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Nitrogen and Curd Compactness of Cauliflower (*Brassica oleracea* var. *botrytis*) F_1-hybrid

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Summary

To investigate the effect of nitrogen on curd compactness and the onset of cauliflower bolting, (*Brassica oleracea* var. *botrytis*) greenhouse trials in nutrient solution were conducted at optimum (6.5 g plant^{-1}) and at limiting (2.6 g plant^{-1}) N supply. With limiting N supply, bolting started four days earlier than at optimum N supply. The transfer from limiting to optimum N supply delayed bolting by four days. The foliar application of the gibberellic acid GA_3 (10 mg plant^{-1}) and the gibberellin synthesis blocker chlorcholinchloride (CCC, 100 mg plant^{-1}) did not affect the onset of bolting. The application of the cytokinin benzylaminopurine (BA, 40–320 µg plant^{-1}) using the stem-infusion technique delayed bolting by three and four days at optimum and limiting N supply, respectively. The effect of BA increased with increasing amount of cytokinin infused. The data suggest that promoted bolting at limiting N supply might be attributed to a limited export of cytokinin from the root to the shoot due to N shortage.

Zusammenfassung

Stickstoff und Kopffestigkeit bei Blumenkohl (*Brassica oleracea* var. *botrytis*) F_1-Hybride. Der Einfluß des Stickstoffangebotes (optimal, 6.5 g Pflanze^{-1} und suboptimal, 2.5 g Pflanze^{-1}) auf Kopffestigkeit und Schossbeginn bei Blumenkohl wurde in Nährlösungsversuchen im Gewächshaus untersucht. Bei suboptimalem N-Angebot setzte das Schossen vier Tage früher ein als bei optimalem N-Angebot. Der Wechsel von optimal auf suboptimales N-Angebot bei 3 cm Kopfdurchmesser verzögerte den Schossbeginn um vier Tage. Die Blattbehandlungen mit Gibberellinsäure GA_3 (10 mg Pflanze^{-1}) und Chlorcholinchlorid (CCC, 100 mg Pflanze^{-1}) als Gibberellinsynthese-Hemmer hatten keinen Einfluß auf den Schossbeginn. Die Stamminfusion mit dem Cytokinin Benzylaminopurin (BA, 40–320 µg Pflanze^{-1}) dagegen verzögerte den Schossbeginn um drei Tage bei optimalem bzw. um vier Tage bei suboptimalem N-Angebot. Die schossverzögernde Wirkung nahm mit steigender Cytokinin-Zufuhr zu. Die Ergebnisse lassen vermuten, dass das beschleunigte Schossen bei limitiertem N-Angebot zurückzuführen ist auf einen durch Stickstoffmangel induzierten, geringeren Export von Cytokinin aus der Wurzel in den Sproß.

Key words. cauliflower – nitrogen – curd compactness

Introduction

In field trials with cauliflower, nitrogen (N) shortage resulted in a significantly higher proportion of loose curds before harvesting compared to optimum N supply (RATHER et al. 1999). BÖHMER et al. (1981) also observed an increase in loose curds at low N supply. This suggested that limiting N supply accelerates curd looseness by elongation of first and higher-order branches, which can be regarded as the onset of bolting. With several brassica species bolting is promoted by exogenous applied gibberellic acid (FRIEND 1985; ROOD et al. 1989). Because gibberellin synthesis is inhibited by high N supply with *Gibberella fujikuroi* (BRUCKNER and BLECHSCHMIDT 1991; CANDAU et al. 1992), the accelerated bolting in the case of limiting N supply might have been due to promoted gibberellic acid synthesis.

A curd of cauliflower is composed of first and higher-order branches and whose tips are shortened considerably (SADIK 1962). Lateral branching, however, is regulated by the ratio of cytokinin to auxin, as is known for apical dominance (CLINE 1994; KLEE and ROMANO 1994; BARENDSE and PEETERS 1995). In this context, cytokinin stimulates lateral branching and reduces cell elongation, while auxin together with gibberellin promotes elongation. At limiting N supply, the export of cytokinin from the root to the shoot is reduced (SATTELMACHER and MARSCHNER 1978; SALAMA and WAREING 1979; KUIPER 1988; WAGNER 1991), which would result in a shortage of cytokinin in the shoot. One could therefore surmise that this would increase the relative proportion of auxin compared to cytokinin, which would promote the elongation of first and higher-order branches of the curd.

The aim of the present study was to investigate the effect of nitrogen and the application of phytohormones after curd initiation on the curd compactness and the onset of bolting with cauliflower in nutrient solution culture in the greenhouse.

Materials and Methods

Experiments were conducted in 1995 and 1996 in the greenhouse with the cauliflower F_1-hybrid 'Marine' (Novartis seed) in nutrient solution culture. Plants were sown on 29 March 1995 (trial 1), 17 August 1995 (trial 2) and 23 July 1996 (trial 3) in rockwool blocks (10 cm*10 cm*30 cm) placed in trays with nutrient solution (pH 6.0) which contained in mg l^{-1}: N 75, P 15, K 91, Mg 18, Fe 0.6, B 0.15, Cu 1.6, Mn 0.25, Zn 0.05 and Mo 0.025.

At the stage of five to six leaves, plants were transferred in 8 l pots with nutrient solution (pH 6.0). Plants were pre-supplied with two nitrogen (N) rates. For optimum N supply (N_{opt}), the weekly N demand was calculated from the measured N uptake during cultivation in field trials at optimum N supply of 250 kg N ha^{-1} (RATHER et al. 1999, 2000). A treatment with 40 % (N_{lim}) of the high N rate was established to limit N supply. Thus the total N applied during cultivation was 6.5 g $plant^{-1}$ at optimum N supply (N_{opt}) and 2.6 g $plant^{-1}$ at the limiting N rate (N_{lim}). The nutrient solution was changed weekly and thus the N concentrations were adapted to the expected weekly N uptake. Other nutrients were supplied in sufficient concentrations (mg l^{-1}): P 31, K 183, Ca 120, Mg 60, Fe 5.0, B 0.5, Mn 0.2, Zn 0.2, Cu 0.2 and Mo 0.05. Plants were cultivated for 64 to 74 days after the transfer in 8 l pots in trial 1, 77 to 87 days in trial 2 and 64 to 77 days in trial 3 depending on reaching quality grade 5.

Temperatures were 16/14 °C day/night during germination, 15/10 °C during vegetative plant growth and 18/15 °C during curd growth. On sunny days a cooling system ensured the set temperatures. In trial 2 and trial 3 natural light was supplemented by artificial light with about 155 PAR μEm^{-2} s^{-2} for 12 h.

Nutrient treatment and application of phytohormones

All treatments started at an early stage of curd growth, which was a curd diameter of 5 cm including wrapper leaves.

Trial 1: To investigate the direct effect of N on curd compactness, plants pre-supplied with an optimum N rate (N_{opt}) were transferred to limiting N supply (N_{lim}) and vice versa. In each case there was a control treatment with constant N_{opt} and N_{lim}.

Trial 2: The effect of gibberellic acid (GA_3) and chlorcholinchloride (CCC, an inhibitor of gibberellic acid synthesis) on curd compactness was examined at N_{opt} and N_{lim}. For treatment with gibberellic acid, aqueous solutions were prepared by dissolving GA_3 in 1 % alcohol. Plants were sprayed with GA_3 at a concentration of 100 mg l^{-1} and CCC at 1000 mg l^{-1} on five successive days at 20 ml $plant^{-1}$, which resulted in an amount of 10 mg GA_3 and 100 mg CCC per plant. A wetting agent (cytowet, BASF, 0.25 ml l^{-1}) was added to both chemicals.

Trial 3: N_{opt} and N_{lim} supplied plants were treated with the metabolically stable cytokinine benzylaminopurine (N^6-benzyladenine, SIGMA) (BA). The stem-infusion technique (GRABAU et al. 1986; BOYLE et al. 1991) as modified by DIETRICH et al. (1995) was used, except that there was only a single infusion site at the internode of the fifth and sixth leaf from the bottom of the plant. This method ensures that the exogenous cytokinin enters the target tissue, since BA is translocated via xylem and is less mobile in the phloem (WANG 1988; DIETRICH et al. 1995).

For stem-infusion cytokinin stock solutions (100 µM) were prepared in 1 N KOH and neutralized with 1 N H_3PO_4 to pH 4.2 and diluted into 10 mM K_2HPO_4/10 mM malic acid buffer (pH 4.2) just prior to injection. Control plants received phosphate/malate buffer only. BA was continuously infused at a constant concentration of 10 µM and injection reservoirs were replenished daily. The infused amounts per plant were recorded.

Curd quality and diameter

The daily measurement started at a curd diameter of 3 cm (including wrapper leaves); in addition, the compactness of the curd was visually assessed with grade 1 to 5 (WIEBE 1973). Grade 1: very compact curd; grade 2: compact curd; grade 3: onset of looseness at the edge of the curd (limit of marketability); grade 4: continued looseness of the curd (onset of bolting, loss of marketability) and grade 5: looseness of the whole curd surface. The market standards of the European Union impose a curd diameter of at least 11 cm and the grade not higher than 3 (ANONYMOUS 1992).

Dry matter and total N content

The plants were harvested when the curds had reached grade 5. Each plant was cut at ground level and divided into wrapper leaves, rest of leaves, curd, and stem. The number of leaves was counted. The fresh weight of each plant organ was recorded and after homogenisation of the sample, a subsample was taken to determine dry matter content after drying for 48 h at 70 °C. Analysis for total N content was conducted with a modified Kjeldahl method including nitrate.

Statistics

Experimental design was a randomised, complete block with four replicates of each treatment and three plants per replicate. Analysis of variance was carried out with the statistical program package SAS (SAS Inst. Inc., Cary, North Carolina). The comparison of treatments was carried out for the time needed to reach a specific grade. Mean comparisons were performed using the Tukey test ($p<0.05$). Least significant differences (LSD) are given. Linear (Pearson) regressions were computed.

Results

Total dry matter yield, N concentration in leaf dry matter and N uptake

In all trials the total dry matter was significantly reduced at limiting N supply (N_{lim}) (Table 1). The N content in leaf dry matter was in a range of 20 to 29 g kg^{-1} with limiting N supply, whereas it was significantly higher at optimum N supply. The N uptake in total shoot dry matter amounted to 2.4 g $plant^{-1}$ and 6.2 g $plant^{-1}$ with limiting and optimum N supply, re-

Table 1. Total shoot dry matter (dm), N content in leaf dm (wrapper leaves + rest of leaves) and N uptake at optimum (N_{opt}) and limiting (N_{lim}) N supply. Plants were harvested at grade 5.

Trial	N supply	Total shoot dm (g plant^{-1})	N content in leaf dm (g N kg^{-1})	N uptake (shoot) (g plant^{-1})
1	N_{lim}	109 b*	20 b	2.5 b
	N_{opt}	170 a	42 a	6.3 a
2	N_{lim}	83 b	26 b	2.3 b
	N_{opt}	137 a	48 a	6.0 a
3	N_{lim}	87 b	29 b	2.3 b
	N_{opt}	156 a	46 a	6.3 a

*) Different letters indicate significant differences separately for each trial and parameter at $p < 0.05$

Table 2. Effect of the change in N supply on total shoot dry matter (dm), curd dm, N content in leaf dm (wrapper leaves + rest of leaves) and N uptake in comparison to a continuous limiting (N_{lim}) and optimum N supply (N_{opt}). Plants were harvested at grade 5.

N supply	total shoot dm (g plant^{-1})	curd dm (g^{-1})	N content in leaf dm (g N kg^{-1})	N uptake (shoot) (g plant^{-1})
N_{lim}	109 b*	47 b	20 b	2.5 b
$N_{lim} \rightarrow N_{opt}$	130 a	55 a	33 a	3.9 a
N_{opt}	170 ns	78 ns	42 a	6.3 a
$N_{opt} \rightarrow N_{lim}$	179	84	32 b	4.9 b

*) Different letters indicate significant differences separately for each trial and parameter at $p<0.05$, ns means non-significant differences.

spectively. In trials 2 and 3, which were conducted in autumn, total dry matter was lower than in trial 1 and the plants tended to a higher N concentration in leaf dry matter at both N levels. The final number of leaves was not different between the N levels and was 22 to 25 leaves per plant at harvest.

N supply and curd compactness

The change over time of curd compactness at optimum N supply (N_{opt}) and limiting N supply (N_{lim}) is presented in Fig. 1A. At both N levels the curd compactness decreased with time, which was indicated by a higher grade. The curd diameter also increased due to steady curd growth. At limiting N supply grade 4 and thus the onset of bolting and loss of marketability was already reached after ten days. At optimum N supply, however, bolting was delayed and started after 14 days. This could have been an effect of curd growth, because at optimum N supply the curd diameter was significantly higher than at limiting N supply. The curd weight measured at grade 5 (Table 2) was also higher than at limiting N supply ($p<0.05$).

Fig. 1B shows that a transfer from limiting to optimum N supply (Nlim→Nopt) significantly retarded the onset of bolting by four days and thus grade 4 was reached after 14 days. This was the same time at which grade 4 was reached at continuous optimum N supply (Fig. 1A). The curd diameter did not significantly change as a result of the transfer to optimum N supply, whereas curd weight increased (Table 2). The change in N supply also increased the total dry matter, the N content in leaf dry matter and the N uptake.

A transfer from optimum to limiting N supply ($N_{opt} \rightarrow N_{lim}$) did not affect the onset of bolting and the curd diameter (Fig. 1C). Also, the total dry matter and curd dry weight (Table 2) were not changed, but the alteration to limiting N supply decreased the N content in dry matter and consequently N uptake was reduced.

Effect of gibberellic acid and chlorcholinchloride on curd compactness

In trial 2 the acceleration of bolting at limiting N supply was confirmed and grade 4 was reached on average three days earlier than at optimum N supply (Fig. 2A, B). At both N levels, treatment with GA_3 did not promote bolting and the application of CCC was ineffective in delaying bolting (Fig. 2A, B).

In this trial the limiting N supply resulted in a significant reduction of total dry matter, curd dry weight, N concentration and N uptake (Table 1). The treatment with GA_3 and CCC, however, had no effect on these parameters at both N levels (data not shown).

Effect of benzylamiopurine on curd compactness

A continuous supply with limiting N supply resulted in an onset of bolting at grade 4 after 12 days, which was again distinctly earlier than at optimum N supply

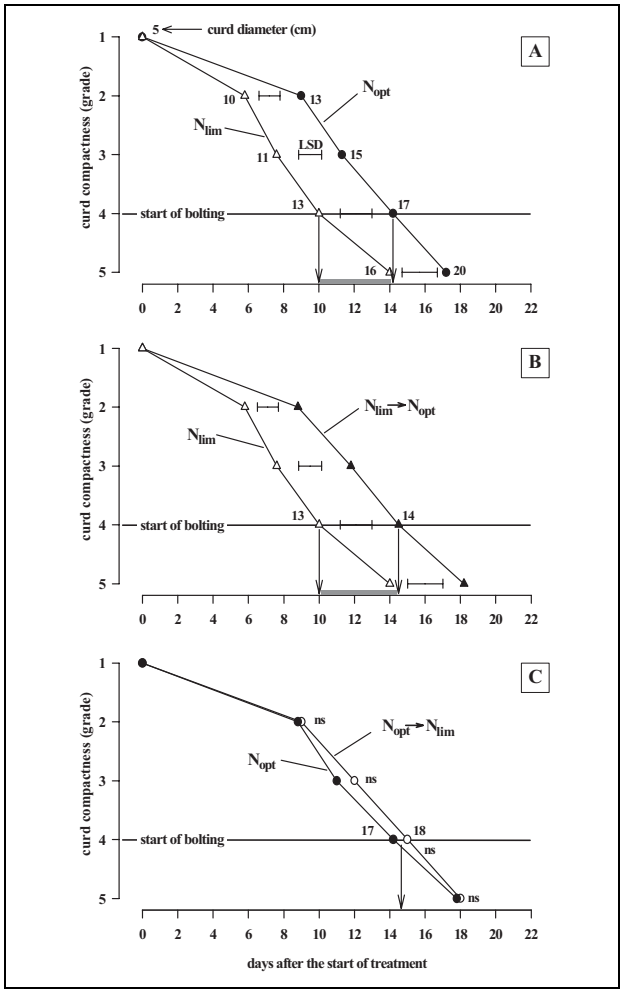


Fig. 1. Curd compactness at continuous optimum (N_{opt}) and limiting (N_{lim}) N supply (A) compared to an alteration in N supply from N_{lim} to N_{opt} (B), and from N_{opt} to N_{lim} (C).

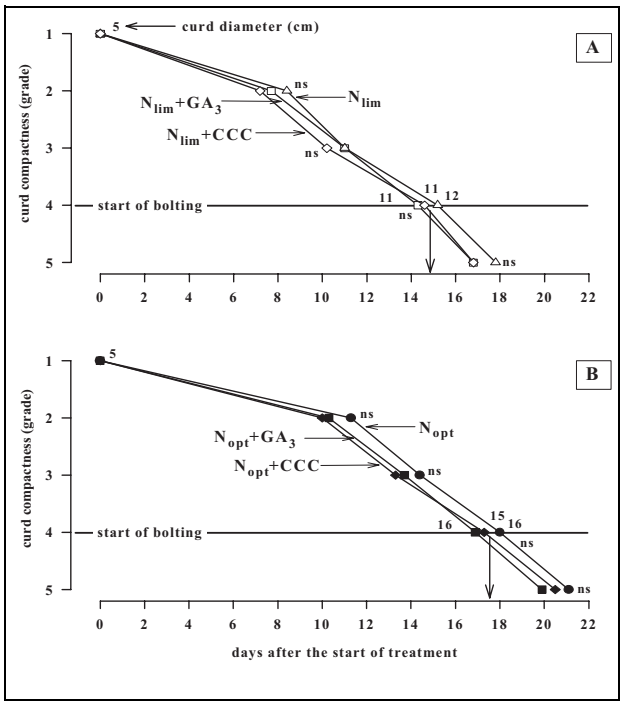


Fig. 2. Effect of a foliar application of GA_3 and CCC at continuous limiting (N_{lim} + GA_3, N_{lim} + CCC) (A) and optimum N supply (N_{opt} + GA_3, N_{opt} + CCC) (B) on curd compactness in comparison to limiting (N_{lim}) and optimum (N_{opt}) N supply.

($p<0.05$) (Fig. 3A, B). The stem infusion with the cytokinin benzylaminopurine significantly delayed bolting by four days at limiting and by about three days at optimum N supply (Fig. 3A, B). This was not due to differences in curd growth, since the curd diameter was not significantly different. At both N levels the total dry matter, the curd dry weight, the N concentration and N uptake did not differ from the untreated control (Table 3).

The volume of BA solution infused varied by up to a factor of three between plants. Thus the amounts of BA infused into each plant were plotted against the retardation of bolting at each N level and a positive correlation between amount of BA infused and delay of bolting was indicated (Fig. 4A, B).

Discussion

Dry matter yield and N content in leaf dry matter

The N content in leaf dry matter with plants receiving optimum supply indicated sufficient N supply, since a content of 30 to 45 g kg^{-1} N in leaf dry matter at harvest is reported to be optimum with cauliflower leaves (GERALDSON et al. 1973; BÖHMER 1980). At limiting N supply the N content was significantly lower and indicated N shortage.

The total N uptake per plant in the greenhouse was in a similar range to the field experiments (RATHER et al. 2000), which were taken for calculating the N supply in this research. Thus, the objective of differentiating between the continuous limiting N and optimum N supply relevant for cauliflower production in the field was achieved. This quantity concept ensures a differentiation in the N supply during the entire plant growth.

The lower dry matter production in trial 2 and trial 3 (Table 1) could be explained by the late growing period in autumn with less global radiation resulting in a higher N concentration due to less dilution, since the amounts of N taken up were similar.

Effect of N supply on curd compactness

In all the trials, continuous limiting N supply accelerated the onset of bolting by three to four days compared to optimum N supply. BÖHMER et al. (1981) also showed that at limiting N supply the time until the loss of marketability was shorter than with optimum N supply. The accelerated bolting could have been the result of an earlier curd induction, which would be indicated by a lower final number of leaves (WIEBE 1972a, b; BOOIJ 1987). In the present investigation,

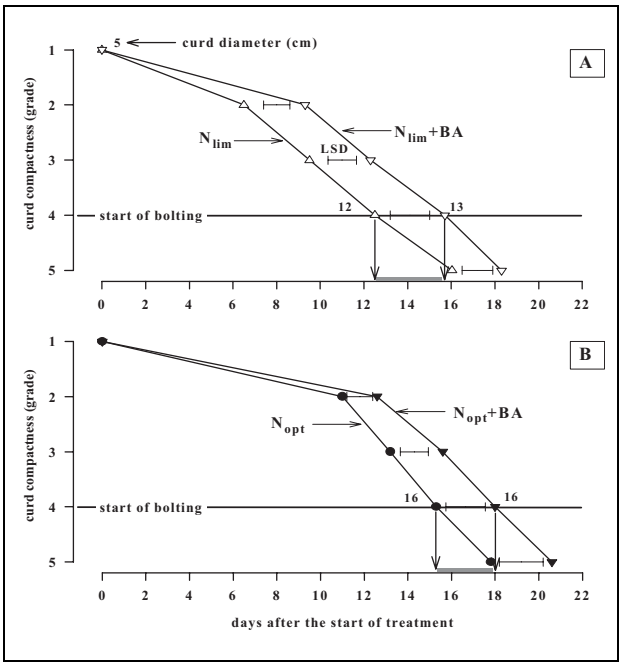


Fig. 3. Effect of stem infusion of benzylaminopurine (BA) at continuous limiting (N_{lim}+BA) and optimum (N_{opt}+BA) N supply on curd compactness in comparison to limiting (N_{lim}) and optimum (N_{opt}) N supply.

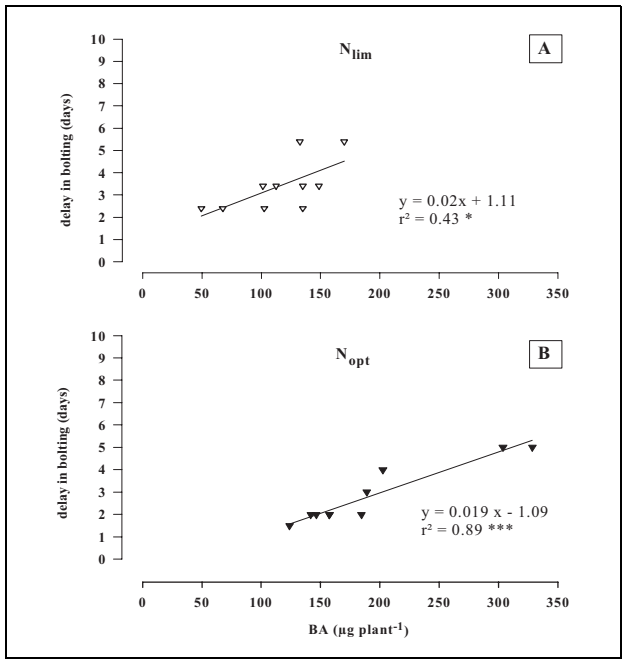


Fig. 4. Relationship between the amounts of BA infused at limiting (N_{lim}, A) and optimum (N_{opt}, B) N supply and the delay in bolting compared to the respective control treatment without BA. (*: $p<0.05$; ***: $p<0.001$).

however, the final leaf number did not differ between limiting and optimum N supply. Thus an earlier curd induction was not assumed to affect the process of bolting.

The transfer from limiting to optimum N supply at a curd diameter of 5 cm significantly retarded bolting (Fig. 1B), which was not due to an increase in the curd diameter, although the curd weight increased (Table 2). The delay in bolting was related to an increase in the N concentration in leaf dry matter to a level, which was optimum with cauliflower (GERALDSON et al. 1973; BÖHMER 1980). In contrast, the transfer from optimum to limiting N supply did not affect the process of bolting and plant growth parameters, but it resulted in a decrease in N concentration in leaf dry matter due to dilution. The N content of 32 g kg^{-1}, however, was still optimum with cauliflower. Since the content of phytohormones is closely linked with the N status of the plant, it could be supposed that bolting is related to the action of phytohormones.

In the case of high N supply, the synthesis of N compounds like amino acids, amines and mediated polyamines is enhanced. Several studies in the literature implied that polyamines significantly affect flower formation (EVANS and MALMBERG 1989). These results, however, are mostly restricted to the effect of polyamines on floral transition and the cytological events during floral initiation (GALSTON and KAUR-SAWHNEY 1995). Additionally, polyamines appear to play a role in cell division and not in cell elongation (SMITH et al. 1985). One could thus conjecture that polyamines might not be responsible for the retarded elongation of first and higher-order branches at high N supply with cauliflower. Phytohormones that play a role in elongation, however, are gibberellin and auxin with its antagonist cytokinin.

Effect of GA_3 and CCC on curd compactness

The foliar application with GA_3 did not have an effect on the start of bolting (Fig. 2). The effect of gibberellin, however, is dependent on the plant species, the cultivar, and the kind of gibberellin (ROOD et al 1989; MANDEL et al. 1992). With brassica species a treatment with 100 mg l^{-1} GA_3 is reported to promote flowering (CHAKRAVARTI 1958; WITTWER and BUKOVAC 1959; KAHANGI and WAITHAKA 1981), while with a tropical cauliflower the effect of GA_3 was dependent on the cultivar (ADITYA and FORDHAM 1995). BOOIJ (1989), however, observed no effect of GA_3 when applied to cauliflower, but the results were restricted to curd initiation. Admittedly, BOOIJ (1989) pointed out that the time of application is critical for the effect of gibberellin, for LESHEM and STEINER (1968) showed that an application with GA_3 56 days after sowing together with a cold treatment promoted flowering. Our own results support the idea that GA_3 and with this gibberellins are not effective in the promotion of bolting, because the treatment with CCC did not affect bolting. This retardant blocks an early step of gibberellin biosynthesis and thus inhibits the synthesis of other active GAs like GA_{4+7} and GA_{20} (SPONSEL 1995). In contrast, HEDDEN (1990) showed an inhibition of bolting with other brassica species. BOOIJ (1989) observed in studies with cauliflower that curd initiation was not affected by CCC, while it was promoted by an application of GA_{4+7}. This conflicts with the inhibiting effect of CCC on the biosynthesis of GA_{4+7}.

Table 3. Effect of stem-infusion of benzylaminopurine (BA) at continuous limiting (N_{lim} + BA) and optimum N supply (N_{opt} + BA) on total shoot dry matter (dm), N content in leaf dm (wrapper leaves + rest of leaves) and N uptake in comparison to limiting (N_{lim}) and optimum (N_{opt}) N supply. Plants were harvested at grade 5.

N supply	total shoot dm (g plant^{-1})		curd dm (g^{-1})		N content in leaf dm (g N kg^{-1})		N uptake (shoot) (g plant^{-1})	
N_{lim}	87	ns*	33	ns	29	ns	2.3	ns
N_{lim} + BA	89		27		28		2.3	
N_{opt}	156	ns	57	ns	46	ns	6.3	ns
N_{opt} + BA	165		65		44		6.4	

*) ns indicates non-significant differences separately for each trial and parameter.

Effect of cytokinin on curd compactness

The application of the cytokinin BA via the stem-infusion technique significantly delayed bolting at both N levels and the effect increased with increasing amounts of BA infused (Fig. 3, 4). The inhibition of bolting by exogenous cytokinin was confirmed by VAN DOORN (VAN DOORN 1996, Novartis Seeds, pers. communication). Cytokinin as an antagonist of auxin prevents elongation and stimulates branching (CLINE 1994; KLEE and ROMANO 1994; BARENDSE and PEETERS 1995). The cytokinin status of the plant, however, is strongly linked with the N supply. A low N supply decreases the cytokinin export out of the roots (SATTELMACHER and MARSCHNER 1978; SALAMA and WAREING 1979; KUIPER 1988; WAGNER 1991), the main sites of biosynthesis (PALNI et al. 1988), and results in a shortage of cytokinin in the shoot. One could thus speculate that this would shift the phytohormone balance in the curd in favour to auxin, which would stimulate the elongation of first and higher-order branches. It has to be borne in mind that plant hormones do not necessarily influence plant responses exclusively via changes in their concentration, but that hormonal regulation may also be exercised via changes in the sensitivity of the target cells (TREWAVAS 1983; DAVIES 1995).

The amounts of BA infused into the plants varied considerably. This may have been the result of the technique used. When the cavity was prepared in the stem with a cork borer it may have happened that different numbers of the radial xylem vessels were reached. Another restricting factor concerning the uptake of BA by infusion may have been the differences between the plants in the production of callus.

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