauliflower leaves to the change of the radiation environment may to some degree be explained by the short growing period of cauliflower which may hamper N translocation from older to younger leaves and generative organs. However, adaptations of leaf N concentrations to changing radiation environments in other species seem to be possible in time spans of about one week (Evans, 1993). But there is also the possibility that the net shading method used was not appropriate to initiate

such adaptations, since there seems to be a closer relationship between the red/far red ratio which single leaves perceive than to the absolute level of radiation intensity (Rousseaux et al., 1999).

Older leaves, located deeper in the canopy, reduce their total N concentration below the [Nm] reference values at much higher levels of soil nitrate than the younger leaf groups, which seem to lower their N concentrations at a soil nitrogen level comparable to the curd (Figures 3, 4 and 6). The response of the leaf protein N concentration, however, is similar for older and younger leaf groups and between leaves in general and the curd. Differential response of total and protein N concentration in cauliflower plant to a decreasing soil nitrate levels may be caused by the existence of two nitrate uptake systems with differing uptake efficiencies (Peuke and Kaiser, 1996). The saturation of the nitrate storage pool within the leaves would therefore require quite high nitrate concentration in the soil solution in order to stimulate the less efficient, less regulated low affinity uptake system.

However, some caution is needed within the interpretation of static, statistical dependencies between soil nitrate levels and plant N concentrations, because they are caused by dynamic processes. The soil nitrate concentration typically declined during the time course of the experiments, because N fertilisation was given once at the beginning of the growing period and from then on the plants continuously exhausted the soil nitrate reserves. The observed different behaviour of the nitrate and protein N pools in the plant may therefore, at least partly, be explained by translocation and assimilation of the nitrate N pool leading to somewhat delayed reaction of the protein N concentration to reduced nitrate availability.

Recently, Devienne-Barret et al. (2000) analysed the functional relationship between the nitrate concentration of the soil solution in 0–30 cm depth below field grown crops and a nitrate uptake rate index in terms of the Michaelis–Menten kinetic. Their estimated K_m values of 0.37, 0.47 and 0.97 mol m^{-3} for wheat, oilseed rape, and maize, respectively, correspond to 13, 16, and 34 kg N ha^{-1} for an assumed soil water content of $0.25 \text{ cm}^3 \text{ cm}^{-3}$. Even a nitrate uptake rate index of one, indicating the absence of N deficiency according to the definition of the authors, is in this study reached at values corresponding to less than 20 kg N ha^{-1} for wheat and oilseed rape and at about 70 kg N ha^{-1} for maize. Our estimated $N_{\text{min,crit}}$ values are higher, at least for the total N concentration (Figures 3 and 4), but in a similar

range for leaf protein N. Alt et al. (2001) analysed a part of the presented data set and estimated K_m values for nitrate uptake of 38.5 kg N/ha. Some of the discrepancies between these studies may be explained by the usage of [Nm] rather than [Nc] dilution curves for identifying $N_{min,crit}$ values.

The observed $N_{min,crit}$ values ranged from 188 kg N ha⁻¹ for leaf groups situated deeper in the canopy (Figure 4) down to values of around 30 kg N ha⁻¹ for the curd and the protein concentration of the leaves (Figures 3 and 6). This raises the question, which of these values may be most useful for diagnostic tissue sampling for yield optimisation. One may argue that positive effects of nitrate N within the plant may be small and should be limited to leaf expansion processes (Palmer, 1996), which are influencing the growth rate especially in early stages. Therefore, the value of about 30 kg N ha⁻¹ may be regarded as a suitable critical level of soil nitrate for cauliflower at later growth stages. These low values are also in accordance with model calculations which predict very low critical soil nitrogen levels for most arable and vegetable crops because of the high mobility of the nitrate ion in the soil solution (Barraclough, 1986, De Willigen and Van Noordwijk, 1987; Kage, 1997). However, here it should be stated again that N deficiency may be induced already at somewhat higher levels of soil nitrate because a time lag between the onset of a restricted N uptake rate and the response of plant protein concentrations. This argument, nevertheless, should also hold for [Nc] values defined by established dilution curves (Colnenne et al., 1998; Justes et al., 1994). They probably underestimate to some extent the plant N concentration which induces a decline of plant dry matter accumulation.

Conclusions

The results of our study indicate that there seems to be an upper limit of total N concentrations within cauliflower plants above a certain threshold value of soil nitrate content. The relative portion of nitrate N in cauliflower leaves can be substantial and is mainly influenced by the irradiance exposure of the leaves. This suggests a differentiation between leaf nitrate and protein N in a model aiming to describe the N dynamics in cauliflower. The [Nm] dilution curves derived in this study may thereby be used to calculate the potential N uptake.

Additionally presented $N_{min,crit}$ values may help to calibrate N uptake models. Such models may then be used to predict variations of $N_{min,crit}$ values caused by differences in rooting pattern, soil moisture and the N uptake rate of a crop.

Acknowledgements

The technical assistance of E. Diedrich, I. Lippert and ML. Lehmann is gratefully acknowledged. Financial support was gratefully given by the Deutsche Forschungsgemeinschaft. Two unknown reviewers gave valuable comments for improving the manuscript.

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Section editor: B. Sattelmacher