DEVELOPMENT OF CAULIFLOWER AND ITS CONSEQUENCES FOR CULTIVATION

Promotoren:

dr.ir. P.C. Struik
hoogleraar in de akkerbouw (gematigde klimaatsgebieden)

dr.ir. H. Challa
hoogleraar in de tuinbouwplantenteelt in het bijzonder de beschermde teelt

remmie booij

DEVELOPMENT OF CAULIFLOWER AND ITS CONSEQUENCES FOR CULTIVATION

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Abstract

From a number of cauliflower crops, grown during several years, plant development was related to the environmental conditions (mainly temperature). After transplanting three developmental phases could be recognized: juvenility, curd induction and curd growth. Variation in time of curd maturity was mainly due to a variation in time of curd initiation (morphological transition of the apex). Time of curd initiation was determined by the time on which juvenility (characterized by the number of initiated leaves) ended and temperature during the period after juvenility. Higher temperatures during the period of curd induction delayed curd initiation and increased the total number of initiated foliage leaves of a plant.

Curd induction could be affected by a GA_{4+7} application, resulting in an advance of curd maturity, especially when curd initiation of a crop was delayed due to high temperature.

Curd weight at maturity was reduced if plant weight at the time of curd initiation was low, conditions which enhanced development but reduced growth caused buttoning.

Bracting was induced by high temperature, and when ethephon was applied just after all plants within a crop had initiated a curd, bracting incidence was enhanced severely. Genetic differences in sensitivity for bracting induced by ethephon were apparent.

Prospects of cultural measures to reduce the variation in time of maturity in relation to rapidly changing environmental conditions are discussed.

Descriptors: Cauliflower, *Brassica oleracea* var. *botrytis*, temperature, growth regulators, gibberellins, ethephon, flowering, bracting, buttoning, timing, planning, maturity, harvest, breeding

STELLINGEN

1. De onderscheiden ontwikkelingsfases van de bloemkoolplant verschillen in gevoeligheid voor omgevingsfactoren, met name temperatuur. Omdat bovendien omgevingsfactoren fluctueren varieert de tijdsduur van uitplanten tot oogstrijpheid sterk.

   Dit proefschrift

2. De hoeveelheid bloemkool die op de markt wordt aangevoerd is vroegtijdig te voorspellen, als men beschikt over informatie aangaande het tijdstip van koolaanleg.

   Dit proefschrift

3. Hoge temperaturen verlaten de koolaanleg van bloemkool; dit effect kan gedeeltelijk worden tegengegaan door toediening van gibberellinezuren.

   Dit proefschrift

4. Regressiemodellen en eenvoudige ecofysiologische modellen zijn het meest geëigend voor betrouwbare voorspellingen ten behoeve van teeltbegeleiding.

   C.J.T. Spitters, Crop growth models: their usefulness and limitations. Acta Horticulturae (1990) 267: 349-368

5. Uit de door De Zeeuw & Leopold uitgevoerde experimenten kan niet éénduidig worden geconcludeerd dat auxine de duur van de jeugdfase beïnvloedt; het is niet uitgesloten dat auxine een effect heeft tijdens de bloei-inductiefase.

   D. de Zeeuw & A.C. Leopold, Altering juvenility with auxin. Science (1955) 22: 925-926

6. Door regelmatig kool te consumeren verkleint men de kans op het krijgen van bepaalde vormen van kanker.

   J.H. Koeman, Chemische gevaren in de voeding. Chemisch Magazine (1984) : 135-141

7. Processen welke ten grondslag liggen aan fenologische verschijnselen worden onvoldoende begrepen om in een verklarend model te vervatten.

   F.W.T. Penning de Vries et al., Simulation of ecophysiological processes of growth in several annual crops. (1989) pp. 73-82

8. De maximale termijn waarover een bruikbare weersvoorspelling mogelijk is, is vrijwel bereikt.

   T. Opsteegh, De atmosfeer; een metafoor voor het gedrag van creatieve systemen. Uit: H.Tennekes (ed.) De vlinder van Lorenz. (1990) pp. 84-102

9. De fiets is in het woon-werkverkeer meestal een goed alternatief voor auto én openbaar vervoer, daar het gebruik van dit vervoermiddel zowel het milieu als de volksgezondheid tengoede komt.

10. Door de tweede hoofdwet van de thermodynamika is het werk van organisatiedeskundigen even onmisbaar als onvolkomen.

11. Het is niet vanzelfsprekend dat een beter inzicht in het functioneren van het geheel kan worden verkregen door intensief een onderdeel ervan te bestuderen.

12. Er wordt onvoldoende duidelijk gemaakt dat de consument het "kijkgeld" betaalt voor commerciële televisie.

13. Gezien de mazen in de belastingwetgeving, verdient het aanbeveling dat de overheid meer achter het net vist.

Stellingen behorend bij het proefschrift van Remmie Booij:
'Development of cauliflower and its consequences for cultivation'.

Wageningen, 25 september 1990.

Aan Jette, Chris en Marga

Curriculum vitae

Remmie Booij werd op 6 oktober 1953 geboren te Wapserveen (Dr.). Na het eindexamen HAVO in 1971 en Atheneum B in 1973 werd in het laatste jaar begonnen met een studie aan de Landbouwhogeschool in Wageningen.

Gedurende de studie, richting Landbouwplantenteelt, werd in 1977 de praktijktijd doorgebracht op het Instituut voor Bodemvruchtbaarheid in Haren (Gr.) en het Plant Breeding Institute in Cambridge (UK). In 1980 werd het doctoraalexamen in de vakken Landbouwplantenteelt, Plantenfysiologie en Bodemvruchtbaarheid afgelegd.

Vanaf 1 februari 1980 tot 1 juni 1987 was de auteur werkzaam op het Proefstation voor de Akkerbouw en de Groenteteelt in de Vollegrond in Lelystad. Hij was hier belast met teeltkundig onderzoek aan vollegrondsgroentegewassen en in het bijzonder werd gewerkt aan het gewas bloemkool. Gedurende deze periode werd het onderzoek uitgevoerd dat ten grondslag ligt aan dit proefschrift.

Vanaf 1 juni 1987 wordt door hem op het Centrum voor Agrobiologisch Onderzoek in Wageningen onderzoek verricht naar de bloeiinductie van vollegrondsgroentegewassen. Tevens vond hier de voltooiing van het proefschrift plaats.

Voorwoord

De weg, die moet worden bewandeld vanaf het moment dat het idee aan het brein van de onderzoeker ontspruit tot het moment waarop de resultaten van het onderzoek zijn gepubliceerd, is alleen begaanbaar dankzij de medewerking van velen. Een aantal van die onmisbare schakels die aan het tot stand komen van dit proefschrift hebben bijgedragen wil ik graag met name noemen.

Allereerst wil ik mijn beide promotoren, prof.dr. P.C. Struik en prof.dr. H. Challa danken voor hun bereidheid als zodanig te willen optreden. Hoewel het experimentele werk vrijwel voltooid was op het moment dat ik hen benaderde, is hun inbreng tijdens het schrijven van het proefschrift onmiskenbaar geweest. Moge de begeleiding vanuit de twee verschillende vakgebieden symbolisch zijn voor de huidige plaats van het onderzoek aan vollegrondsgroenten.

De probleemstelling, welke ten grondslag heeft gelegen aan het onderzoek was afkomstig uit de praktijk en de primaire doelstelling was dan ook het aandragen van een oplossing. Tijdens de experimentele fase van het onderzoek was er sprake van aan de ene kant het zoeken naar een oplossing en aan de andere kant de bevrediging van een wetenschappelijke nieuwsgierigheid. Ik wil daarom bestuur en directie van het PAGV danken voor de vrijheid die ik heb gekregen om vooral ook aan het laatstgenoemde aspect te mogen toegeven. Naar ik hoop is dit proefschrift een aanwijzing dat beide aspecten tot op zekere hoogte verenigbaar zijn. Mijn overstap naar het CABO is evenwel bepalend geweest voor de voltooiing van het proefschrift, mijn dank gaat uit naar dr.ir. J.H.J. Spiertz, als directeur van het CABO, voor het in mij gestelde vertrouwen en de ruimte die mij is geboden. Ik ben mij er van bewust dat het wat meer tijd heeft gekost dan oorspronkelijk was gepland.

Dr. Siebe van de Geijn en ir. Peter Dekker ben ik zeer erkentelijk voor de wijze waarop ze de manuscripten van het nodige commentaar voorzagen.

Natuurlijk zijn een aantal mensen in de uitvoerende sfeer onmisbaar geweest, waarvoor ik hun hartelijk dank wil zeggen. Pierre Bakker en medewerkers van het PAGV proefbedrijf voor de aanleg en verzorging van de vele veldproeven. Medewerksters van de typekamer en met name Cora Hermsen voor de moeite om de tekstverwerker en printer dat te laten doen wat ik me voorstelde. Ko Engelsman voor de zorgvuldige wijze van het tekenen van de figuren, iets waar m.i. geen computer tegenop kan. Peter Stad en medewerkers van de fotodienst voor de snelle en accurate afhandeling van de fotografische werkzaamheden. En tenslotte Joke Braber en Leo van der Heijden voor de laatste puntjes op de i.

De soms heftige discussies welke ik samen met mijn oud-collega's van de afdeling Teeltonderzoek Groenten heb gevoerd over de ontwikkeling van het onderzoek in de vollegrondsgroente heb ik bijzonder gewaardeerd. Hoewel de tijd die ik op het PAGV heb doorgebracht tamelijk turbulent van aard was, denk ik er met veel genoegen aan terug.

Tenslotte ben ik aan Jette veel dank verschuldigd voor de wijze waarop zij het thuisfront voor haar rekening heeft genomen in de afgelopen jaren, alleen daardoor kon ik mij met veel, soms misschien met te veel, energie op het werk richten, waarvan de voltooiing van dit proefschrift een belangrijk onderdeel uitmaakte.

De uitgave van dit proefschrift is mede mogelijk gemaakt door een financiële bijdrage van het LEB-Fonds.

Contents

Chapter 1

Introduction

Introduction

The mean annual supply of cauliflower at the Dutch auctions was 42.6 $\pm$ 0.35 million heads during the period 1979-1988. This production was achieved on an annual acreage of 2520 $\pm$ 135 ha. The given standard errors indicate a rather stable acreage and production during this period. The supply per week, averaged over a ten year period (1980-1989), appeared to be fairly constant during the season (Fig. 1).

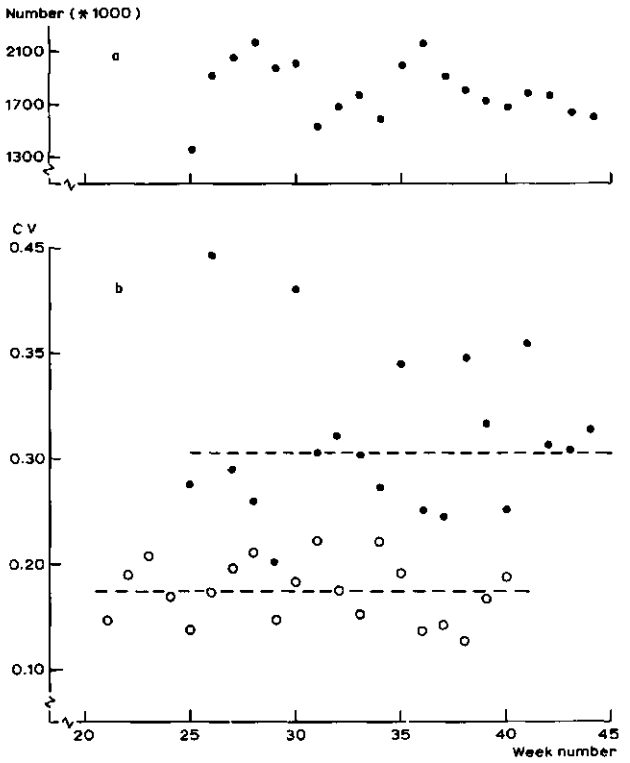

Figure 1
Weekly cauliflower supply (number of heads) at the auctions during the season averaged over the period 1980-1989 (a) and the coefficient of variation (cv) in weekly supply in the same period for cauliflower (●) and lettuce (○) (b).
Source: PGF

However, the coefficient of variation in supply during a certain week was high and variable. In comparison, the relative variation in the number of heads of lettuce supplied

weekly at the auctions during the same period was only half of the variation in the number of cauliflower heads (Fig. 1). The main difference between these two crops is the marketable part of the plant; the whole sprout of lettuce is harvested, while from the cauliflower plant the inflorescence is harvested.

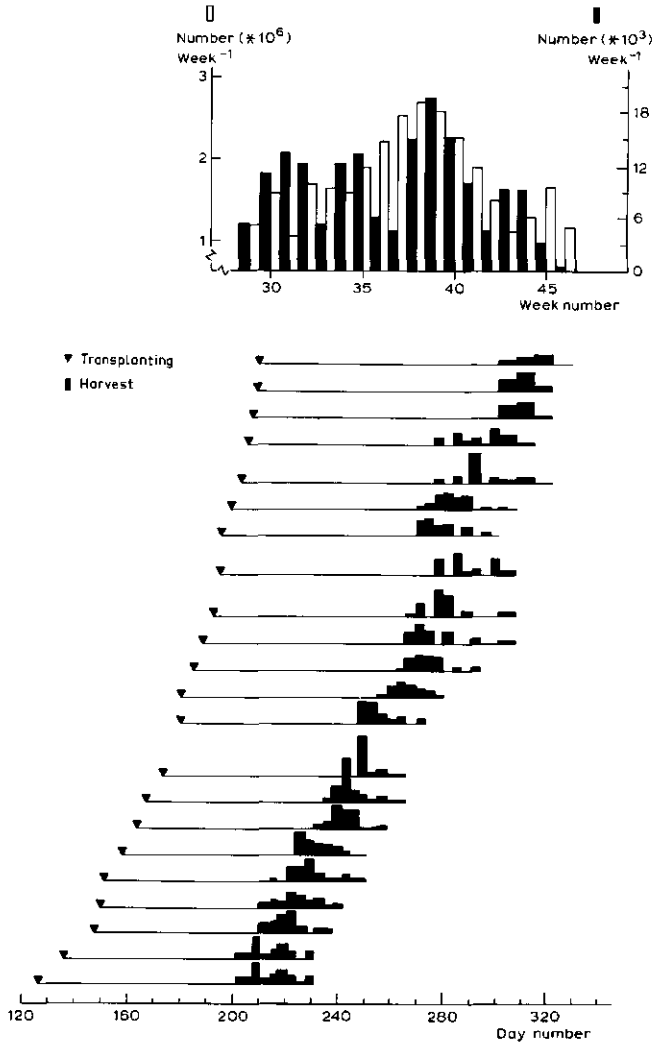

Figure 2
Relation between transplanting date (Ordinal date: January 1 is Day 1) and time of harvest for a number of crops of an individual farm. Total weekly production (number of heads week^{-1}) on the farm and total weekly supply at the auctions (number of heads week^{-1}) in the same period of time is given on top.

A large part (about 60 %) of the cauliflower production is concentrated in a small area ("de Streek"). Most growers are highly specialized and grow continuously cauliflower throughout the season. As the harvest requires a lot of hand labour, its timing is important. Two variables should therefore be known for each crop in advance, namely *i*, the time between transplanting and maturity and *ii*, the time interval between maturation of the first and the last curds. The planning of production of a single farm is mainly based on the experiences in the past; by transplanting at regular time intervals he aims at a regular supply during the season. A production scheme and the outcome of the plan is given in Figure 2. The weekly production varied in spite of regular transplanting. The length of the growing period (number of days between transplanting and harvest) and the length of the period during which plants of a single crop matured (harvest period) varied from crop-to-crop. Adding the production of all the single crops results in the production of the whole farm. Fluctuations in the number of harvested heads per week on the farm were obvious and corresponded with the fluctuations in weekly supply at the auctions in the same period (Fig. 2). A similarity between the situation of the individual grower of his fellow growers in a certain area is illustrated, when the length of the growing period of the crops is regarded. A pattern could be recognized when the length of the growing period was plotted against the transplanting date (Fig. 3), a pattern that depended on the season concerned. Some changes in length of the growing period are remarkably sudden.

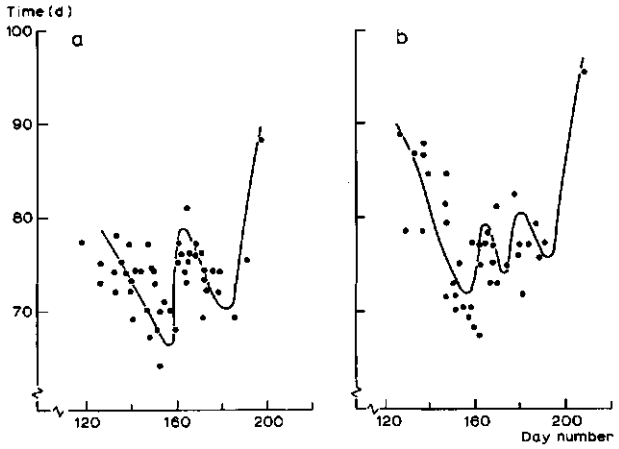

Figure 3
Relation between transplanting date (Ordinal date: January 1 is Day 1) and time (d) between transplanting and harvest for a number of crops grown by different growers during 1981 (a) or 1983 (b). Each point represents a crop.

The edible part of the cauliflower plant is the inflorescence which takes shape through a process of repetitive branching (Sadik, 1962), so that an enormous number of shoot apices cover the surface. Before formation of the curd a transformation of the

stem apex is necessary; instead of leaf primordia secondary primordia are initiated, which will form the base structure of the curd (Margara & David, 1978). This transition from the vegetative to the generative phase (curd initiation) only occurs when the requirements for induction of the inflorescence are satisfied. The plant should pass the juvenile phase first, before inductive conditions will be effective (Wiebe, 1972a). Therefore should the plant have initiated a certain number of leaves, as the end of juvenility is characterized by the number of initiated leaves (Hand and Atherton, 1987). Temperature is the most important environmental factor affecting curd induction, higher temperatures retard or even prevent induction, while lower temperatures accelerate the induction (Wiebe, 1972b).
Curd diameter increases after curd initiation until the strong elongation of the branches of the inforescence starts. Flowers are formed only on a few branches after elongation started. The curd is said to mature just before this elongation starts and harvest can not be delayed, because afterwards quality deteriorates quickly. Size and quality of the curd at maturity determine the ultimate yield. The scope of the present study is to relate plant development to time of maturity, as affected by the environment, which was put into the following questions:

- How does the variation in time on which phase transitions occur, affect the variation in time of maturity of crops and of single plants within a crop?
- How is the transition from the vegetative to the generative phase influenced by the environment?
- How can time of curd maturity be manipulated in the field?
- What are the relations between the rate of plant development and size and quality of the curd?

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Chapter 2

Environmental factors in curd initiation and curd growth of cauliflower in the field

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Environmental factors in curd initiation and curd growth of cauliflower in the field

R. Booij

Research Station for Arable Farming and Production of Field Vegetables (PAGV), P.O. Box 430, NL 8200 AK Lelystad, Netherlands

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Key words: cauliflower, data of harvesting, growth regulation, temperature, flower initiation, curd initiation, *Brassica oleracea* L. var. *botrytis*

Abstract

In 1982, 1983 and 1984, seedlings of two cauliflower (*Brassica oleracea* L. var. *botrytis*) cultivars were transplanted at several dates during the summer. Physiological events like end of juvenility, curd initiation and maturity were recorded.

Date of curd initiation was correlated with mean temperature in the period after initiation of the 19th leaf. At higher temperatures, curd initiation was later. The number of leaves initiated before curd initiation was best correlated with mean maximum day temperature in the period between initiation of the 19th leaf and curd initiation. The variation in duration of curd growth was less than the variation of the period between transplanting and curd initiation. The duration of curd growth could just as well be explained by the date of curd initiation as by a temperature-time product or by the mean irradiance.

Introduction

The rate at which cauliflowers become ready for marketing can vary enormously during the summer and autumn (Booij, unpublished; Hartmann & Wuchner, 1965; Salter et al., 1972; Wiebe, 1980). This variation occurs in spite of regular transplanting schedules and causes problems in marketing and labour organization.

Variation in growing period (number of days between transplanting and harvest) in a continuous cauliflower schedule cause most of the variation in supply (Booij, unpublished).

Temperature plays an important role (Liptay, 1981; Wiebe, 1973) in disturbing the planning. Because the product to be harvested is an inflorescence, the transition from vegetative to generative stage is necessary. The time of transition depends on the physiological age of the plant and on the temperature at certain times (Fujime, 1983; Wiebe, 1972a,b; Wurr et al., 1981).

This paper describes the effects of environmental factors on this transition and its influence on harvest date. An attempt is made to measure these effects.

Materials and methods

The trials were carried out in 1982, 1983 and 1984 at the research station in Lelystad, on a fertile marine clay soil. The cauliflower cultivars 'Delira' (Rijk Zwaan, De Lier) and 'Elgon' (Royal Sluis, Enkhuizen) were studied by transplanting bare-rooted plants 5 to 6 weeks old at several dates (Table 1). During the period between three weeks after transplanting and a 100% curd initiation, a sample (12 plants) was taken twice a week for dissecting. The total number of leaves (including leaf primordia) and the developmental state of the apex (vegetative or generative) were determined.

When the first secondary primordia became visible, determined with a binocular microscope (magnification ×50), the apex was considered to have reached the generative state (curd initiation) (Fujime, 1983; Margara & David, 1978). The final number of leaves is the number of leaves initiated before curd initiation and was estimated as soon as all plants of a sample had initiated a curd. At harvest, plants were individually assessed for maturity three times a week and were cut as they matured.

Initiation date of the 19th leaf was the date on which the mean total number of leaves in a sample from a plot was 19. Curd initiation date of the population was defined as the date when half of the plants had initiated a curd, harvest date as the date when half of the plants had been harvested.

The weather data were obtained from an official meteorological station situated about 6 km from the research station.

The calculated correlations between weather components and plant development were restricted to linear regressions.

Temperature-time product for curd initiation and curd growth was calculated according the following method (Robertson, 1968). The contribution T_{eff} of every day (i) between two developmental stages to the temperature-time product (T_{sum}) depends on the day temperature (T_i) and a set base (T_b) and maximum (T_m) temperature under the following conditions.

If	: $T_i \leqslant T_b$	$T_b < T_i \leqslant T_m$	$T_i > T_m$, then:
T_{eff} for curd initiation	: $T_m - T_b$	$T_m - T_i$	0
T_{eff} for curd growth	: 0	$T_i - T_b$	$T_m - T_b$

$$T_{sum} = \sum_{i=1}^{n} T_{eff}$$

where i = 1 is the first day and n the last day of the considered period. The parameters T_b and T_m are unknown. Different values of T_b and T_m were chosen and with these values the T_{sum} was calculated for every transplanting. The aim was to find values of T_b and T_m that resulted in a minimum standard devation of T_{sum}, by judging the coefficient of variation (standard deviation relative to the mean value, Reinink et al., 1986).

Results

The period between transplanting and harvest can be divided into two parts: between transplanting and curd initiation, and between curd initiation and harvest. These two periods are dealt with separately.

Curd initiation

The number of days between transplanting and curd initiation varied between 25 and 46 days (Table 1). The period was not related to the transplanting date. Curd initiation date of 'Elgon' tends to be a few days later than 'Delira'. The final number of leaves varied considerably too (Table 1); for 'Elgon' the values were higher than for 'Delira'.

The time (days) between transplanting and curd initiation not significantly correlated to the mean temperature in that period (Table 2). The period between transplanting and curd initiation can be subdivided into two parts: between transplanting and the initiation of the 19th leaf, and between initiation of the 19th leaf and curd initiation. The length of the second period significantly correlated with mean temperature during the period considered and with mean temperature in the period three weeks after transplanting and curd initiation (Table 2). The positive correlation coefficients indicate a later curd initiation at higher mean temperatures. Both cultivars showed the same highly significant correlations. The mean temperature in the periods better correlated with the final number of leaves (Table 3). The highest correlation was again found if mean temperature in the period between initiation of the 19th leaf and curd initiation was taken as explanatory variable. The final number of leaves even better correlated with mean daily maximum temperature during this period (Table 4). Using either the daily mean temperature or the daily maximum temperature to explain the variation in length of this period did not make any difference.

The sum of the total daily radiation largely explained the variation in final number of leaves and the variation in time (Table 4).

In Fig. 1, the scatter diagram and the best-fitting regression lines are given for the most important relations. The slope of the regression line between final number and temperature is for 'Elgon' nearly twice as steep as for 'Delira' (Fig. 1A, B). For time (Fig. 1C, D), the slope for 'Elgon' was nearly three times as steep.

It would be interesting to look at the effect of varying the starting point (higher or lower number of leaves) for calculations. The mean number of leaves could not, however, be varied to start with, because data of all the transplantings were not available. However, if some days before or after the time the 19th leaf was initiated were included in the calculations, the correlation coefficients did not change very much. For 'Elgon' also correlation coefficients were calculated starting at the day the 25th leaf was initiated, but the correlation coefficients were then hardly significant.

Temperature-time products did not much reduce the variation in the time between initiation of the 19th leaf and curd initiation. It was not possible to find coefficients of variation lower than 0.25 by varying T_b and T_m.

Table 1. Effect of transplanting date on the length (number of days) of different periods and the final number of leaves. The results of the two cultivars are separately presented.

Date	'Delira'				Date	'Elgon'			
	time (days) between transplanting and		final number of leaves	time (days) between curd initiation and harvest		time (days) between transplanting and		final number of leaves	time (days) between curd initiation and harvest
	initiation 19th leaf	curd initiation				inititation 19th leaf	curd initiation		
1982-05-12	20	33	31.5	42	1981-06-15	23	46	45.9	47
1982-05-18	21	30	27.5	41	1982-06-22	20	38	43.5	49
1982-05-26	21	25	25.0	40	1982-06-29	–	35	40.9	49
1982-06-01	23	28	27.0	41	1982-07-06	–	38	44.6	52
1982-06-08	18	26	27.5	39	1982-07-13	–	36	41.2	53
1982-06-15	20	36	36.2	47					
1982-06-22	18	35	33.8	44					
1982-07-13	21	35	33.3	49					
1983-05-11	28	40	30.5	38	1982-05-20	23	38	40.1	44
1983-05-20	23	31	31.3	42	1983-06-14	21	40	44.8	43
1983-05-30	21	31	31.7	40	1983-06-21	24	43	45.5	47
1983-06-02	24	34	31.4	42	1983-06-28	17	35	44.9	47
1983-06-07	28	41	36.5	44	1983-07-05	20	36	40.4	48
1983-06-14	25	35	35.8	45	1983-07-14	19	31	39.5	53
1983-06-21	24	38	37.6	42					
1983-07-14	22	29	31.5	49					
1984-05-08	28	41	27.9	44	1984-06-19	–	30	31.2	41
1984-05-15	25	32	27.5	45	1984-06-26	25	33	31.8	45
1984-05-23	25	36	27.4	40	1984-07-03	19	28	34.1	49
1984-05-29	28	32	24.8	45	1984-07-10	25	40	39.8	55
1984-06-05	27	33	23.4	40					
1984-06-12	28	41	25.8	37					
1984-06-19	23	32	27.3	39					
1984-07-10	28	38	33.3	52					

Table 2. Correlation coefficients between the length of several periods (days) and the mean temperature in the periods considered. The coefficients are separately presented for the two cultivars.

Time (days) between:	Mean temperature in the period between:			
	transplanting and initiation of 19th leaf	transplanting and curd inititation	21 days after transplanting and curd inititation	initiation of 19th leaf and curd initiation
'Delira'				
Transplanting and initiation of 19th leaf	−0.363*	−0.371*	−0.211	−0.189
Transplanting and curd initiation	−0.185	−0.047	0.288	0.319
Initiation of 19th leaf and curd initiation	0.099	0.281	0.567**	0.584**
'Elgon'				
Transplanting and initiation of 19th leaf	−0.475	−0.508	−0.355	−0.310
Transplanting and curd initiation	−0.071	0.250	0.479	0.574*
Initiation of 19th leaf and curd initiation	0.201	0.516	0.775**	0.850**

Significant correlation coefficient: $*P < 0.05$; $**P < 0.01$.

Table 3. Correlation coefficients between final number of leaves of the cultivars and the mean temperatures in several periods.

Cultivar	Mean temperature in the period between		
	transplanting and initiation of 19th leaf	transplanting and curd initiation	initiation of 19th leaf and curd inititation
'Delira'	0.505**	0.686**	0.874**
'Elgon'	0.360	0.724**	0.879**

Significant correlation coefficients: $**P < 0.01$.

Table 4. Correlation coefficients for several weather components in the period between initiation of the 19th leaf and curd initiation. (a) the final number of leaves; (b) time (days) between initiation of the 19th leaf and curd initiation; (c) curd growth with the same weather components during curd growth.

	Mean day temperature	Maximum day temperature	Minimum day temperature	Mean daily radiation	Sum of daily total radiation	Sum of rainfall
(a) Final number of leaves						
'Delira'	0.874**	0.906**	0.650**	0.459*	0.738**	−0.196
'Elgon'	0.879**	0.904**	0.756**	0.408	0.890**	0.420
(b) Time (days)						
'Delira'	0.584**	0.574**	0.480**	0.213	0.919**	0.243
'Elgon'	0.850**	0.850**	0.766**	0.416	0.953**	0.396
(c) Curd growth						
'Delira'	−0.645**	−0.583**	−0.662**	−0.815**	−0.484**	0.766**
'Elgon'	−0.836**	−0.856**	−0.828**	−0.928**	−0.782**	0.618**
'Delira' + 'Elgon'	−0.722**	−0.664**	−0.750**	−0.896**	−0.659**	0.714**

Significant correlation coefficient: $*P < 0.05$; $**P < 0.01$.

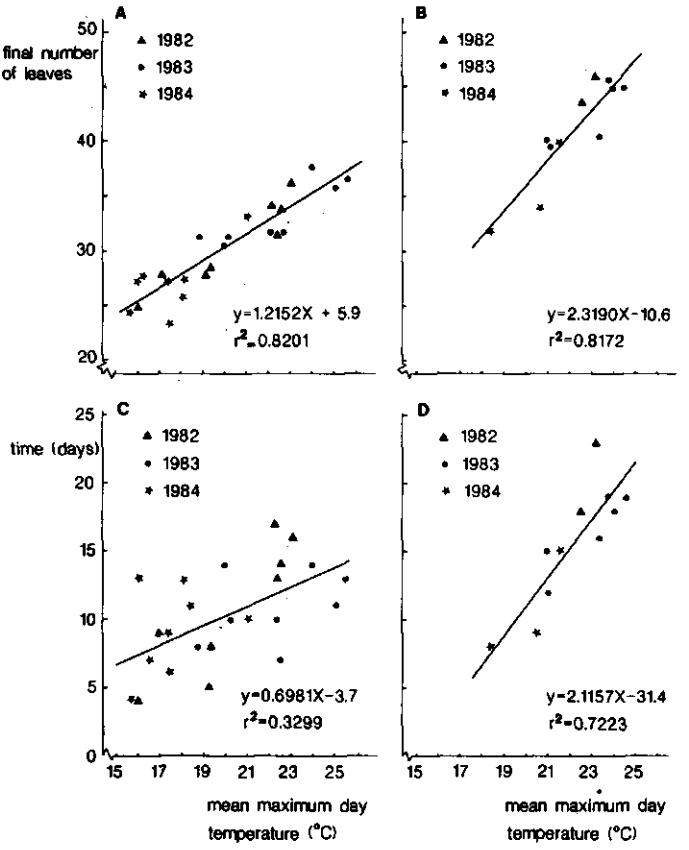

Fig. 1. Relationship between the mean maximum day temperature in the period between initiation of the 19th leaf and curd initiation and the final number of leaves (A, B) or the length of the period (C, D) for 'Delira' (A, C) and 'Elgon' (B, D).

Curd growth

Curd growth lasted 37 to 55 days (Table 1). Its duration seems to be fairly constant for 'Delira' (Table 1); only at the last transplanting date was the growing period a few days longer. The growing period of 'Elgon' tends to be longer at later transplanting dates (Table 1).

The duration was fairly constant when the curd was initiated before Day* 205 (24 July), but when the curd was initiated at later dates, there was a significant positive correlation between duration of curd growth and curd initiation date (Fig. 2). The first part consists mainly of 'Delira' data and the last mainly of 'Elgon' data. The differences between the two cultivars are, however, small. The duration of curd growth significantly correlated with all the weather components studied (Table 4).

* Ordinal date: 1 January is Day 1.

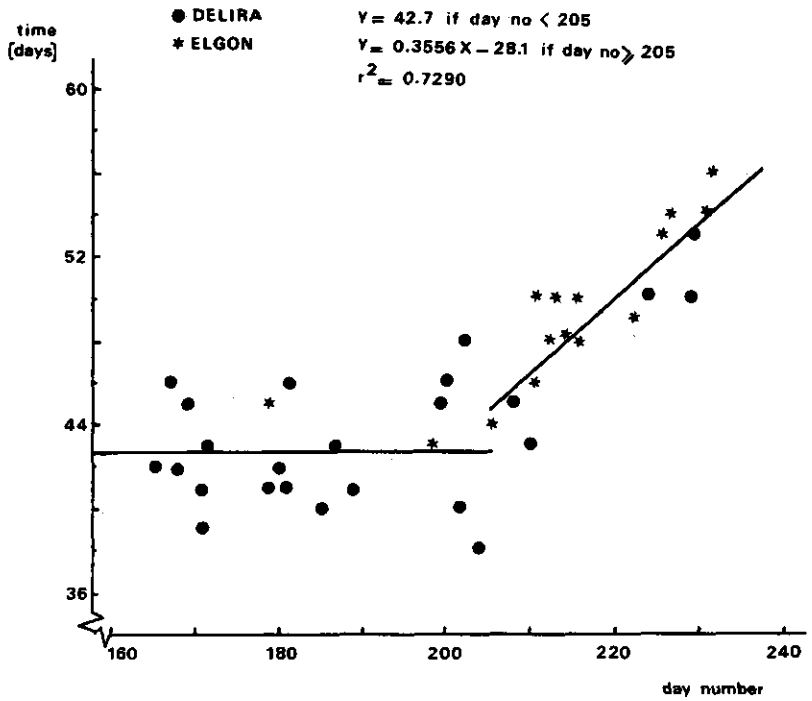

Fig. 2. Relationship between the day number (ordinal date: 1 January is Day 1) of curd initiation and the duration of curd growth of 'Delira' and 'Elgon'.

The highest correlation coefficient was found between duration of curd growth and mean irradiance during curd growth. The duration of curd growth decreased with increasing mean irradiance (Fig. 3). With higher irradiance there is still considerable variation around the regression line.

Another approach is to calculate the temperature-time product to explain the variability. The lowest coefficient of variation (0.062) was found on two occasions, namely with a T_b of 0 °C and a T_m of 19 °C and with a T_b of 5 °C and a T_m of 16 °C. In the latter case, the mean temprature-time product had a value of 445 °C·d.

In fact, there are now three variables to explain the variation in duration of curd growth, namely curd initiation date, mean irradiance, and the temperature-time product. To compare these three methods, the residual standard errors are compared. For the relation with curd initiation date (Fig. 2), the residual standard error was 2.29 days; for mean irradiance (Fig. 3), the error was 2.07 days. For the temperature-time product, the coefficient of variation was 0.062 and the mean T_{sum} 445 °C·d, i.e. a standard deviation of 27.6 °C·d. Translation of this value into a certain number of days depends on the day temperature. At a constant temperature of 16 °C, it corresponds to a standard error of 2.63 days. Lower temperatures result in higher values; higher temperatures give the same value.

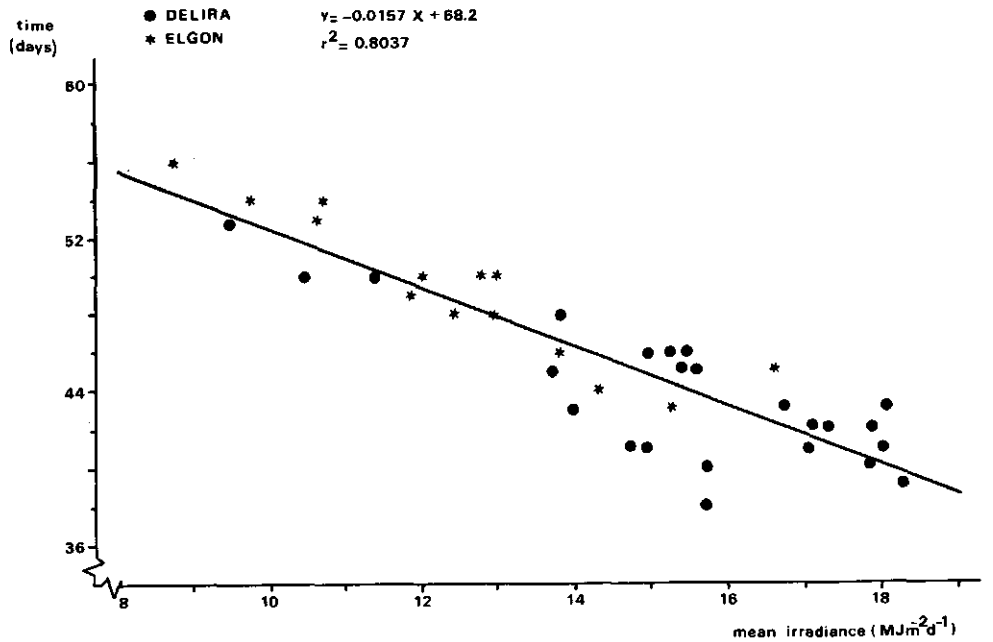

Fig. 3. Relationship between mean irradiance in the period between curd initiation and harvest and its duration (days) for 'Delira' and 'Elgon'.

The differences between the three methods are small, although mean irradiance gave the least residual standard error.

Discussion

During growth of a cauliflower crop in the field, two major transitions occur: the end of juvenility and curd initiation. Three developmental stages can therefore be recognized after transplanting: the juvenile phase, the curd induction phase, and the curd growth phase (Wurr et al., 1981). The date (i.e. number of days after transplanting or sowing) at which the phase transitions take place has consequences for the harvest date.

The correlations of temperature with curd initiation (Tables 2 and 3) show that the effect of temperature depends on the developmental stage of the plant. This clearly suggests the existence of a juvenile phase. Experiments under controlled conditions showed that the plant should reach a certain physiological age before the curd could be initiated by lower temperatures (Fontes et al., 1967; Fujime, 1983; Sadik, 1967; Wibe, 1972a), although Fujime & Hirose (1979) were able to enhance curd induction by cold treatment of germinating seeds. The physiological age at

which the plant reaches the end of the juvenile phase can best be characterized by the number of leaves that have been initiated (Wiebe, 1972a). In our trials the best correlation was when the end of the juvenile phase was set at 19 initiated leaves. None of the variables studied satisfactorily explained the date at which the 19th leaf was initiated. Although leaf initiation rate depends on temperature (Wiebe, 1972c), in our experiments the time at which growth restarts after transplanting plays a role.

Temperature in the period after the end of the juvenile phase influenced the time of curd initiation; high temperatures delayed curd initiation, as has been found in trials under controlled conditions (Fujime, 1983; Wiebe, 1972b). Final number of leaves better correlated with mean temperature in this period. Atherton et al. (in prep.) too found less variable responses to temperature with the final number of leaves than with the time to curd visibility. This implies that the effect of a day at a certain temperature on curd initiation depends also on the leaf initiation rate during the curd induction period, and this is why temperature-time products were not satisfactory. So final number of leaves does not only give information about the time of curd initiation, but also about the temperature conditions during the curd induction period, although often a higher final number of leaves is accompanied by a delay in curd initiation.

The relation between the mean temperature and the final number of leaves depends on cultivar (Fig. 1), as is also found in the literature (Fujime, 1983). The difference in slope indicates that 'Elgon' is more sensitive to temperature than 'Delira'. A temperature increase of, for instance, 1 °C results in a larger increase in final number of leaves for 'Elgon'. Temperature sensitivity is related to earliness: later cultivars are more sensitive to higher temperatures and have higher final number of leaves (Fujime, 1983).

With a wider range of temperatures then under Dutch conditions (11-19 °C), the relation between temperature and final number of leaves is not linear (Atherton et al., in prep.; Wiebe, 1972c). However, when linear regressions are calculated with the data within the range 11-19 °C, the slopes of their regression lines are of the same magnitude.

The good correlation with mean temperature during the different periods suggests that variation in temperature is not so important. Wiebe (1974) and Fujime (1983) have shown that diurnal variation in temperature gave the same results as a constant temperature with the same mean. Also when days with different temperatures were alternated, the results were similar (Wiebe, 1974).

In the correlation between day of curd initiation and duration of curd growth, two phases could be recognized with a rather distinct transition (Fig. 2). This correlation between date of curd initiation and duration of the curd growth indicates that the effects of variable weather factor like temperature and radiation are of less importance. Several authors have found relations between temperature and rate of curd growth (Salter, 1960; Salter, 1969; Wiebe, 1973).

It is necessary to distinguish between the effect of temperature on the increase in curd size and on maturity date. From the data presented by Wurr & Fellows (1984), duration of curd growth can be calculated. The duration of curd growth was fairly

constant and independent of mean curd weight at harvest (in spite of buttoning).

The effect of temperatures between 15 and 25 °C on harvest date are small, even if the effect on curd weight at harvest is big (Fujime, 1983); lower temperatures increase the duration of curd growth. The temperatures during our trials were within this range and this may explain the fairly constant duration of curd growth.

The relation between duration of curd growth and radiation (Fig. 3) was mainly determined by the transplantings, which had initiated the curd at a later date (Fig. 2). Daylength decreases very rapidly after the beginning of August and total daily radiation is closely correlated with daylength. So the relation between duration of curd growth and radiation might be an effect of daylength determining maturity of the curd (elongation of the inflorescence).

A temperature-time product could not explain the variation in duration of growth any better. Although Salter (1969) found a good relation between temperature-time product and curd weight during curd growth, temperature-time product did not determine harvest date. The T_b and the T_m that we found were quite close to the values that Salter (1969) found (2.8 °C and 15.6 °C).

The good relation between duration of curd growth and curd initiation date has promising consequences: harvest date can be predicted fairly accurately 6 to 8 weeks in advance, according to the given relation.

To get a better harvest planning of cauliflower, the length of the period between transplanting and harvest date should be regulated. The only way to do so is by regulating the time of curd initiation, because if the curd is initiated at the proper time, harvest will be close to the desired date. To regulate time of curd initiation, it is necessary to regulate the length of the juvenile phase and of the curd induction period. So, especially if curd initiation is delayed by high temperatures, artificial induction is required. If the end of the juvenile phase is determined by a certain number of leaves, regulating of the length of the juvenile phase will have consequences for number of leaves and could have implications for problems like buttoning (Wurr & Fellows, 1984).

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Chapter 3

Cauliflower curd initiation and maturity: variability within a crop

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Cauliflower curd initiation and maturity: variability within a crop

Summary

Between 1982 and 1986 seedlings of two cauliflower (*Brassica oleracea* L. var. *botrytis*) cultivars were transplanted at several dates during the summer. Plant development was recorded by dissecting plants at regular time intervals. The number of initiated leaves of vegetative plants was linearly related to the number of leaves longer than 1 cm. Variation in curd diameter within a crop was largely accounted for by regression on the number of leaves longer than 1 cm and the final number of leaves of the plant. A method for estimating curd initiation date of a plant was developed, based on the final number of leaves and the number of leaves longer than 1 cm. Also a procedure for estimating the leaf number that characterises the end of the juvenile phase is decribed. Cv. Delira had 17 and cv. Elgon 19 leaves initiated at the end of juvenility. In most crops the variation of curd initiation date was caused by both plant-to-plant variation in end of juvenility and by variation in the mean daily maximum temperature after the end of juvenility.

About 55 % of the variance in duration of the harvest period of a crop could be explained for by the combined effect of variation in the duration of the curd initiation period and in the temperature during curd growth.

The complexity of environmental factors determining the duration of the harvest period is discussed in relation to the possible effects of cultural factors.

Introduction

Within a cauliflower crop the time of maturity of plants, varies considerably and because the standing ability of the curd is short, many selective hand harvests are required. The harvesting costs are a large part of the total costs of production (Wheeler and Salter, 1974). Much research has been carried out aiming at a reduction of the variability, with once-over harvest as the ultimate goal. Depending on transplanting date the duration of the harvest period can vary considerably during the season (Booij, 1984). Attempts have been made to reduce the duration of the harvest period using cultural techniques (Salter and Fradgley, 1969; Lindfors, 1975), for example using seed grading, direct drilling, different plant raising methods and plant selection, however, with variable success.

Special attention has been paid to the effect of a cold treatment before transplanting on the duration of the harvest period (Salter and James, 1974; Salter and Ward, 1972; Wiebe, 1973; Wurr et al., 1981a; Wurr et al., 1981b; Wurr et al., 1982). This was promoted by the idea that the duration of the harvest period is related to the duration of the curd initiation period, and that the plant-to-plant variation in curd initiation within a crop is due to differences in cold requirement.

The aim of the present investigation was to analyse the effects of plant characteristics and environmental factors on the variability of curd initiation and curd maturity within the crop, under a range of field conditions.

Materials and methods

Trials were carried out during the years 1982 through 1986 at the Research Station for Arable Farming and Production of Field Vegetables (PAGV) in Lelystad, on a light fertile marine clay soil. The cauliflower cultivars 'Delira' (Rijk Zwaan, De Lier, NL) and 'Elgon' (Royal Sluis, Enkhuizen, NL) were studied under different conditions by transplanting batches of plants on the dates mentioned below.

1982	'Delira'	12-5;	18-5;	26-5;	1-6;	8-6;	15-6;	22-6; 13-7
	'Elgon'	15-6;	22-6;	29-6;	6-7;	13-7		
1983	'Delira'	11-5;	20-5;	30-5;	2-6;	7-6;	14-6;	21-6; 14-7
	'Elgon'	20-5;	14-6;	21-6;	28-6;	5-7;	14-7	
1984	'Delira'	8-5;	15-5;	23-5;	29-5;	5-6;	12-6;	19-6; 10-7
	'Elgon'	19-6;	26-6;	3-7;	10-7			
1985	'Delira'	22-5;	29-5;	5-6;	13-6;	19-6		
	'Elgon'	5-6;	13-6;	19-6;	28-6;	4-7		
1986	'Delira'	21-5;	27-5;	3-6;	10-6;	18-6		
	'Elgon'	3-6;	10-6;	18-6;	24-6;	1-7		

Transplants were grown from 1982 through 1984 in cold frames, during 1985 and 1986 in an unheated glasshouse.

Five- to six-week old transplants were transplanted by hand in a square arrangement at a plant density of 2.5 m^{-2}. A sample of 12-15 plants was taken at transplanting and twice a week during the period between about three weeks after transplanting and 100 % curd initiation. On all individual plants in a sample the number of leaves longer than 1 cm (including scars; excluding cotelydons) was counted, and by dissecting the plant, the number of leaves shorter than 1 cm (leaf primordia) was counted.

The developmental stage of the apex was assessed and the diameter of the apex or the young curd was measured. The total number of leaves of a vegetative plant is the sum of the leaf scars, the number of leaves longer than 1 cm and the number of leaf primordia shorter than 1 cm. When the first secondary primordia became visible with a binocular microscope (magnification x 50), the apex was considered to have reached the generative stage (curd inititation) (Fujime, 1983; Margara and David, 1978). The final number of leaves on a generative plants is the number of leaves initiated below the first leaf with a secondary primordium in its axil.

At harvest of the 1982-1984 trials, plants were individually assessed for maturity three times a week and were cut as they matured. In 1985 and 1986 curds were not cut, but twice a week, each curd was scored for quality and size. The curd was considered to be mature on the date of the highest score for quality and size.

Weather data were obtained from a meteorological station situated about 6 km from the experimental site.

Regression analysis was carried out with GENSTAT (Lane et al., 1987).

Results

Curd diameter and number of leaves

After a certain time, the proportion of generative plants in samples from a crop increased and thereafter, within a sample, the diameter of the developing curd was variable. On samples with more than 90 % generative plants and with less than 10 % of plants with no leaves shorter than 1 cm, curd diameter was regressed on number of leaves longer than 1 cm, on final number of leaves on the plant and on the combination of these two variables. Vegetative plants and plants with no leaves shorter than 1 cm were excluded from analysis.

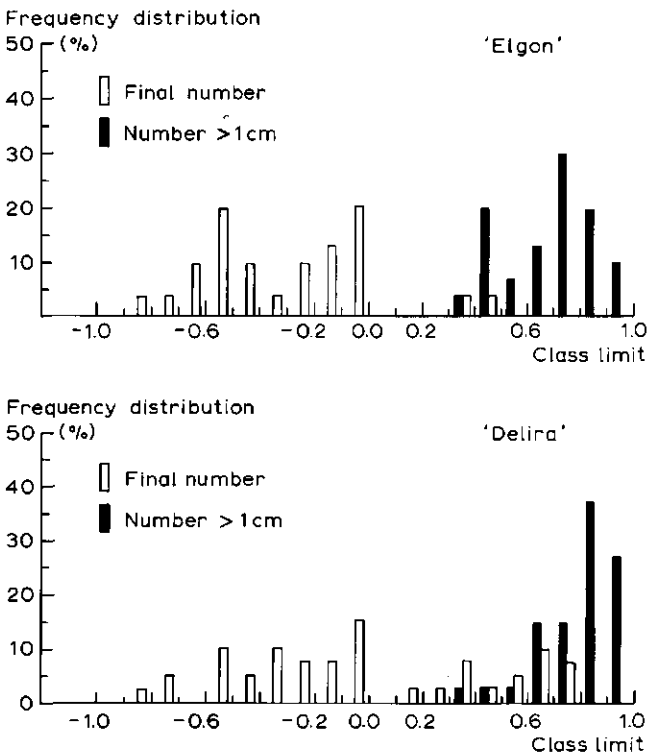

Figure 1
Relative frequency distribution (%) of correlation coefficients (r). For each sample (12-15 plants), consisting of more than 90 % of generative plants and less than 10 % plants with no leaves shorter than 1 cm, the correlation coefficient between the number of leaves longer than 1 cm or the final number of leaves and the curd diameter of the plant was calculated. A frequency distribution of all correlation coefficients ('Delira': 41; 'Elgon': 31) was made with a class size of 0.1. (Significant ($P<0.05$) coefficients: $r<-0.5$ or $r>0.5$)

The relative frequency distributions of the correlation coefficients calculated for all the samples that met these criteria are given in Figure 1. In most samples there was a significant positive correlation between the diameter of the curd and the number of leaves longer than 1 cm (Fig. 1). For 'Elgon' this relation was somewhat less pronounced than for 'Delira'. Significant correlations between curd diameter and final number of leaves were found in a few samples. These correlation coefficients were positive as well as negative. The combination of the number of leaves longer than 1 cm and the final number of leaves could explain 70-90 % of the diameter variation in most samples.

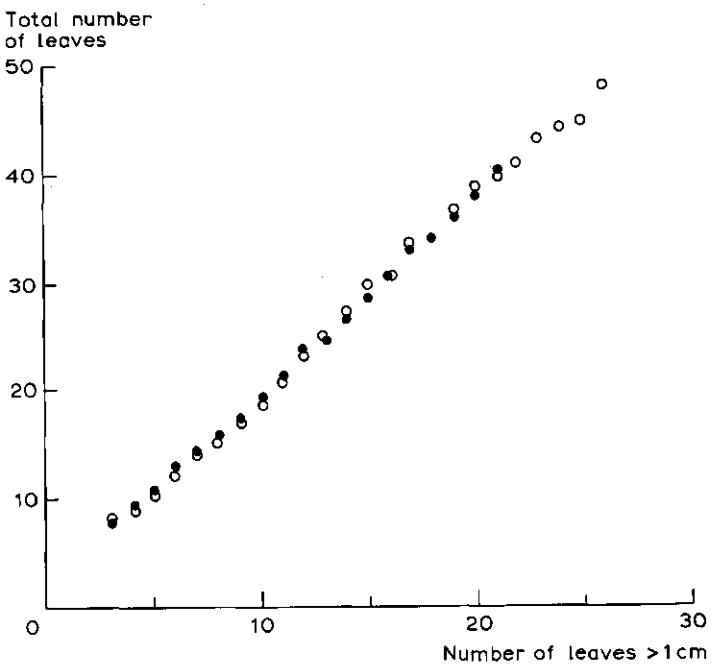

Figure 2
Relationship between the number of leaves longer than 1 cm and the total number of leaves of vegetative plants, for 'Elgon' (○) and 'Delira' (●). Each point represents the mean of plants with a certain number of leaves longer than 1 cm. The regression equations are:
$Y=(1.80\pm0.009)X + (1.69\pm0.097)$; $R=0.97$; $N=2559$; 'Delira'
$Y=(1.86\pm0.009)X + (1.24\pm0.135)$; $R=0.98$; $N=1761$; 'Elgon'

The data from all dissected generative plants with more than 1 leaf shorter than 1 cm were combined for each variety and the curd diameter (CD (mm)) was regressed on the number of leaves longer than 1 cm (LN) and the final number of leaves (FN), giving the following regression equations:

$CD=2.25 + 0.446LN - 0.304FN$ ($R^2=0.741$; $N=1226$; 'Delira')
$CD=3.72 + 0.309LN - 0.259FN$ ($R^2=0.751$; $N=834$; 'Elgon')

This showed that, on average, the curd diameter of an individual plant increased with increasing number of leaves longer than 1 cm, but for a given number of leaves longer than 1 cm the diameter decreased with increasing final number of leaves.

Curd initiation date

A relation between FN and LN at curd initiation is found when the diameter of a newly initiated curd (0.4-0.6 mm (Salter, 1960; Wiebe, 1972c)) is substituted for CD. The final number of leaves (FN) of a plant is fixed by curd initiation. On a generative plant, which still has leaves shorter than 1 cm when dissected, LN at curd initiation can be calculated when a set curd diameter, e.g. 0.40 mm, and the measured final number of leaves are substituted in the above regression equations. Curd initiation date of such a plant can be estimated if the relationship between of leaves longer than 1 cm (LN) and time is known. The problem of using this approach is doubt over which preset diameter should be chosen for curd initiation.

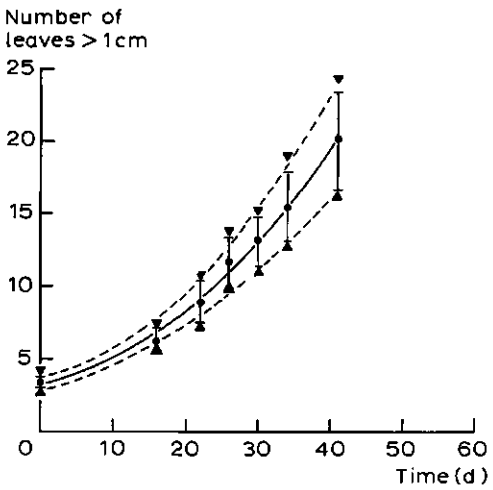

Figure 3
Relationship between time (days after transplanting) and the mean number of leaves longer than 1 cm for the whole sample (45 plants) (●); the 15 largest plants (▼) and the 15 smallest plants (▲) within the sample. Data obtained from the first transplanted crop in 1982. Vertical bars indicate ± standard error. The regression equations are:
(●): $Y = 0.00789X^2 + 0.088X + 3.3$ ($R^2 = 0.996$; $N = 7$)
(▼): $Y = 0.01049X^2 + 0.056X + 3.9$ ($R^2 = 0.997$; $N = 7$)
(▲): $Y = 0.00586X^2 + 0.098X + 2.9$ ($R^2 = 0.992$; $N = 7$)

An approach that avoids choosing an arbitrary diameter for curd initiation is as follows. The number of leaves initiated by vegetative plants correlates closely with the number of leaves longer than 1 cm (Fig. 2). The initiation date of the first leaf with a secondary primordium in its axil (i.e. a bract) will be very close to the curd initiation

date. The number of leaves longer than 1 cm on a plant at the initiation of the first bract can be estimated by substituting (final number of leaves + 1) for total number of leaves in the equation given in Figure 2. To estimate the initiation date of this leaf, the relation between numbers of leaves longer than 1 cm and time should be known for the each plant. The relationship was estimated as follows:
For the first transplanted crop in 1982, the relation between the mean number of leaves longer than 1 cm and time after transplanting was described by a second order polynomial (Fig. 3). The same was true for the subsample consisting of the 15 plants with the smallest number of leaves longer than 1 cm or for the subsample of the 15 plants with the largest number (the total number of plants being 45).

The standard error of the number of leaves longer than 1 cm increased at later sampling dates (Fig. 3), but the coefficient of variation appeared to be fairly constant with time (about 0.17). On this basis it was assumed that, for each plant within the population, the number of leaves longer than 1 cm increased according a second order polynomial, and that its relative deviation from the population mean for number of leaves longer than 1 cm was constant during time.

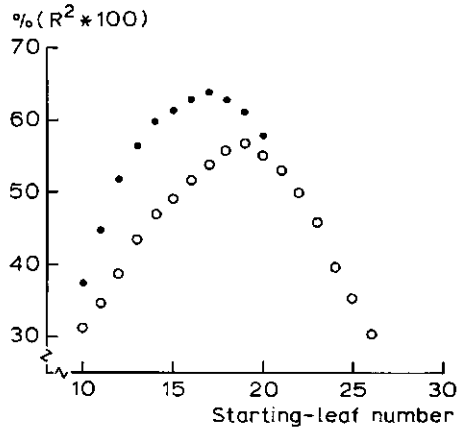

Figure 4
Percentage of variance in final number of leaves accounted for by the mean maximum day temperature during the period between the estimated initiation date of the starting-leaf number and the estimated curd initiation date for different starting leaf numbers ('Delira' (●) and 'Elgon' (○)). The number of observations were for 'Delira' 1128 and for 'Elgon' 799.

For each crop the relation between time and the mean number of leaves longer than 1 cm could be described by such a second order polynomial (R^2 for each crop > 0.98). For every plant a relation between time and the number of leaves longer than 1 cm could be estimated using its relative deviation from the mean of the relevant sample along with the polynomial relating the mean number of leaves longer than 1 cm to time for the crop. This estimate was substituted into the linear relation between the number of leaves longer than 1 cm and the total number of initiated leaves (Fig. 2), and the date on which a certain leaf was initiated was estimated. As stated earlier, the estimated curd initiation date was assumed to be the date on which the first bract was initiated.

An indication of the error associated with the estimated initiation date of a given leaf was obtained using the data presented in Figure 3. The data from the last sample (41 days after transplanting) for the 15 largest and the 15 smallest plants and the polynomial for the mean were used to estimate the date on which the 15 smallest plant and the 15 largest plants had 4.6 (i.e. about 10 initiated leaves) leaves longer than 1 cm (Fig. 2). These values were compared with the calculated values using the different regression equations for the two subsamples (Fig. 3). The

difference was 1.8 days for the largest plants and 1.0 for the smallest plants. Therefore the method using the mean polynomial seems reasonably accurate particularly since by the final sampling date discrepancies would be at a maximum.

Final number of leaves, temperature and juvenility

The final number of leaves of a cauliflower plant is determined by temperatures after the end of the juvenile phase (Wiebe, 1972b; Atherton et al. 1987). The end of the juvenile phase can be characterized by a certain fixed number of leaves initiated (Wiebe, 1972a; Hand and Atherton, 1987). For all generative plants, which had leaves shorter than 1 cm on dissection, the curd initiation date and the initiation date of the 10th - until the last true leaf (final number) was estimated using the procedure described in the previous section. The mean daily maximum temperature during the interval between the estimated date of initiation of a certain leaf and the estimated date of curd initiation was calculated for each plant.

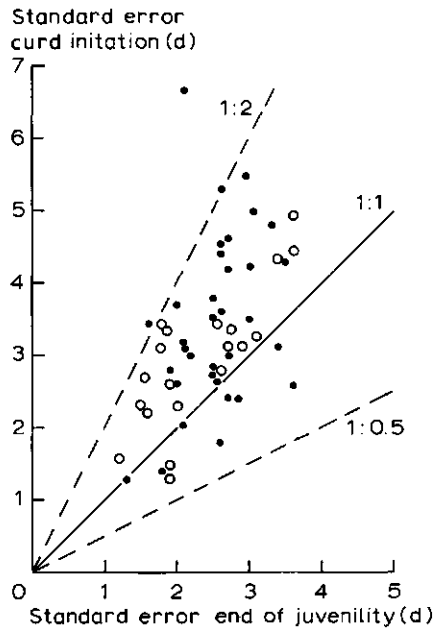

Figure 5
Relationship between the standard error of the estimated end of juvenility (i.e. the estimated date on which the plant had initiated 17 leaves for 'Delira' (●) or 19 leaves for 'Elgon' (○)) and the standard error of the estimated curd initiation date within a crop; each point represents a crop.

By varying the starting date of this interval i.e. by starting at different leaf numbers, the period over which final leaf number is most sensitive to temperature can be determined. The mean temperature during each interval was regressed on the final number of leaves and the proportion of the variance in final number leaves accounted for by mean temperature was determined (Goldwin, 1982). Mean maximum day temperature could explain the final number of leaves better than just mean day temperature (Booy, 1987).

The final number of leaves of an individual plant varied between 18 and 43 for 'Delira' and between 24 and 53 for 'Elgon'. The mean daily maximum temperature during the intervals ranged between 13.5 °C and 24.8 °C, so that linear regressions were appropiate (Booij, 1987). The final number of leaves was positively correlated with the mean maximum day temperatures in these intervals. The proportion of the variance in final number of leaves accounted for by these mean daily maximum temperatures increased with increasing starting leaf number until a maximum at leaf 17 for 'Delira' and 19 for 'Elgon', with a decrease with further increase in starting leaf number (Fig. 4). These maxima for

percentage variance accounted for were regarded as estimate of the leaf number at the end of the juvenile phase.

Curd initiation and harvest period

Within each crop there was a plant-to-plant variation in the date on which juvenility ended (i.e. when 17 or 19 leaves had initiated respectively for 'Delira' and 'Elgon') and there was variation in the date of curd initiation. The standard error of the estimated curd initiation date increased with increasing standard error of the estimated date for the end of juvenility (Fig. 5). The standard error of curd initiation date was larger than that for end of juvenility in most crops.

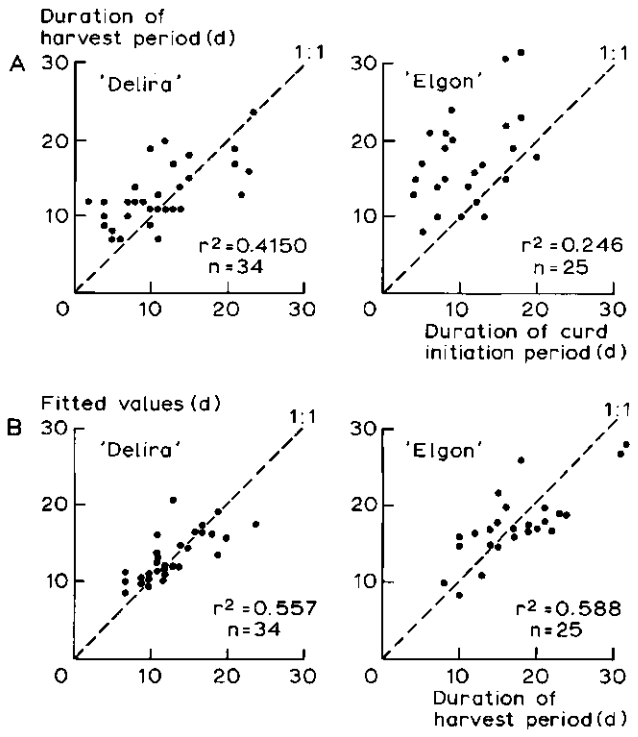

Figure 6

A. Relationship between the duration of the curd initiation period and the duration of the harvest period.

B. Relationship between the duration of the harvest period and the fitted values for duration of the harvest period calculated with the regression equations mentioned in the text.

The durations of the curd initiation period and of the harvest period, respectively, defined as the number of days between 10 % and 90 % of the plants having a curd initiated or harvested. The percentage of generative plants within successive samples was used to determine the length of the curd initiation period. The duration of the

harvest period correlated significantly ($P < 0.05$) with the duration of the curd initiation period (Fig. 6).
The correlation was relatively weak for both cultivars and the coefficient was highest for 'Delira'. In most crops the harvest period was longer than the curd initiation period, especially for 'Elgon'.

By including the mean temperature during curd growth along with duration of the initiation period in the regression model, about 55 % of the variation in duration of the harvest period could be explained. These regression equations were:

'Delira':
$HP = -1.78 + 0.416IP + 1.90T_{10} - 1.31T_{90}$
($R^2 = 0.557$ N = 34)

'Elgon' :
$HP = 0.10 + 0.224IP + 5.44T_{10} - 4.81T_{90}$
($R^2 = 0.588$ N = 25)

(HP = duration of the harvest period; IP = duration of the initiation period; T_{10} = mean temperature (°C) between 10 % initiation and 10 % harvest; T_{90} = mean temperature (°C) between 90 % initiation and 90 % harvest).

The relation between the measured values and the fitted values for duration of the harvest period is presented in Figure 6.

Discussion

The curd initiation date of a cauliflower plant depends on the date the juvenile phase comes to an end and the temperature in the following period (Wiebe, 1972b; Hand and Atherton, 1987). Plant-to-plant variation within a cauliflower crop in respect of curd initiation date is due to both differences in date on which the juvenile phase ends and differences in temperature the individual plants experience subsequently. Variations could be partly due to genetic variability within the crop for the end of juvenility and/or cold requirement. Salter (1969) found a positive correlation between curd initiation date (and curd diameter) and final number of leaves in most crops, and he ascribed variation within a crop to differences in cold requirement; thus plants with a higher cold requirement initiated more leaves before curd initation. These differences were probably mainly genetically determined. Aamlid (1952), Jensma (1957), Watts (1965), Wurr et al. (1981c) and Wurr et al. (1982) found that earlier cultivars had lower leaf numbers and that later cultivars had a greater cold requirement (Wiebe, 1972b). Also within a crop of one cultivar, Jensma (1957) found a positive correlation between earliness and final number of leaves, probably due to variation in cold requirement (Sadik, 1967). However within inbred lines from cultivars both positive and negative correlations between number of leaves and earliness were recorded.

In the present work significant correlations were found between curd diameter and final number of leaves in a few crops (Fig. 1), and the variation in curd diameter was ascribed mainly to a variation in the end of juvenility. The conflicting results of Salter's work and the present may be caused by the cultivars used. Modern cultivars are likely to be genetically more uniform. In these cultivars there may be minor variations in cold requirement, but these are probably outweighed by the environmental effects.

The final number of leaves depends on temperature after the juvenile stage (Fig. 4). When individual plants within a crop reach the end of the juvenile stage on different dates, they will experience different temperatures subsequently, and this will influence the within-crop correlation between curd diameter and final number of leaves.

Sudden temperature changes during a transition period, for example, when only some plants have reached the end of juvenility or when only some plants have completed curd induction could cause considerable variation in curd initiation over and above that associated with variation in end of juvenility (Fig. 5).

The duration of the harvest period is determined only partly by the duration of the curd initiation period (Fig. 6). Temperature during curd growth also modified the duration of the harvest period (Fig. 6). Salter (1969) found a positive correlation between duration of the initiation period and duration of the harvest period (both expressed on a day-degree base), but there was still a considerable residual variation and the relation was cultivar dependant. Wurr et al. (1981c) did not find a relation between duration of the initiation period and the harvest period for winter heading cauliflower cultivars, and only a weak correlation was found in an experiment with different cultivars and cold treatments (Wurr et al., 1981a).

Although in the present experiments variations in duration of the initiation period combined with temperature during curd growth could explain much of the variation in duration of the harvest period, about 45 % remained unexplained. This relatively high residual variation can in part be attributed to the small size of the samples (12-15 plants) taken to estimate the duration of the curd initiation period.

The duration of the harvest period is determined primarily by the factors date of end of juvenility, temperature after the end of juvenility and temperature during curd growth, possibly all interacting with a genetic component. This makes it difficult to find techniques that can consistently reduce the duration and variability of the harvest period.

Variation in the time growth resumes after transplanting as well as the variations in growth conditions within a field will cause plant-to-plant variation in the date on which the juvenile stage ends. Measures to produce uniform transplants can be largely nullified by conditions in the field. The variation within a crop will tend to increase during growth, so the longer it takes to reach the end of juvenility, the less the effects of increasing uniformity of transplants will be. Also the more variable the environmental conditions (weather) are, the less predictable will be the effects of transplant uniformity.

The method used to estimate curd initiation date, based on the final number of leaves and the correlation between the number of visible leaves and the total number of initiated leaves, could be used for other species with a terminal flower or inflorescence. For example in tobacco, Singer and McDaniel (1986) found a good correlation between the number of visible leaves and the total number of leaves. A small time lag between initiation of the last true leaf and initiation of the inflorescence or flower is also necessary. The method could especially be useful, when plant numbers are restricted as in phytotron experiments, since the initiation date can be estimated without sampling and dissecting plants. For this purpose it is necessary to record the number of visible leaves per plant during growth.

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Chapter 4

Effects of temperature on leaf and curd initiation in relation to juvenility of cauliflower

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Effects of temperature on leaf and curd initiation in relation to juvenility of cauliflower

R. Booij and P.C. Struik

Summary

Cauliflower plants (*Brassica oleracea* L. var. *botrytis* subvar. *cauliflora*, cv Delira) were grown at 14 °C or 22 °C to study the effect of temperature on leaf and curd initiation. The rate of leaf initiation depended on the leaf number: the first 11 leaves were initiated at a lower rate than the following leaves. A linear relationship was found between the number of leaves longer than 2 cm the total number of initiated leaves of vegetative plants. The slope of the regression line was independent of temperature and different from unity. The time between initiation of a leaf and its attaining a length of 2 cm increased linearly with leaf number.

The relation between dry matter production or leaf area and the number of leaves longer than 2 cm was hardly influenced by temperature.

By transferring plants from weak curd-inducing conditions (22 °C) to strong curd-inducing conditions (14 °C) at different times, the number of leaves at which the juvenile phase ended, could be estimated by assessing the effect of the number of initiated leaves at the moment of transfer on the final number of leaves. For this cultivar the juvenile phase ended when 16-18 leaves were initiated.

During the juvenile phase the linear relation between the number of initiated leaves and the diameter of the apical dome was independent of temperature. After the juvenile phase the apical dome diameter of vegetative plants at 22 °C increased more slowly than at 14 °C. The maximum dome diameter of vegetative plants was between 0.35 and 0.40 mm at both temperatures.

Introduction

Many plant species requiring cold to induce flowers have a juvenile phase, a period during which the plant is unable to respond to a promotory stimulus from the environment (Lang, 1965; Napp-Zinn, 1973; Bernier et al. 1981). It is useful to know when the change from juvenile to mature occurs. Using chronological age seems inadequate, because the duration of juvenility depends on the environmental conditions (e.g. light intensity; Wellensiek and Higazy, 1961; Pierik, 1967). The number of initiated leaves probably is the best estimate (Bernier et al., 1981). For example, the reduction in length of the juvenile phase of *Lunaria biennis* at higher light intensities can be explained by the effect of light intensity on the time needed to initiate a certain number of leaves (combine Table 1 and 2 of Higazy, 1962).

Many Brassica species have a juvenile phase, varying considerably in length (Friend, 1985). The existence of a juvenile phase for cauliflower (*Brassica oleracea* L. var. *botrytis* subvar. *cauliflora*) and its relation to plant development was demonstrated by Kato (1964); the number of initiated leaves at the end of the juvenile phase has been determined for cauliflower by Sadik (1967), Wiebe (1972a), Hand and Atherton (1987).

Time of curd initiation depends on the length of the juvenile phase and the length of the curd induction phase (Wurr et al., 1981) and the final number of leaves (i.e. number of leaves below the curd) is the sum of the number of leaves at the end of juvenility and the number of leaves initiated during the induction period (Lang, 1965). The final number of leaves is mainly determined by the temperature before curd initiation (Aamlid, 1952; Wiebe, 1972b; Atherton et al., 1987; Booy, 1987) and increases at increasing temperatures.

If the end of juvenility is marked by the number of initiated leaves (Hand and Atherton, 1987) and the final number of leaves is determined by the temperature during the induction phase (Atherton et al., 1987), a change from non-inducing temperatures to inducing temperatures should not affect the final number of leaves, if the change was made before the end of juvenility.

The aim of the present study was to test this hypothesis and to establish relations between some plant features and the end of juvenility. Data about leaf initiation, leaf appearance, dry matter production, leaf area and curd initiation were obtained from plants grown at two different temperatures.

Materials and methods

Plants of the cauliflower cultivar Delira (Rijk Zwaan, De Lier NL) were grown in 1.7 L pots containing potting compost. Five seeds were sown per pot and were thinned to one per pot after emergence. Nutrient solution and water were provided adequately. During the early growth the plants were sprayed once a week with a solution of 0.112 mg L^{-1} sodium molybdate.

The experiment was carried out in growth rooms at a light intensity of 40 W m^{-2} in the waveband 400-700 nm during a 16 h day. The relative humidity was kept between 60 and 70 %. One growth room was kept at a temperature of 14 °C during the night and 16 °C during the day while another room was kept at 22 °C during the night and 24 °C during the day. Treatments are coded by their night temperatures (14 °C and 22 °C). The pots were placed on carts that were circulated within each growth room twice a week to reduce position effects. Plant density was adjusted to plant growth. At 10 different times plants were transferred from the 22 °C room to the 14 °C room. Six groups of 5 plants each were selected randomly. Three groups of 5 were transferred while the rest was used for dissecting. Per group of 5 plants the leaf area and dry weight were determined and of each individual plant the number of leaves longer than 2 cm (including scars; excluding cotelydons), the number of leaves shorter than 2 cm (leaf primordia), the developmental stage of the apex (vegetative or generative) and the diameter of the apical dome were determined. The last three parameters were measured with a binocular microscope (magnification x50). When the first secondary primordia became visible, the apex was considered to have reached the generative state (Fujime, 1983; Margara and David, 1978). Samples for an analysis as mentioned above were also taken from the plants that had been retained at 14 °C from sowing.

From each individual plant at 14 °C the number of leaves longer than 2 cm was counted weekly until the final harvest. At the final harvest the number of leaves longer than 2 cm and the number of leaves below the curd (final number of leaves) both including scars were counted. Treated plants were harvested when the most advanced plant per treatment had exposed the curd.

Means, standard errors and regression coefficients were calculated with GENSTAT5 (Lane et al., 1987).

Results

Leaf initiation at a constant temperature

The number of initiated leaves increased linearly with time; while at both temperatures a sudden change in leaf initiation rate could be recognized (Fig. 1A).

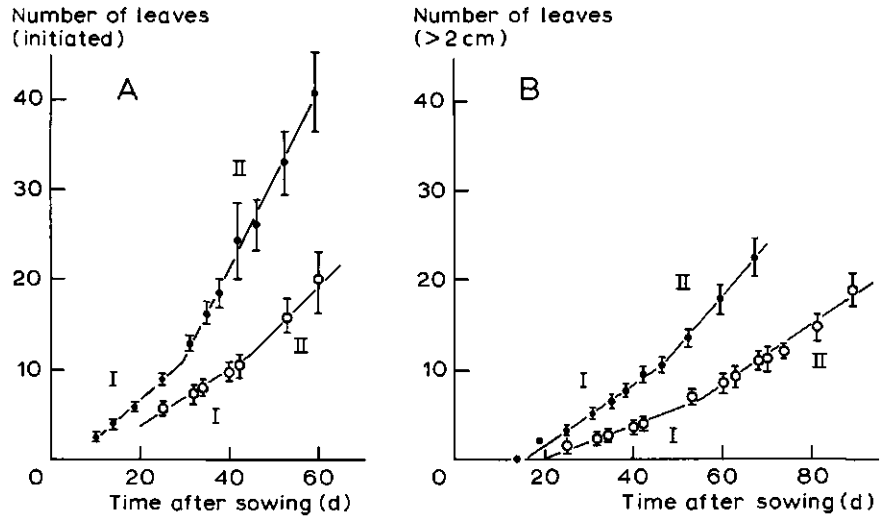

Figure 1
Number of initiated leaves (A) and number of leaves longer than 2 cm (B) of plants growing at 14 °C (○) or 22 °C (●). Each point represents the mean of 15 plants and the vertical bars indicate ± SE.
The regression equations for the two (I and II) best fitting lines are:
A. 22 °C: I: Y=0.436X- 1.91; II: Y=1.006X-18.72; R^2=0.997; N=11
14 °C: I: Y=0.305X- 2.21; II: Y=0.586X-14.87; R^2=0.999; N=7
B. 22 °C: I: Y=0.328X- 4.67; II: Y=0.606X-17.87; R^2=0.998; N=11
14 °C: I: Y=0.176X- 3.16; II: Y=0.346X-12.61; R^2=0.992; N=13

The number of leaves at which the change occurred was determined by using the nonlinear fit option of GENSTAT (Lane et al.,1987). The point of intersection of the two lines (I and II in Fig. 1A) was at 11.1±0.96 and 11.6±1.02 initiated leaves for 22 °C and 14 °C, respectively.

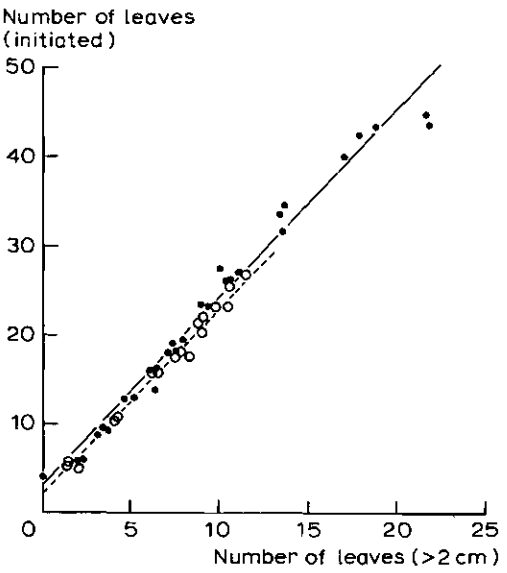

Figure 2
Relationship between the number of leaves longer than 2 cm and the number of initiated leaves of vegetative plants grown at 14 °C (o) or 22 °C (●). Each point represents the mean of the vegetative plants within a sample.
The regression equations are:
22 °C: $Y=2.076X+3.11$; $R^2=0.980$; $N=29$
14 °C: $Y=2.053X+2.41$; $R^2=0.985$; $N=17$

The slopes of both regression lines were significantly higher at 22 °C than at 14 °C. The change in rate of leaf initiation, however, was more pronounced at 22 °C than at 14 °C.

A similar plot was made for the relation between the number of leaves longer than 2 cm and time (Fig. 1B). Again, two distinct lines with significantly different slopes could be recognized, intersecting at 10.2 ± 0.84 and 6.9 ± 0.62 leaves for 22 °C and 14 °C, respectively. The slopes of the two lines were both significantly higher at 22 °C than at 14 °C and again the changed rate of increase was more pronounced at the higher temperature. The convergence towards the point of intersection during the nonlinear fit procedure was clearer for the number of initiated leaves than for the number of leaves longer than 2 cm.

The rate of increase of the number of initiated leaves was significantly higher than the rate of increase of the number of leaves longer than 2 cm. The time needed from initiation of a certain leaf to attain a length of 2 cm increased linearly with increasing leaf number, which is illustrated by the following equations.

The number of initiated leaves (N_i) and the number of leaves longer than 2 cm (N_v) are both linearly related to time (t) (Fig. 1).

$$N_i = a*t + b \quad (1)$$

$$N_v = c*t + d \quad (2)$$

If at t_1 $N_i=N$ and at t_2 $N_v=N$, then the time period $\Delta t=t_2-t_1$, i.e. the time between initiation of N leaves and the moment at which N leaves have attained a length of 2 cm, is expressed as:

$$\Delta t = N/c - d/c - N/a + b/a = (1/c - 1/a)*N - d/c + b/a \quad (3)$$

When c=a, the time needed (Δt) is constant. The slope (1/c-1/a) of the linear relation depends on temperature and the range of leaf numbers, as c and a depend on these (Fig. 1).

Combining eqn 1) and 2) results in a relation between the number of leaves longer than 2 cm (N_v) and the number of initiated leaves (N_i).

$$N_i = a*N_v/c - d*a/c + b \quad (4)$$

So the slope of the line depends on the leaf iniatiation rate (a) and the rate of increase of the number of leaves longer than 2 cm (c). This implies that the breaks as found in Figure 1 should be reflected in a relation between N_v and N_i (Fig. 2), namely at 22 °C a

break at about 11 initiated leaves and when about 10 leaves had attained a length of 2 cm. At these leaf numbers the mutual relation between the rates (a and c in eqn 4) changes. The slope of the line should increase at the first mentioned number of leaves and decrease again at the second. However, the variation as given in Figure 2 was too large to reveal the breaks and the relation could be described by a straight line.

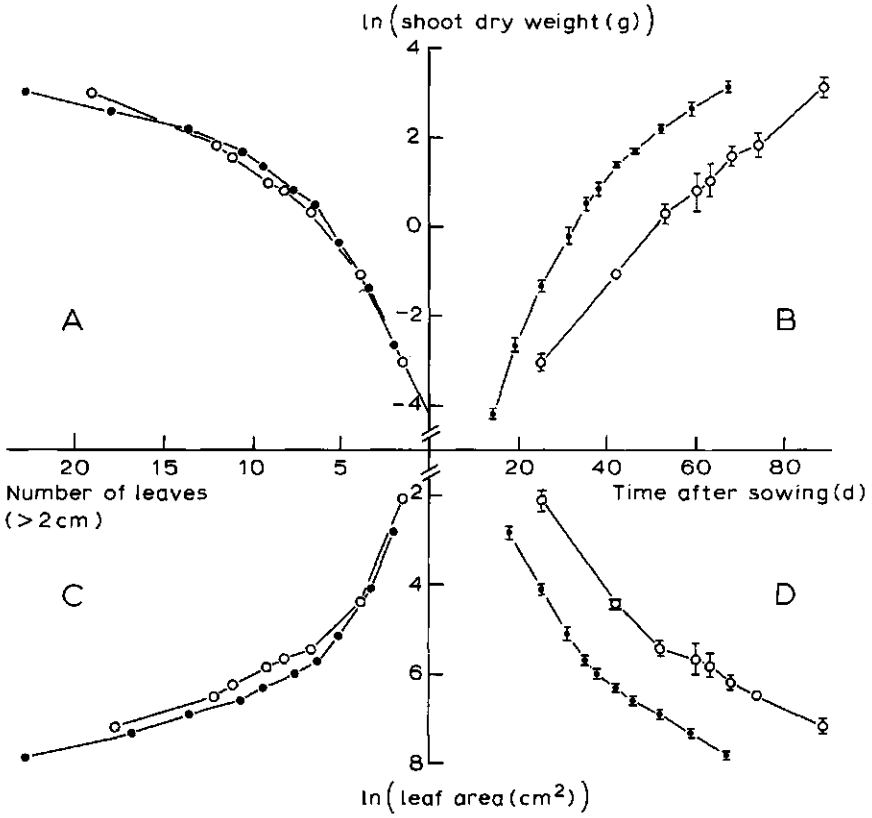

Figure 3
Natural logarithm of shoot dry weight per plant and leaf area per plant in relation to days after sowing (B,D) or in relation to the number of leaves longer than 2 cm (A,C) of plants grown at 14 °C (○) or 22 °C (●). Each point represents the mean of 5 plants and the vertical bars indicate ±SE.

There was no significant effect of raising temperature on the slope of the regression line (Fig. 2); the intercept was slightly, but significantly, smaller for the plants grown at 14 °C. As the slope (a/c in eqn 4) was not affected by temperature, it means that the parameters a and c in eqn 4 are influenced to the same extent by temperature.

Growth and development at a constant temperature

The shoot dry-matter production per plant and the increase of leaf area during the experiment is presented in Figure 3. The lower relative growth rate (slope of the line) at 14 °C, especially in the early growing period resulted in lower shoot dry weights of plants grown at 14 °C than at 22 °C.

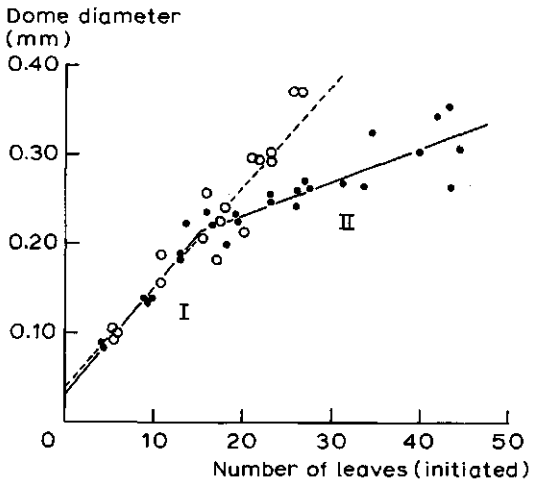

Figure 4
Relationship between the diameter (mm) of the apical dome of vegetative plants and the number of initiated leaves of plants grown at 14 °C (○) or 22 °C (●). The two different lines at 22 °C are indicated by I and II. Each plant represents the mean of the vegetative plants within a sample. The regression equations for the best fitting lines are:
22 °C I: $Y=0.012X+0.034$; II: $Y=0.004X+0.160$; $R^2=0.929$; $N=29$
14 °C $Y=0.011X+0.031$; $R^2=0.900$; $N=17$

The natural logarithm of the total area of green leaves increased linearly at two distinct rates (Fig. 3). The transition appeared to be at a leaf area of about 180 cm^2 $plant^{-1}$ at 14 °C and at 370 cm^2 $plant^{-1}$ at 22 °C. The slopes of the regression lines, indicating the relative rates of increase, were somewhat lower at 14 °C. The main differences in leaf areas between the two temperatures originate with the early growth phase.

The effect of growing temperature was eliminated when the shoot dry weight was plotted against the mean number of leaves longer than 2 cm (Fig. 3). Regarding leaf area, a difference between the two temperatures remained, but the effect of growing temperature was much smaller.

The mean diameter of the apical dome of the shoot apex of vegetative plants depended on the number of initiated leaves (Fig. 4). The increase of the diameter was independent of temperature until 15-20 leaves were initiated; beyond this point the diameter of the plants grown at 14 °C continued to increase at a similar rate, while the increase of plants grown at 22 °C was significantly lower. Using the nonlinear fit option of GENSTAT, the point of intersection of the two lines at 22 °C appeared to be at 15.0 ± 1.9 initiated leaves. The slope of the line at lower numbers of leaves did not differ significantly from the slope of the regression line calculated for the plants grown at 14 °C. The variation in diameter increased when the number of initiated leaves was more than 15. The highest mean apical dome diameter of vegetative plants was about 0.37 mm (Fig. 4).

Effects of temperature changes on number of leaves

The effect of temperature changes from 22 °C to 14 °C on the formation of leaves longer than 2 cm is presented in Figure 5. To keep the figure readable, not all results

are given. After the first four transferring dates the relations between time and the number of leaves longer than 2 cm revealed a sudden change in rate similar to the plants grown continuously at 14 °C. When transferred later, there was no obvious break and a single linear relation was observed. The slope of the lines increased at later transferring dates.

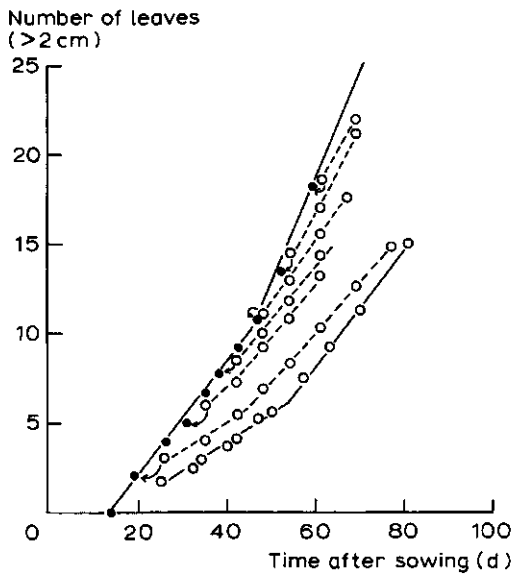

Figure 5
Number of leaves longer than 2 cm of plants grown at 14 °C (○) or 22 °C (●). The plants grew continuously at 14 °C or 22 °C (solid lines) or at 14 °C after a transfer from 22 °C (dashed lines). Each point represents the mean of 15 plants. Arrows indicate the number of leaves > 2 cm at the respective transfer dates.

At the final harvest the final number of leaves was counted. In Figure 6 the effect of the number of initiated leaves at the time of transfer on the final number of leaves is presented. The final number of leaves decreased slightly until 15 leaves were present at the transfer date; at higher number of leaves the final number increased. Two significant linear relations could be recognized intersecting at (17.9±0.86) initiated leaves at the time of transfer.

When the first secondary primordia are initiated (i.e. curd initiation) the final number of leaves of a plant is fixed. The number of leaves longer than 2 cm at the time the last foliage leaf (i.e. final number) was initiated can be estimated using the relation in Figure 2. As from each plant the number of leaves longer than 2 cm was counted weekly, the time at which this number of leaves longer than 2 cm was reached can be estimated.

The same can be done for the final number plus one, being the first bract. The estimated curd initiation time of a plant was considered to be the time at which the first bract was initiated. The procedure for estimation of time of curd initiation was carried out for each plant in the sample at the final harvest.

The estimated time at which 10 %, 50 % and 90 % of the plants had initiated a curd in relation to the time of transfer is presented in Figure 7. The number of days until 50 % of the plants had initiated a curd decreased until the plants were 35 days old at the transfer and afterwards the number of days increased. Plants transferred 14 days after sowing initiated curds at nearly the same time as plants grown continuously at 14 °C. The advance due to the higher growing temperature during the first 14 days was lost, probably because the very young plants suffered from the temperature shock.

The estimated time at which 50 % of the last transferred lot of plants (day 59) had initiated a curd was very close to the transferring date and the initation time of a part of this lot was estimated to be before the transfer (Fig. 7). In the dissected sample at the last transfer date only 1 out of 15 plants had actually initiated a curd.

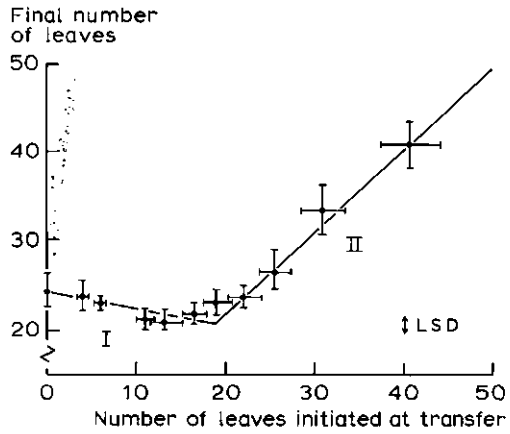

Figure 6
Relationship between the number of initiated leaves at 22 °C before the transfer to 14 °C and the final number of leaves. Each point represents the mean of 15 plants and the vertical and horizontal bar indicate ±SE. LSD: Least Significant Difference P< 0.05. The regression equations for the two (I and II) best fitting lines are:
I: Y=-0.184X+24.26; II: Y= 0.893X+ 4.92; R^2=0.986; N=11

All the plants at 22 °C had initiated a curd at the termination of the experiment (87 days after sowing). These plants had a final number of leaves of 48.1±4.5 and an estimated mean initiation time of 67 days after sowing. However, in a dissected sample at 67 days after sowing only 30 % of the plants had initiated a curd. Thus the estimated curd intiation time seems to be a few days earlier than the visible appearance of secondary primordia. At 14 °C the dissecting was done more frequently during the period of curd initiation. This enabled a better comparison of the two methods: dissecting at regular time intervals and estimation using the final sample (100 % generative plants). In this case the estimation of the 50 % initiation by dissecting yielded a 1.1 days later time than the estimation using the final sample.

The length of the initiation period (between 10 and 90 % of the population) was longer for the plants growing continuously at 14 °C and for the first two transferred lots (Fig. 7). This is probably due to a higher plant to plant variation caused by a slight molybdenum deficiency that occurred during the early growth at 14 °C in particular for the first transferred lot.

Discussion

The difference between the rate of leaf initiation (Fig. 1A) and the rate of increase of the number of leaves longer than 2 cm (further referred to as leaf appearance rate) (Fig. 1B) indicates that the time from initiation of a leaf until it reaches a length of 2 cm increases as leaf number increases. A similar relation was found for lettuce (Bensink, 1971). When the length of an individual leaf increases exponentially during the early growth (Erickson and Michelini, 1957; Williams, 1975) the difference between the two rates of Fig. 1 indicates a decreasing relative growth rate of the individual leaves with increasing leaf numbers. As the time between initiation and appearance increases linearly with leaf number (eqn 3), the relative growth rate of the individual leaf should decrease proportionally to the reciprocal of the leaf number. Thereby one of the conditions for using the Plastochron Index, namely a constant relative growth rate of successive leaves (Lamoreaux et al., 1978), is not satisfied. Whether this condition is met can be assessed by means of the relation between the number of initiated leaves

and the number of leaves of a certain length. A difference between the initiation rate and the rate of appearance results in a slope different from unity (Fig. 2). Singer and McDaniel (1986) also found a significant correlation between number of leaves of tobacco longer than 3 cm and the number of initiated leaves with a slope of about 1.5.

The rate of leaf initiation was lower at the lower temperature (Fig. 1). At both temperatures, two phases with different rates of leaf initiation could be distinguished; the transition was at the same number of initiated leaves. This transition was also found by Hand and Atherton (1987) and the value at which the transition occurred (11-12 leaves) is close to the value we found.

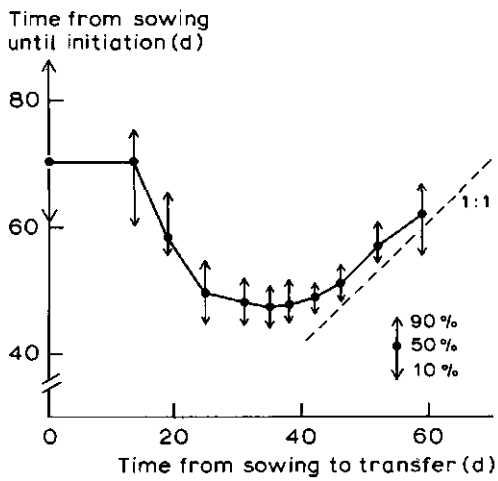

Figure 7
Effect of time of transfer (days after sowing) from 22 °C to 14 °C on the estimated curd initiation time (days after sowing) for 10 %, 50 % and 90 % of the plants. The estimation is made for the 15 plants at the final harvest. Dashed line represents the line through the origin and slope 1.

The method we used to estimate curd initiation date after the temperature change is based on the assumption that the relation between the number of initiated leaves and the number of leaves longer than 2 cm is not influenced by the change. The rate of appearance depends on the leaf initiation rate. A number of leaves attaining a length of 2 cm after the transfer, were still initiated at 22 °C, so that the rate of appearance is higher for these plants than for plants grown continuously at the lower temperature (Fig. 5). Marc and Palmer (1978) found that the rate of leaf initiation of sunflower after a temperature change was the same as the one for plants grown continuously at this temperature, independent of the timing of the change. If this holds true also for cauliflower, the relation between the number of leaves longer than 2 cm and the number of initiated leaves should be different after the change for a certain time from plants growing continuously at the lower temperature. However, as was seen for plants grown continuously at 22 °C, changes in leaf initiation rate hardly influenced the relation between the number of leaves longer than 2 cm and the number of initiated leaves (Fig. 2). As the differences in rate between the two temperatures were of the same magnitude (Fig. 1), the mentioned assumption should not result in large errors.

The relation between the number of leaves longer than 2 cm and the number of initiated leaves was independent of temperature (Fig. 2), meaning that the initiation rate and the rate of appearance are influenced in a similar way by temperature. This confirms the results of Pieters (1974) with poplar, who showed that the relation between leaf elongation rate and leaf initiation rate was independent of temperature.

The length of the vegetative period (i.e. until curd initiation) decreased at increasing length of the stay at the higher temperature and later increased when the plants remained at this temperature even longer (Fig. 7). As the end of juvenility is characterized by the number of initiated leaves (Wiebe, 1972a; Hand and Atherton, 1987), plants transferred early will need more time to reach a certain leaf number because at a lower temperature the initiation rate is lower (Fig. 1A). Curd initiation of mature plants is stimulated by lower temperatures (Wiebe, 1972b; Atherton et al., 1987; Booij, 1987), so the longer the plant remains at non- or weakly inducing conditions, the longer the vegetative period. The number of leaves at the time of transfer affected the final number of leaves until 17-18 leaves were initiated only to a small extent (Fig. 6) and therefore can be concluded that the stated hypothesis, that a switch of temperature before the end of juvenility does not affect the final number of leaves, appears to be true. The point of intersection of the two lines in Figure 6 therefore represents the number of leaves at which the juvenile phase ends. The value for the end of juvenility is very close to the value found by Booij (in press) in field trials by regression analysis and in agreement with the values found by Hand & Atherton (1987), Sadik (1967) and Wiebe (1972a) for comparable cultivars.

Explanations for the small, although significant, decrease of the final number of leaves until 17-18 leaves were initiated (Fig. 6) can be: (1) number of leaves is not the only characteristic for end of juvenility; (2) end of juvenility depends on temperature; (3) the effect of the inducing temperature depends on the preceding conditions. Although none of the mentioned explanations can be ruled out based on the experiment described, the last possibility seems most likely. Atherton et al. (1987) showed that nitrogen starvation of cauliflower plants at weakly inducing temperatures could increase the final number of leaves substantially. However, at strongly inducing conditions nitrogen starvation did not influence the final number of leaves. Klinkhamer et al. (1987) could increase the bolting percentage of spear thistle by an increased nitrogen supply after a partial inductive treatment. Both experiments indicate that the growing conditions during or after a certain induction treatment can modify the effect. In our experiment the leaf area at a certain number of leaves was lower at the lower temperature (Fig. 3), perhaps modifying the inducing effect. Further research is needed in this area.

Until about 15 initiated leaves the relation between the number of initiated leaves and the diameter of the apical dome was not influenced by temperature (Fig. 4). From 15 initiated leaves onwards the increase of the diameter of the apical dome was less at 22 °C than at 14 °C. It seems that the diameter should be 0.35-0.40 mm before the secondary primordia can be formed, the number of plastochrons needed to reach this value depends on temperature. The number of initiated leaves at which the effect of temperature becomes apparent is perhaps related to the end of juvenility as this number of initiated leaves is close to the value found in Figure 6.

Hand and Atherton (1987) related the sudden change in rate of leaf initiation (Fig. 1A) to the end of juvenility. However, when they tried to establish the number of leaves at which juvenility was supposed to end, using a temperature change they found a value being at least 3 leaves more than the value at which the change in rate of leaf initiation occurred. In our work the difference appeared to be more than 7 leaves, so it is unlikely that the change in rate of leaf initiation is related to juvenility.

The most frequently used method to determine the end of juvenility is a transfer from a non-inducing to an inducing temperature at different ages followed by a non-inducing temperature after a certain period. This method has a few disadvantages: (1) during the

cold treatment the plants continue to initiate leaves, so that the end of juvenility can be reached during the low temperature treatment; (2) due to plant variability there will be a range of leaf numbers resulting in a percentage of curd initiation between 0 and 100 %; (3) devernalization after the treatment is possible; (4) risk of an abnormal inflorescence (e.g. bracting of cauliflower; Hand and Atherton, 1987). These disadvantages are irrelevant to our method of determining the end of juvenility.

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Chapter 5

Influence of transplant size and temperature on cauliflower curd weight

In press: Gartenbauwissenschaft

Influence of transplant size and temperature on cauliflower curd weight

Summary

Two field trials were conducted, using an early cauliflower cultivar; in the first trial the effect of temperature before transplanting on curd weight was studied and in the second trial the effect of a low temperature treatment before transplanting was examined in dependence on the age of the plants.

Curd weight was reduced when plants were subjected to low temperatures before transplanting. Especially plants with a high number of visible leaves at transplanting, which had been subjected to low temperatures, produced small curds. These small curds matured earliest within a crop and had the lowest leaf weight at maturity. A lower plant weight at the time of curd initiation reduced curd weight at maturity. The number of days between curd initiaton and maturity did not depend on curd weight at maturity. The results are discussed in relation with buttoning.

Introduction

The cauliflower curd can be regarded as an inflorescence that will ultimately form flowers and produce seed (Sadik, 1962). Maturity of the curd from the point of view of the grower is reached just before the internodes of the inflorescence start to elongate and the curd becomes loose (Sadik and Ozbun, 1968). The curd should be harvested before this occurs because after this event curd quality deteriorates quickly. Curds can also mature before a minimum marketable size is reached. These so called buttons (Carew and Thompson, 1948) do not have any value and the proportion of plants buttoned influences the financial output greatly. Buttoning is most frequent in crops which are grown during the early part of the season, when mainly large transplants of early cultivars are used (Jensma, 1957; Sandwell, 1961) to obtain an early production. Much research was focussed on the effects of the cultivation techniques during transplant raising on the incidence of buttoning (Carew and Thompson, 1948; Jensma, 1957; Salter, 1960; Sandwell, 1961; Skapski and Oyer, 1964; Birkenshaw et al., 1982). In general, buttoning was promoted by the use of large transplants. Wiebe (1981, 1983) made an attempt to predict buttoning before transplanting based on plant characteristics; higher values for plant weight, number of leaves and diameter of the apex indicated a higher risk of buttoning. Wurr and Fellows (1984) showed that buttoning was more frequent when curd initiation took place sooner after transplanting. Curd initiation is promoted by low temperatures (Wiebe, 1972b). However, first the juvenile phase, which can be characterised by the number of initiated leaves (Hand and Atherton, 1987) should come to an end (Wiebe, 1972a).

The present paper describes the study of the relation between development (leaf and curd initiation) and vegetative growth (plant weight) on curd weight at maturity. Variations in growth and development were created by different temperatures and durations of the raising period.

Materials and methods

The experiments were carried out on a light sandy soil at the Research Station for Arable Farming and Field Production of Vegetables in Alkmaar. Experiments were conducted in 1980 (Experiment 1) and 1981 (Experiment 2). The cauliflower cultivar used was the Alpha-selection Raket (Sluis & Groot, Enkhuizen, NL).

Seeds were sown in 5.0 cm peat blocks and the plants were raised in a heated greenhouse. Plants were transplanted in the field in a square arrangement at a plant density of 2.8 plants m^{-2}. Between the rows extra plants were planted for dissecting purposes. 10-15 plants were dissected at the start of the treatment, at transplanting and at regular time intervals after transplanting. The plants were considered generative when the first secondary primordia became visible (binocular microscope, magnification x 50) (Margara and David, 1978; Fujime, 1983). The final number of leaves was considered to be the number of initiated leaves below the curd. A curd was harvested when it matured, i.e. just before the curd started to become loose and not exceeded a diameter of 20-22 cm.

Experiment 1

The aim of the experiment was to study the effect of temperature prior to transplanting on curd maturity time and on curd and leaf weights at maturity.

Seeds were sown on April 6 and plants were raised at a minimum temperature set-point of 20 °C. Four weeks after sowing a batch of these plants was transplanted while the remaining plants were treated and transplanted afterwards. Plants were subjected to 5, 10 or 15 °C $\pm$ 1 °C for 14 days in a cold store with additional light (TL33; 16 h day^{-1} ; 18 W m^2). Relative humidity was kept between 85 and 95 %. Treated plants were transplanted in unreplicated plots consisting of 72 plants for harvest at maturity. From dissected plants the number of leaves longer than 1 cm, the number of initiated leaves and the developmental stage of the apex were determined. At maturity leaf and curd fresh weight were determined for each plant.

Experiment 2

The aim of the experiment was to examine the effect of transplant age in combination with a cold treatment before transplanting on growth and development after transplanting, on time of curd maturity and on curd and leaf weights at maturity. Sowing dates were chosen so that plants were 21, 28, 32 or 35 days old at the start of the treatment or for untreated plants at the transplanting date. Plants were raised until emergence at 20 °C and after emergence until 3 weeks after sowing at a minimum temperature set-point of 10 °C and subsequently at a minimum temperature set-point of 20 °C until start of the treatment or transplanting.

Plants were subjected to 5 °C $\pm$ 1 °C for 10 days in a cold store with additional light (TL33; 16 h day^{-1}; 18 W m^{-2}). Relative humidity was kept at 95 %. All treatments were transplanted on June 1 and treatments were replicated 3 times and each plot consisted of 32 plants for harvest at maturity. From dissected plants the number of leaves longer than 1 cm, the number of leaf initials, the developmental stage of the apex, the diameter of the apex and the fresh weight were determined. Plants in the field were labeled and from each plant the number of leaves longer than 1 cm was recorded at transplanting and leaf and curd weight was determined at maturity.

The number of leaves longer than 1 cm is further referred to as the number of visible leaves.

Results

Experiment 1

The first curds of the treated plants matured between 35 and 40 days after transplanting, while the curds of the control plants did not mature before 50 days after transplanting (Fig. 1).

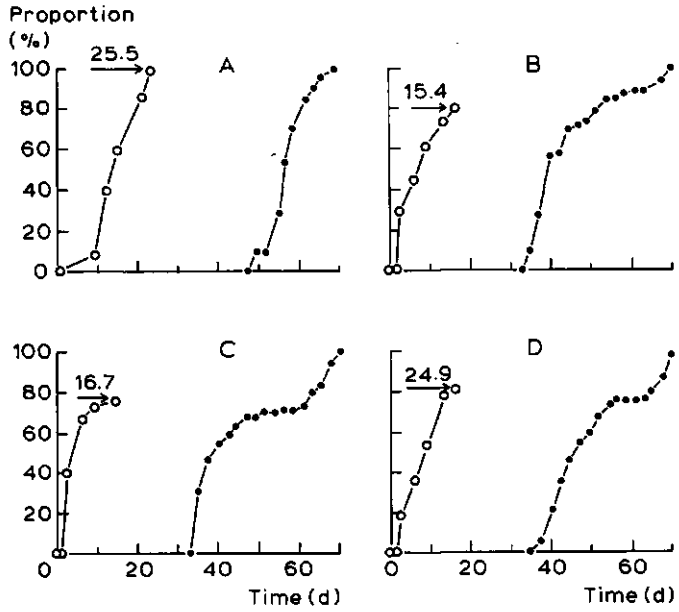


Figure 1
Relationship between time (days after transplanting) and the proportion of the number of plants in a crop that had initiated a curd (○) or that had matured (●). Plants were untreated (A) or subjected to 5 °C (B), 10 °C (C) or 15 °C (D) before transplanting. Mean final number of leaves of generative plants on the last sampling date is given. (Exp. 1)

Curd and leaf weights of treated plants were much lower at maturity than of untreated plants, in particular of the first maturing curds (Fig. 2). Leaf weight at the time of curd maturity increased linearly with time (Fig. 2A) and the relation for treated plants was not significantly ($P<0.05$) different from untreated plants. When curd weight at maturity was plotted against leaf weight it appeared that for treated plants curd weight increased at increasing leaf weights (Fig. 2B). For untreated plants the range of observed curd weights was small and there was no relation between leaf and curd weight (Fig. 2B).

Figure 3 (opposite page)
Cumulative frequency distribution of curd weight in relation to plant age and treatment (A). Maturity date (days after transplanting) (B), fresh weight of leaves at curd maturity (C) and number of visible leaves at transplanting (D) averaged per class of curd weights at maturity for each treatment.
Treatment: 1-4 cold treated, respectively 21, 28, 32 or 35 days after sowing; 5-8 untreated, transplanted respectively 21, 28, 32 or 35 days after sowing.
Curd weight classes: a: ≤200 g; b: 200< weight≤300; c:.. etc.; h: 800<weight≤900 g.(Exp. 2)

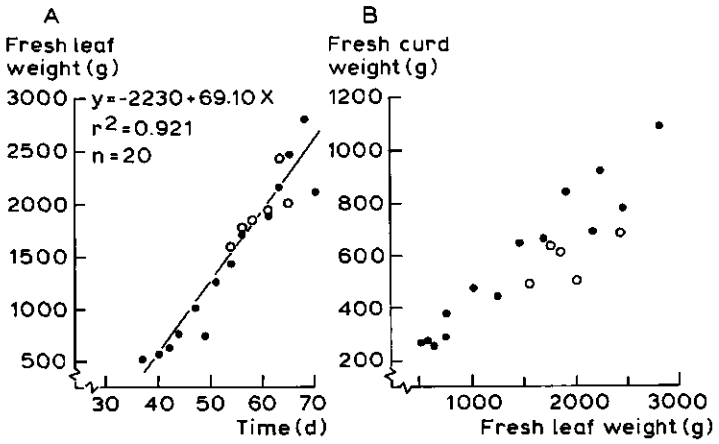
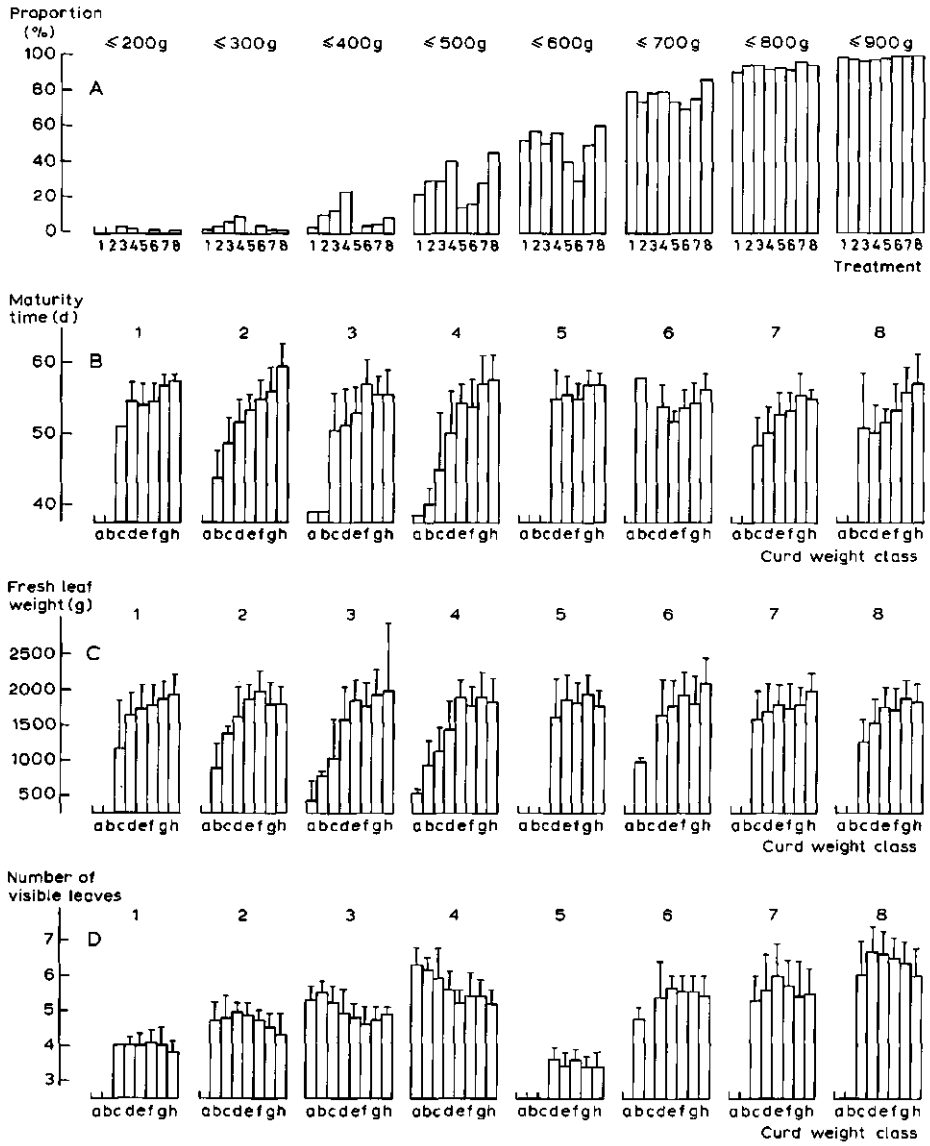


Figure 2
A. Relationship between time (days after transplanting) and the fresh weight of leaves of plants harvested at curd maturity ((●) cold treated; (○) untreated).
B. Relationship between leaf- and curd weight of plants harvested at curd maturity ((●) cold treated; (○) untreated). (Exp. 1)

The pattern of curd initiation reflected to a large extent the pattern of curd maturity (Fig. 1). No plants had initiated a curd at transplanting, but two days after transplanting a large proportion of the treated plants had already initiated a curd (Fig. 1), while in the control plot the first generative plants were observed 10 days after transplanting. Unfortunately information about the initiation date of the last 20 % of the treated plants fails, because no more plants were available for dissection. The final number of leaves at the last sampling date was higher when the temperature during the treatment had been higher (Fig. 1), but was always lower than for the untreated plants.

Curd initiation was observed first in plants with the highest number of visible leaves within a sample and the curd diameter of a dissected plant was positively correlated with the number of visible leaves.


Proportion (%)
≤200g
≤300g
≤400g
≤500g
≤600g
≤700g
≤800g
≤900g
A
12345678
Treatment
Maturity time (d)
B
abcdefgh
Curd weight class
Fresh leaf weight (g)
C
Curd weight class
Number of visible leaves
D
Curd weight class

Experiment 2

The analysis of variance (data not shown) revealed a significant ($P<0.05$) effect of transplant age on mean 50 % maturity date, mean curd diameter and mean curd weight at maturity. Only for mean curd weight there was a significant effect of the cold treatment.

Table 1

Mean date of curd maturity (days after transplanting ± SE) as affected by transplant age (days after sowing) and the number of visible leaves at transplanting. (Exp. 2)

Age (d)	Number of visible leaves					
	3	4	5	6	7	8
Cold treated						
21	-	54.8±2.7	52.4±3.7	-	-	-
28	-	56.6±4.7	52.4±3.4	-	-	-
32	-	57.8±3.2	53.2±4.9	45.7±6.2	-	-
35	-	61.0±3.1	56.4±3.3	47.1±5.5	39.8±1.5	-
Untreated						
21	57.0±2.1	54.8±2.4	-	-	-	-
28	-	-	54.8±2.4	52.6±2.2	-	-
32	-	51.8±5.2	53.6±4.2	53.1±2.5	50.8±3.1	-
35	-	-	56.7±7.7	54.1±4.2	50.5±3.4	46.0±0.0

The cumulative frequency distribution of curd weight at maturity for each treatment is presented in Figure 3A. The proportion of small curds (e.g. < 400 g) increased significantly ($P<0.05$) at increasing age and this proportion was significantly ($P<0.05$) higher for cold treated plants than for untreated. When the observations per plant were sorted according to curd weight at maturity and a number of weight classes were made, mean maturity time, mean leaf weight at maturity and the mean number of visible leaves at transplanting was calculated per curd weight class. Smaller curds matured earlier in all treatments (Fig. 3B). This effect was most clearly for the cold treated plants of 5 weeks old. For curds smaller than 500 g leaf weight increased with increasing curd weights (Fig. 3C). At increasing curd weight the mean number of visible leaves at transplanting decreased (Fig. 3D). For plants that were not cold treated, an increase in the number of visible leaves at transplanting was observed at increasing curd weight, followed by a decrease at higher curd weights.

The observations per plant obtained at maturity were sorted on the number of visible leaves of the plant at transplanting and the mean maturity time was calculated for each group of plants with the same number of visible leaves. Curds matured earlier when the number of visible leaves was higher at transplanting (Table 1). This effect was more pronounced for cold treated plants than for untreated plants.

In summary small curds within a crop matured earliest, had a low leaf weight and the plants producing the smallest curds had the highest number of visible leaves at transplanting, especially when the plant was cold treated before transplanting.

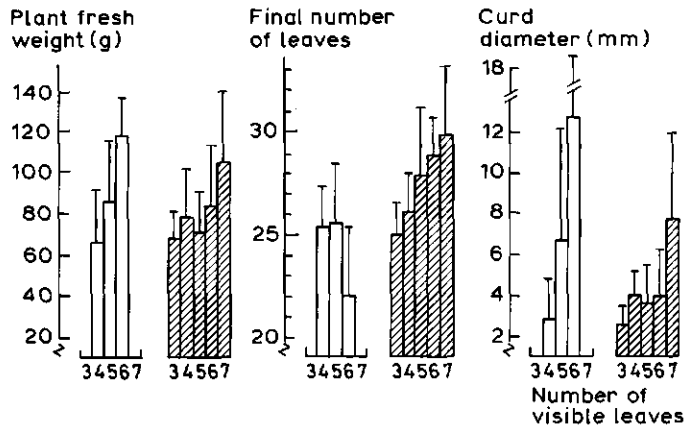


Figure 4
Mean fresh weight (g) per plant (A); mean final number of leaves (B) and mean curd diameter (mm) (C) at 23 days after transplanting (all plants generative) as related to the number of visible leaves at transplanting for cold treated and untreated plants (shaded).

The number of visible leaves determined of each plant at transplanting can be used as a marker to establish relations between curd size at maturity and earlier events during crop growth.

At 23 days after transplanting when all plants had initiated a curd, plant fresh weight of treated and untreated plants increased with increasing number of visible leaves at transplanting (Fig. 4). Final number of leaves of untreated plants increased at increasing number of visible leaves at transplanting, but decreased for cold treated plants. In particular for cold treated plants there was an effect of number of leaves at transplanting on curd diameter just after all plants had initiated a curd.

Plants with a higher number of visible leaves at transplanting initiated earlier a curd, especially when plants were cold treated, and had attained earlier a certain fresh weight (Fig. 5). A combination of the upper and lower part of Figure 5 reveals that plant fresh weight of cold treated plants was lower at the time the first curds were initiated, especially if the number of leaves at transplanting was higher. The broken vertical lines in Figure 5 indicate the mean fresh weight at the time 50 % of the plants had initiated a curd. Fresh weight of untreated plants at the time 50 % of the plants had initiated a curd decreased at decreasing number of visible leaves at transplanting, but fresh weight was higher again when the plants had 3 or 4 visible leaves at transplanting.

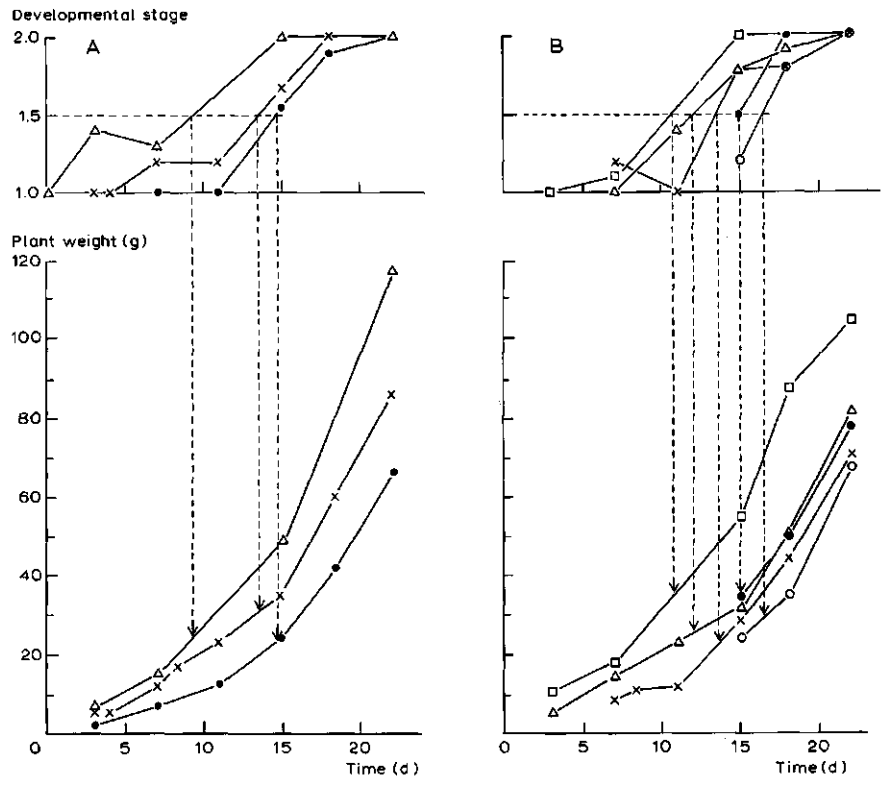


Figure 5
Relationship between time (days after transplanting) and mean developmental stage of the apex (1: vegetative; 2: generative) (upper part) and mean plant fresh weight (lower part) of cold treated - (A) or untreated plants (B); for groups of plants, distinguished by the number of visible leaves at transplanting (3 (●); 4 (○); 5 (×); 6 (△); 7 (□)). (Exp. 2)

The mean number of visible leaves at transplanting increased with age (Table 2). With increasing number of visible leaves at transplanting, plant fresh weight, the number of initiated leaves and the diameter of the apical dome increased (Table 2). In none of the treatments curd initiation was observed at transplanting.

The relationship between the number of visible leaves and plant fresh weight could be described by a second order polynomial (Fig. 6). When plants remained longer on the seed bed the increase in plant fresh weight per leaf was particularly less. The number of initiated leaves of vegetative plants was linearly correlated with the number of visible leaves, so that similar conclusions can be drawn for the relation between the number of initiated leaves and plant fresh weight.

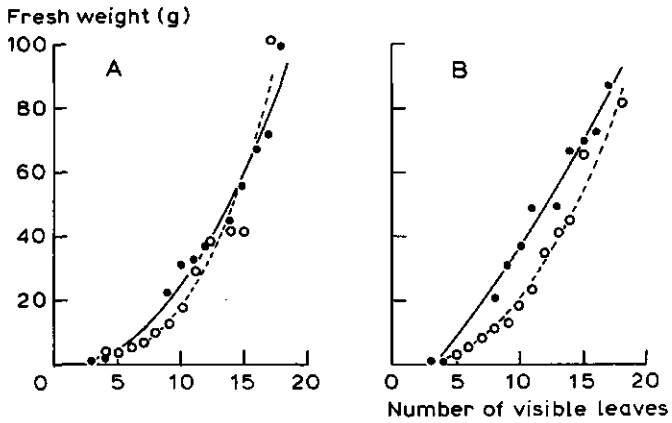


Figure 6
Relationship between the number of visible leaves and fresh weight per plant of 3 (●) and 5 (○) weeks old plants that were cold treated before transplanting (A) or untreated (B).

Table 2
Plant fresh weight, number of initiated leaves and diameter of the apical dome (± SE) as affected by transplant age (days after sowing).
(Exp. 2)

Age (d)	Number of visible leaves	Fresh weight (g)	Number of initiated leaves	Diameter (mm)
Cold treated				
21	4.0±0.3	2.2±0.6	10.7±1.1	0.18±0.03
28	4.5±0.6	2.9±1.0	11.6±1.9	0.20±0.05
32	4.8±0.6	3.5±1.0	12.1±1.7	0.18±0.03
35	5.5±0.6	4.7±1.5	13.5±2.8	0.21±0.06
Untreated				
21	3.2±0.4	1.4±0.3	9.2±0.6	0.16±0.02
28	5.1±0.5	5.0±1.6	12.8±1.7	0.18±0.04
32	6.1±0.8	7.3±2.3	16.1±3.6	0.22±0.05
35	6.5±0.9	7.6±3.0	16.8±4.2	0.24±0.07

The number of days between transplanting and the time on which 10 % of the plants had initiated a curd, decreased at increasing age at transplanting (Table 3). The date on which 90 % of the plants had initiated a curd was not affected by plant age. This means that the length of the curd initiation period (time difference between 10 % and 90 %)

increased at increasing plant age. This effect was more pronounced for the cold treated plants.

As the length of the period between curd initiation and maturity was independent of the proportion of the population regarded (Table 3), the maturity pattern reflected the pattern of curd initiation within the population.

Table 3
Time (days after transplanting) on which 10, 50 or 90 % of the plants in a crop had initiated a curd or had matured and on the period (d) of curd growth as affected by transplant age (days after sowing).
(Exp. 1)

Proprotion	Time of curd initiation (d)				Time of maturity (d)				Period of curd growth (d)			
	Age (d)				Age (d)				Age (d)			
	21	28	32	35	21	28	32	35	21	28	32	35
Cold treated												
10 %	12	11	5	2	51	48	45	40	39	37	40	38
50 %	14	13	14	12	55	54	54	53	41	41	40	41
90 %	20	17	20	20	59	58	60	61	39	41	40	41
Untreated												
10 %	12	10	7	7	53	50	47	46	41	40	40	39
50 %	16	14	13	12	56	53	53	52	40	39	40	40
90 %	20	18	21	20	60	59	58	58	40	41	37	38

Discussion

A low temperature treatment before transplanting could enhance the proportion of small curds drastically (Fig. 1, 3A), especially when plants had a high number of visible leaves at the start of the treatment. The smaller curds were the first maturing curds (Fig. 1, 3B) and it is likely that these curds were initiated first. The earlier initiation can be shown by using the number of visible leaves as a marker, namely plants with the high number of visible leaves at transplanting initiated curds earlier (Fig. 5A) and matured first (Fig. 3). Plant size at the time of curd initiation seems to affect curd weight, as the earlier initiation of cold treated plants was accompanied with lower fresh weights (Fig. 5A). Wurr and Fellows (1984) also showed an increase of the proportion of a crop that buttoned, when curd initiation occurred sooner after transplanting. The relation between growth and development (leaf initiation rate, curd induction) is of crucial importance. Low temperatures accelerate curd induction (Wiebe, 1972b) after the end of the juvenile phase (Wiebe, 1972a). In the present study the relation between the

number of visible leaves and plant fresh weight was affected by the duration of the raising period on the seed bed (Fig. 6), as growth was relatively more affected by seed bed conditions (high plant density) than development (leaf initiation). This means that plant fresh weight at the end of juvenility will be lower if more leaves are initiated during the raising period, as the end of juvenility can be characterised by the number of initiated leaves (Hand and Atherton, 1987). Low temperatures after the juvenile phase will retard growth and promote curd induction, resulting in a low plant fresh weight at curd initiation. If this occurs when the plant still remains on the seed bed, the chance of buttoning is highest. In general, buttoning occurs more frequently when plants remain longer on the seed bed (Carew and Thompson, 1948; Jensma, 1957; Sandwell, 1961; Skapski and Oyer, 1964; Heydecker and Nichols, 1967; Birkenshaw et all, 1982; Wiebe, 1983; Wurr and Fellows,1984). Skapski and Oyer (1964) showed an interaction between plant density on the seed bed and temperature, only when curd inducing conditions prevailed on the seed bed, the extent of buttoning increased at increasing plant size (due to plant density). It is also shown in the present study: the extent of buttoning was lower for untreated plants (Fig. 3A), although untreated plants were larger at transplanting than the cold treated plants (Table 2). Conditions after transplanting until curd initiation such as frosts, transplant check or drought can affect buttoning by reducing growth.

The juvenile phase prevents curd induction of plants with a low number of leaves initiated, therefore a cold treatment had no effect on curd weight when the number of visible leaves was low at the start of the treatment (Fig. 3). This implicates that storage of transplants at low temperatures, e.g. when transplanting has to be delayed, has a low risk when the end of the juvenile phase has not been passed but risk of buttoning will be high when plants are stored after their juvenile phase. If a delay of transplanting is expected, it is better to store plants at low temperatures at an early stage, than allow the plants to continue growth on the seed bed.

A longer juvenile phase (Wiebe, 1972a; Hand and Atherton, 1987) and a higher cold requirement for curd initiation (Wiebe, 1972b) of later cultivars will result in a higher plant weight at curd initiation, therefore the risk of buttoning is lower for later cultivars (Jensma, 1957; Heydecker and Nichols, 1967).

Length of the interval between curd initiation and maturity was independent of curd weight (Table 3; Wurr and Fellows, 1984). As the time to reach maturity was independent of curd weight (Table 3) and the rate of increase of leaf weight was the same for buttoning- and non-buttoning plants (Fig. 2), leaf weight was expected to be lower at maturity for buttoned plants. Therefore reduced leaf weight of buttoned plants does not seem to be due to a reduced leaf growth because of a stronger sink for assimilates of the curd.

Curd size can also be influenced by the growth conditions after curd initiation such as plant density (Salter, 1961); moisture (Salter, 1959); N-fertilization (Carew and Thompson, 1948; Wurr et al., 1988) and soil condition (Wiebe, 1983). Depending on the extent of restriction of a growth factor, buttoning may be the result from a lack of assimilates for curd growth due to reduced leaf growth, while the daily advance towards curd maturity is less affected. Abd El-Hafez and Said (1985) showed that reduction of leaf weight by cutting leaves during curd growth reduced curd weight at maturity.

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Chapter 6

Effect of growth regulators on curd diameter of cauliflower

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Effect of Growth Regulators on Curd Diameter of Cauliflower

R. BOOIJ

Research Station for Arable Farming and Production of Field Vegetables (PAGV), P.O. Box 430, 8200 AK Lelystad (The Netherlands)

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ABSTRACT

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The effect of ancymidol, chlormequat, daminozide, ethephon, gibberellin 3 (GA_3) and a mixture of gibberellins 4 and 7 (GA_{4+7}) on curd diameter of cauliflower was tested. GA_{4+7} increased curd diameter as a consequence of earlier curd initiation. The effect was directly related to the concentration (10–120 mg l^{-1}) of GA_{4+7} and plant age at the time of application. The effect of GA_{4+7} was more pronounced when curd initiation of the untreated cauliflowers was delayed by high temperatures. Multiple application of GA_{4+7} was more effective than a single application. The prospects of using GA_{4+7} to control the growing period of cauliflower and the role of GA_{4+7} in harvest planning are discussed.

Keywords: *Brassica oleracea* L. *botrytis*; cauliflower; flower initiation; gibberellin; growth regulators; harvest planning.

Abbreviations: GA_3 = gibberellin 3; GA_{4+7} = gibberellins 4 and 7.

INTRODUCTION

During growth of cauliflower plants several developmental stages can be distinguished (Wurr et al., 1981). The most important phase transition is from the vegetative to the generative state, as the edible part of the plant is the inflorescence. This transition depends on age of the plant (Wiebe, 1972a) and on temperature (Wiebe, 1972b). Higher temperatures can delay or prevent curd initiation after the juvenile stage. The influence of temperature and physiological age on curd initiation has also been observed in the field (Booij, 1987).

Harvest planning is mainly disturbed by an unpredictable variation in the time interval from transplanting to harvest (Booij, 1984). To reduce this variability, the curd induction must be affected since the time the curd takes to grow is less variable (Booij, 1987). Plant development in the field, in particular initiation of an inflorescence, is difficult to control because only few tools are available. A possibility is the application of a growth regulator, because some growth regulators affect flower initiation (Zeevaart, 1978).

As the information about effects of growth regulators on curd initiation of cauliflower is limited, a range of concentrations and application dates was tested under field conditions. Since the approach was intended as a test of commercial feasibility only commercially available growth regulators were included.

MATERIALS AND METHODS

General. – Trials in 1982 and 1983 with cauliflower cultivar 'Delira' (Rijk Zwaan, De Lier, NL) were carried out at the research station in Lelystad on a fertile marine clay soil. The plants were raised in frames and transplanted by hand 4.5–5 weeks after sowing as bare-rooted plants. The plant density was 2.8 m^{-2} in a square arrangement. The crops were treated as in commercial practice. Samples (12 plants) were taken from the control plots at regular intervals during the period that growth regulators were applied. By dissecting the plants, leaf primordia were counted and the developmental stage of the apex (vegetative or generative) was determined. For the determination a binocular microscope (magnification 50) was used; the apex was considered to have reached the generative state (curd initiation) as soon as the first secondary primordia became visible (Margara and Davids, 1978). The mean final number of leaves, i.e. the number of initiated leaves below the first leaf with a secondary primordium in its axil, was determined when all the plants in a sample had initiated secondary primordia.

The growth regulators were dissolved in water and wetting agent (Cytowet) was added to a concentration of 0.25 mg l^{-1}. Each plant of a plot was treated separately with a propane-driven sprayer at a constant overpressure of 0.1 MPa. The dose per plant was 15–18 ml of the solution.

A once-over harvest of all the plots was executed before the first curds of the most advanced plot reached maturity. Only the curd was cut and the diameter of the curd (without leaves on it) was measured and averaged for each plot. A part of the control plots was harvested about 1 week before and another part about 1 week after the main harvest. The data were used to calculate the growth rate of the curd. Differences between treatments and control were tested for significance by Student's *t*-test (Dixon and Massey, 1957); variance was analysed (ANOVA) with GENSTAT (Alvey et al., 1982). The trials in the 2 years were not the same in design and therefore the layout will be treated separately.

1982. – Two trials included the variables type of growth regulator, concentration and date of application. Trial 1 was transplanted on 4 June 1982 and Trial 2 on 15 July 1982. The growth regulators and the range of concentrations of the regulators are listed below.

Ethephon: 50; 100; 200; 400; 800 mg l^{-1}
Chlormequat: 125; 250; 500; 1000 mg l^{-1}
GA_3: 10; 20; 40; 80 mg l^{-1}
GA_{4+7}: 10; 20; 40; 80 mg l^{-1}
Daminozide: 500; 1000; 2000; 4000 mg l^{-1}
Ancymidol: 5; 10; 20; 40 mg l^{-1}

Daminozide was tested only in Trial 1 and ancymidol only in Trial 2. The growth regulators were applied 14, 18, 21, 24, 26 or 28 days after transplanting in the first trial and 15, 18, 20, 22, 26 or 29 days after transplanting in the second.

An unreplicated split-split-plot design was used; the main plot (application date) was split into 7 subplots (regulators and control) and each subplot was divided into 4 sub-subplots (concentration). Each sub-subplot had 20 plants. The first trial was harvested 55 days after transplanting and the second 76 days after transplanting.

1983. – In 1983, 3 trials, transplanted on 13 June, 30 June and 13 July, analysed the effect of a single application of GA_{4+7} at different concentrations (0, 15, 30, 60 or 120 mg l^{-1}) and with different application dates (21, 25, 28 or 31 days after transplanting). An unreplicated split-plot design was used; the main plot (application date) consisted of 5 subplots (concentration and control).

In these 3 trials also the effect of multiple application (twice, thrice and four times) of GA_{4+7} at concentrations of 10, 20, 40 or 80 mg l^{-1} was tested. The first application was for all treatments 21 days after transplanting and the others 25 (2, 3 and 4 sprayings), 28 (3 and 4 sprayings) and 31 days (4 sprayings) after transplanting. An unreplicated split-plot design was used; every main plot (number of applications) was split in 5 subplots (concentration and control). Each subplot contained 16 plants.

The plants in the 3 trials were harvested 70, 69 and 70 days after transplanting, respectively.

RESULTS

Because of limits in space and time the number of plants treatment^{-1} was restricted. By so doing the best comparisons could be made between treatments on one hand and the control on the other; comparing treatments was less re-

liable. A difference between the control and each treatment could be tested for significance, because the controls were replicated.

In the first trial of 1982, only a few treatments (2 out of 120) resulted in a significantly larger diameter than the control. The highest concentration (800 mg l^{-1}) of ethephon caused severe bracting.

In the second trial of 1982, spraying with GA_{4+7} at 80 mg l^{-1} resulted in a significantly larger curd when applied at the last 3 dates (Table 1). From the other growth regulators only 1 treatment with chlormequat and 2 treatments with ancymidol resulted in just-significant larger diameters. These just-significant values were ignored further, because no clear pattern could be recognized. Some plants had initiated curds at the last 3 dates of application in the first trial, but none had initiated curds at the application dates in the second trial (Table 1).

Because only GA_{4+7} consistently affected curd diameter in the 1982 trial, GA_{4+7} was tested further in 1983.

The results of the trials in 1983 are presented in Table 2 for a single application of GA_{4+7} and in Table 3 for multiple application. Especially in the first trial, a single application of GA_{4+7} increased mean curd diameter (Table 2). The effect was most distinct if the highest concentration was applied 28 or 31 days after transplanting. In the second trial only with the highest concentration applied at the first 2 dates were significantly higher mean curd diameters than control found. In the third trial, no pattern was detected. Variance was

TABLE 1

Effect of GA_{4+7} concentration and time of application on mean curd diameter in cm (1982)

	Trial 1						Trial 2					
	14[1] days	18 days	21 days	24 days	26 days	28 days	15 days	18 days	20 days	22 days	26 days	29 days
Concentration (mg l^{-1})												
0	7.5	7.1	9.7	5.1	6.9	5.7	11.1	9.6	10.9	9.3	-	10.5
10	6.5	5.2	7.1	6.9	5.1	6.9	8.8	8.6	10.1	10.5	10.2	9.8
20	7.0	6.9	6.4	6.6	3.2	5.9	8.2	10.3	10.8	11.8*	10.5	10.4
40	6.5	7.9	8.2	5.7	4.6	5.6	8.7	10.1	9.4	10.7	11.9*	10.8
80	6.3	6.7	7.6	6.8	4.3	6.5	9.4	10.3	10.9	12.1*	12.2*	13.2*
Total no. of leaves[2,3]	15.1	15.8	21.6	23.8	24.7	27.0	14.9	16.2	18.1	19.1	21.2	24.8
Proportion of plants generative (%)[2]	0	0	0	35.7	50.0	64.0	0	0	0	0	0	0

[1]Time of application (days after transplanting).
[2]At the time when GA_{4+7} was applied.
[3]Including scars and primordia.
*Significantly ($P < 0.05$) higher than control.

TABLE 2

Effect of GA_{4+7} concentration and time of application on mean curd diameter in cm (one application, 1983)

	Trial 1				Trial 2				Trial 3			
	21[1] days	25 days	28 days	31 days	21 days	25 days	28 days	31 days	21 days	25 days	28 days	31 days
Concentration (mg l^{-1})												
0	5.6	6.8	6.7	6.4	11.2	9.8	11.3	9.4	7.8	7.6	8.4	7.9
15	7.8	5.8	8.5*	5.9	10.9	9.6	11.6	12.6*	8.9	7.8	8.8	6.9
30	7.7	8.2	9.2*	6.8	10.7	11.1	11.8	10.6	5.6	9.5	9.2	4.7
60	7.5	9.6*	11.3*	8.1	11.9	11.8	11.0	11.2	10.4*	9.2	8.6	7.0
120	9.8*	9.0*	10.2*	10.6*	15.0*	12.5*	11.5	8.8	6.3	8.9	10.8*	7.3
Total no. of leaves[2,3]	15.8	20.6	23.0	26.7	17.6	25.8	29.3	34.4	21.1	25.3	26.6	29.1
Proportion of plants generative (%)	0	0	0	0	0	0	0	22.2	0	0	16.7	68.7

[1]Time of application (days after transplanting).
[2]At the time when GA_{4+7} was applied.
[3]Including scars and primordia.
*Significantly ($P<0.05$) higher than control.

TABLE 3

Effect of number of applications and concentration of GA_{4+7} on mean curd diameter in cm. For growth and development of control plants see Table 2 (1983)

Concentration (mg l^{-1})	Trial 1			Trial 2			Trial 3		
	2[1]	3	4	2	3	4	2	3	4
0	5.6	6.7	6.4	11.2	11.3	9.4	7.8	8.4	7.9
10	7.8	7.3	7.7	9.9	11.6	12.5	7.2	10.0	5.7
20	8.4	9.1*	9.3*	9.3	11.4	10.0	8.4	9.6	6.1
40	11.9*	12.5*	10.1*	13.5*	13.2*	13.0*	5.8	10.1*	8.1
80	12.3*	11.5*	12.3*	-	15.4*	14.9*	12.5*	11.7*	10.5*

[1]No. of applications.
*Significantly ($P<0.05$) higher than the control.

analysed with the 3 trials treated as blocks. The residual errors were not related to the fitted values and were normally distributed. The analysis revealed a significant effect of GA_{4+7} concentration ($P=0.012$), but the effect of application date ($P=0.065$) was just not significant. There was no significant interaction ($P=0.844$) of the 2 factors.

The effect of multiple application of GA_{4+7} is presented in Table 3. At a concentration of 80 mg l^{-1}, GA_{4+7} resulted in a larger diameter than the control in all 3 trials. In the first 2 trials, lower concentrations gave also diameters

significantly different from the control. The number of treatments with a mean diameter significantly different from the control was highest in the first trial and lowest in the last trial. For these 3 trials, variance was analysed, the trials being treated as blocks. The residual errors were not related to the fitted values and were normally distributed. There was a significant ($P<0.01$) effect of concentration, but there was no significant effect ($P=0.157$) of the number of applications; the 2 factors did not interact ($P=0.960$). Figure 1 gives the relation between concentration of GA_{4+7} and curd diameter for single and multiple application. The effect of concentration of GA_{4+7} after multiple application was larger than after a single application.

In the first trial, no plants of the control had initiated curds at the application dates; in the second trial, curds were initiated at the last date; in the third trial, curds were initiated at the last 2 application dates (Table 2).

The treatments with GA_{4+7} reduced the final number of leaves substantially (Table 4). Multiple application reduced the number of leaves more than a single application, but more than 2 applications did not result in a further decrease.

The difference in mean curd diameter between the treated plants and the controls corresponds to a difference in earliness, because a larger curd means the treated plants were more advanced. The daily rate of increase in diameter of the control is given in Table 5. Supposing the curd growth rate of the control plants to be the same as the treated plants, a difference in the mean diameter of 1 cm corresponds, in the 3 trials of 1983, with an advance of 1.6, 1.5 and 1.9 days, respectively.

The main stem of the plants treated more than once with GA_{4+7} was longer than usual, and its extension increased with the number of applications. The curd was then less well covered by inner leaves and was exposed earlier.

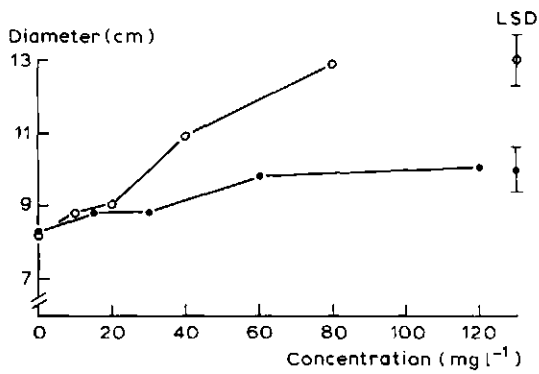

Fig. 1. Relationship between concentration (mg l^{-1}) of GA_{4+7} applied once (●) or more than once (○) and the curd diameter (cm). For each concentration the mean of all application dates is taken where only one application was made, and that of all application frequencies where there were several applications. (means of the 3 trials, 1983) (LSD: $P<0.05$).

TABLE 4

Effect of some GA_{4+7} treatments on final number of leaves at harvest (1983)

Trial	No. of applications	Concentration ($mg\ l^{-1}$)	No. of leaves
2	4	80	25.9
2	Control	0	34.5
3	1[1]	120	29.5
3	1[2]	120	29.6
3	4	80	25.8
3	3	80	26.6
3	2	80	25.8
3	Control	0	31.4

[1]21 days after transplanting.
[2]28 days after transplanting.

TABLE 5

Some data about the control plots of all trials

	1982		1983		
	Trial 1	Trial 2	Trial 1	Trial 2	Trial 3
Mean total no. of leaves 19[1]	20	22	24	23	19
Median plants generative[2]	6	13	15	10	11
Final no. of leaves	26.4	33.3	35.8	35.1	30.3
Mean temperature (°C)[3]	15.3	16.8	19.2	18.9	16.2
Curd growth rate ($cm\ day^{-1}$)	0.82	0.71	0.63	0.68	0.52

[1]Days after transplanting.
[2]Days after initiation of the nineteenth leaf.
[3]In the period between initiation of the nineteenth leaf and median generative time.

DISCUSSION

The increase in diameter of the curd with GA_{4+7} can be caused by an effect on rate of curd growth or on initiation date of the curd. The effect was probably on curd initiation, because: an application of GA_{4+7} long before curd initiation date of the control was most effective and if it was applied when the curd had already been initiated there was no influence on diameter (Tables 1 and 2); an application of GA_{4+7} reduced the final number of leaves substantially (Table 4), indicating that the curd is initiated earlier (Booij, 1987; Wiebe, 1972a,b).

The effect of a single application of GA_{4+7} seemed to depend on the stage of development of the plant; in the second trial of 1982, an effect became visible when the total number of leaves was more than 19 (Table 1). However when

treated with a higher concentration, also at somewhat lower number of leaves there was an effect (Table 2). The influence of plant age (or development) on the effect of a GA_{4+7} treatment fits in with the relation between plant age and the effect of low temperatures on curd initiation (Booij, 1987; Wiebe, 1972a); cauliflower has a juvenile phase (Wurr et al., 1981). For the cultivar used in our experiments, the end of the juvenile phase can be characterized best by about 19 initiated leaves (Booij, 1987).

Time of curd initiation is determined after the end of the juvenile phase mainly by temperature; high temperatures delay curd initiation (Booij, 1987; Wiebe, 1972b). Our experiments show that there was only an effect of GA_{4+7} when it was applied after the end of the juvenile phase and before curd initiation occurs (Tables 1 and 2). Comparing the experiments, the effect of GA_{4+7} application after the end of juvenility on curd diameter was bigger when the difference between the final number of leaves and the number of leaves at the application date was higher (Tables 1, 2 and 5). The higher final number of leaves was due to high temperatures (Table 5). However, within each experiment, there was hardly any effect of application date when applied after the end of juvenility (Tables 1 and 2). The discrepancy between these 2 phenomena could not be explained.

The largest and most consistent effects were found when GA_{4+7} was applied more than once. The difference between 1 and more applications cannot be explained by differences in the total amount of GA_{4+7} dosed. The effect on diameter was bigger when a certain total amount of GA_{4+7} was split (Fig. 1). Other explanations can be: (1) the internal concentration of GA_{4+7} remains longer on a certain level after more applications; (2) the variation within the crop, especially in relation with the sensitivity for GA_{4+7}, as not all plants within a crop will pass the end of juvenility at the same date. More than 2 applications did not enhance the effect (Table 3), so that 2 applications could initiate curds in the maximum number of plants. Our data allow no conclusion on this matter.

Within the crop, the variability in curd diameter was not influenced by the GA_{4+7} treatments (data not shown). If it were possible to replace temperatures inducing curd initiation completely by GA_{4+7}, a reduction in the variability would be expected as happens when temperature suddenly falls (Wiebe, 1973). Gibberellin may only enforce the natural induction of the curd. Under climatic conditions prevailing in The Netherlands, a curd is always initiated; higher temperatures only retard the initiation (Booij, 1987). Gibberellins often do not induce bolting or flowering but only accelerate it in several crops in combination with a cold treatment (van Marrewijk, 1976; Ali and Souza Machado, 1982; Nieuwhof, 1984). The variability of curd diameter within a crop is caused by a variation in curd initiation date (Salter, 1969) and if the variation in curd initiation date is mainly caused by variation in date of end of juvenility, GA_{4+7} will not be able to reduce the variability in curd diameter.

Leshem and Steiner (1968) tried to accelerate flowering of an English cul-

tivar of winter cauliflower by using GA_3 at 50 mg l^{-1}, flowering was significantly accelerated but the final number of leaves was reduced only in combination with a cold treatment. Salter and Ward (1972) studied the effect of GA_3 and GA_{4+7} (5–50 mg l^{-1}), but they did not find any effect. The main differences between the experiments of Salter and Ward (1972) and ours were the concentrations and dates of application of GA_{4+7}; Salter and Ward (1972) treated younger plants with lower concentrations of GA_{4+7}. The failing of an application of GA_3 was in agreement with our experiments, so probably the kind of gibberellin used is important, as has been concluded for the flowering process in other species (Zeevaart, 1978).

Endogenous gibberellins are likely to play a role in curd initiation. Kato (1965) found an increase in the content of gibberellin-like compounds during the period that the curd was initiated. At non-inducing temperatures (25°C) the content of gibberellin-like compounds was lower than at lower temperatures (Kato, 1965). Fontez et al. (1970) and Thomas et al. (1972) found an increase in the content of these compounds after a cold treatment. However Fontez and Ozbun (1970) and Fontez et al. (1970) increased endogenous gibberellins substantially by application of daminozide and curd initiation was even partially prevented. Although chlormequat, ancymidol and daminozide are able to inhibit or depress biosynthesis of GA (Sembdner et al., 1980), no reduction in curd diameter was found in our experiments.

The time cauliflower takes to grow is determined mainly by the moment of curd initiation (Booij, 1987). GA_{4+7} can probably be used in regulating the growing period, especially in a warm climate or season when high temperatures retard curd initiation, and therefore can be a tool for correcting harvest planning of cauliflower. For commercial application more information is needed about the effect on quality. However field trials to optimize the GA_{4+7} application will be difficult, because the effect depends strongly on the weather conditions (mainly temperature) after the end of juvenility.

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Chapter 7

Effects of gibberellic acids on time of maturity and on yield and quality of cauliflower

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Effects of gibberellic acids on time of maturity and on yield and quality of cauliflower

Summary

The effect of an application of gibberellic acids (GA_{4+7}) on cauliflower was studied in a number of crops of the cultivars Delira and Elgon, grown in spring and summer of the years 1984, 1985 and 1986. Crops varied in timing of the end of the juvenile phase and of curd initiation and differed in final number of leaves and length of the growing period. In most crops the period between transplanting and harvest was shortened, when GA_{4+7} was applied twice after the end of juvenility at a concentration of 80 mg l^{-1}. The shortening of the growing period varied from crop-to-crop and increased when the difference between the number of leaves initiated at the time of application and the final number of leaves of the untreated crop increased. GA_{4+7} reduced the final number of leaves. Quality of the curds was hardly affected in most crops, but when crops were treated which displayed bracting, the bracting incidence was reduced. In crops of cv Delira with a low final number of leaves, size and quality of the curds was reduced.
The results are discussed in relation to the harvest planning of cauliflower.

Introduction

The cauliflower supply can fluctuate tremendously on farms, where cauliflowers are grown continuously during the season, despite of the use of transplanting schedules, which are based on earlier experience (Booij, 1984; Hartmann & Wuchner, 1965; Salter et al., 1972). The variation is mainly due to an unpredictable variation in length of the growing period of a crop and, to a lesser extent, to a variation in length of the period during which individual plants within a crop mature (Booij, 1984). The interval of time between transplanting and maturity (harvest) is mainly determined in a crop by the time of curd initiation (Booij, 1987; Grevsen, in press). The time interval between maturation of the first and the last curds within a crop (harvest period) is affected mostly by the length of the period in which curds are initiated within the crop (Salter, 1969; Booij, in press). Time of curd initiation is influenced by temperature during induction; higher temperatures retard curd induction and temperatures above a certain limit can even prevent curd induction (Booij, 1987; Wiebe, 1972). The final number of leaves is also influenced by temperature: this number of leaves increases at increasing temperatures (Atherton et al., 1987; Booij, 1987). Induction of the curd can only be achieved after a certain minimum number of leaves has been initiated (Hand and Atherton, 1987). This minimum number of leaves characterizes the end of the juvenile phase. The variation in time on which the phase changes, like end of juvenility and curd initiation, occur from crop-to-crop and within a crop from plant-to-plant affects largely the variation in time of maturity. Regarding the phase transitions, temperature plays a predominant role. An option to obtain a more even cauliflower supply during the season is a reduction of the variation in length of the growing period by reducing the variation in time of curd initiation. Booij (1989) showed that curd induction could be affected by GA_{4+7} applications, if applied after the end of the juvenile phase. Especially when curd

induction was delayed, due to high temperatures, a GA_{4+7} application advanced the time of curd maturity. Due to natural variations in environmental conditions during the season, crops vary in timing of several developmental transitions, like end of juvenility, curd induction and maturity. The aim of the present described experiments is to relate the effect of GA_{4+7} on time of curd maturity, curd size and curd quality of a crop to developmental characteristics of the crop.

Materials and methods

Trials were carried out at the Research Station for Arable Farming and Production of Field Vegetables (PAGV) on a fertile marine clay soil in 1984, 1985 and 1986. Plants of cv Delira (Rijk Zwaan, De Lier, NL) and cv Elgon (Royal Sluis, Enkhuizen, NL), were raised in frames in 1984 and in an unheated glasshouse in 1985 and 1986; bare rooted transplants were planted by hand on several dates (Table 1) in a square arrangement at a density of 2.5 plants m^{-2}, 5 to 6 weeks after sowing. The crops were treated as in commercial practice.

Samples (10-12 plants) were taken from the control plots at regular intervals starting three weeks after transplanting, until all plants in a sample had initiated a curd. By dissecting the plants, the number of leaves initiated and the developmental stage of the apex (vegetative or generative) were determined, by using a binocular microscope. The apex was considered to have reached the generative phase (curd initiation) as soon as the first secondary primordia became visible (Margara & David, 1978). The mean final number of leaves, i.e. the number of leaves initiated below the first leaf with a secondary primordium in its axil, of a crop was determined when all the plants in a sample had initiated secondary primordia.

GA_{4+7} (from Berelex GA 4/7 (ICI); 9 g l^{-1} GA_{4+7}) was diluted to 80 mg l^{-1}, and 0.25 ml l^{-1} wetting agent (Cytowet, BASF) was added. Each plant was treated separately with a propane-driven sprayer at a constant overpressure of 0.2 MPa, at a dose of 15-18 ml of the solution. GA_{4+7} was applied twice to the same plant, with the second application 4 days after the first.

At harvest of the 1984 trial, plants were individually assessed three times a week and were cut just before the curd would become loose (maturity) and were judged by size and quality. In 1985 and 1986 curds were not cut, but twice a week each curd was scored for quality and size. The curd was considered to be harvestable on the date of the highest score for quality (class I; no defects; class II: minor defects; class III: unmarketable) and size (Size 6: 17-20 cm; Size 8: 14-17 cm; Size 10: 11-14 cm diameter). Bracting, riceyness, looseness and malformations were regarded as quality defects.

For each crop a cumulative frequency distribution of the number of harvested curds was made and the time on which 10 % (H10), 50 % (H50) or 90 % (H90) of the curds had been harvested was estimated. The interval between the time on which 10 % and 90 % of the curds had been harvested is regarded as the harvest period (HP).

Regression analysis and analysis of variance (ANOVA) were carried out with the statistical program package GENSTAT (Lane et al., 1987).

Trial 1 (1984)
From 240 plants, transplanted on each date (Table 1), one third was treated and two thirds were left untreated. The first of two GA_{4+7} applications was given at about 21 days after transplanting. Treatments were unreplicated.

Trial 2 (1985)
From each plot (100 plants), half was treated and half was left untreated. Cv Delira plants were treated for the first time when they had initiated about 19 leaves and cv Elgon plants when they had initiated about 26 leaves.

Trial 3 (1986)
With cv Delira the effect of time of the GA_{4+7} application was studied and with cv Elgon the effect of application time and GA_{4+7} concentration was examined. The first of the two GA_{4+7} applications was given at the time when about 19 leaves had been initiated (T1), 2 (T2) or 4 (T3) days later, but at the earliest 20 days after transplanting. The GA_{4+7} concentrations applied to cv Elgon were 80, 120 or 160 mg l^{-1}. Each treatment was replicated three times and for the final harvest each plot consisted of 42 plants in case of cv Delira and 25 plants in case of cv Elgon. After all untreated plants of cv Delira had initiated a curd, a sample (15 plants) was taken from the treated plots and the final number of leaves was counted.

Results

Time of maturity

Characteristics of the untreated plots are presented in Table 1. The crops varied in time on which the 19th leaf was initiated; in time on which 50 % of the plants within a crop had initiated a curd and the mean final number of leaves.

The effect of a GA_{4+7} treatment on the maturity time (number of days after transplanting) of a crop was expressed as the difference in time of maturity between the untreated- and the corresponding treated plot. Positive values mean an advancement of maturity and negative values a delay. In most crops H10 and H50 was advanced by an application of GA_{4+7}, however, in some crops H10 was delayed (Fig. 1). As not all crops were treated exactly at the same developmental stage (i.e. the number of leaves initiated) and there were also differences between crops in the mean final number of leaves (Table 1), the effect of a GA_{4+7} treatment was related to the difference in these numbers of leaves. From Trial 3 (1986) only the results of T1 were included. In general, the advancement of H10 and H50 increased at increasing difference in the number of leaves. The effect on H50 diminished again when the difference was higher than 15 leaves. Two crops of cv Delira (9 and 13) deviated clearly from the relation; no 9 was severely damaged by pigeons and from no 13 a number of plants was clearly infected with *Rhizoctonia solani*. Therefore these two crops were omitted from the regression analysis. The relationship between the difference in number of leaves and the effect of GA_{4+7} on time of maturity could be described by a second order polynomial for the effect on H10 and by a third order polynomial for the effect on H50. Only significant ($P<0.05$) terms were included.

Table 1
Transplanting date, time (days after transplanting) on which mean number of leaves equaled 19, time on which 50 % of the plants had initiated a curd, mean final number of leaves, time (days after transplanting) of first GA_{4+7} application and number of leaves initiated at that time of all crops studied. (Exp. 1: 1984; Exp. 2: 1985; Exp. 3: 1986)

Crop number	Transplanting date	Initiation leaf 19	Curd initiation	Mean final no of leaves	First application: time	First application: number of leaves
'Delira'						
1	84-05-15	25	32	27.5	21	16.9
2	84-05-23	25	35	27.4	21	15.8
3	84-05-29	28	32	24.8	21	15.0
4	84-06-05	27	32	23.4	21	14.7
5	84-06-19	23	31	27.3	24	20.9
6	84-07-10	28	38	33.3	21	14.4
7	85-05-22	28	35	23.3	26	17.4
8	85-05-29	30	37	28.0	27	17.2
9	85-06-05	29	40	33.0	29	18.2
10	85-06-13	26	39	31.5	25	18.0
11	85-06-19	27	36	31.1	27	19.2
12	86-05-21	25	37	36.0	26	20.1
13	86-05-27	26	42	36.8	24	18.0
14	86-06-03	21	38	33.9	22	19.5
15	86-06-10	21	34	33.1	21	19.0
16	86-06-18	20	28	30.4	20	19.1
'Elgon'						
1	84-06-19	.	32	31.2	24	27.1
2	84-06-26	25	33	31.8	20	15.3
3	84-07-03	18	27	34.1	21	22.1
4	84-07-10	25	41	39.8	21	17.1
5	85-06-05	28	50	40.8	36	25.2
6	85-06-13	22	36	37.8	28	29.1
7	85-06-19	23	34	36.3	28	26.7
8	85-07-04	.	35	33.2	27	26.1
9	86-06-03	21	41	40.9	22	20.5
10	86-06-10	16	34	39.2	21	22.4
11	86-06-18	16	30	37.7	20	23.3
12	86-06-24	16	30	36.7	21	23.6
13	86-07-01	15	29	36.6	20	23.4

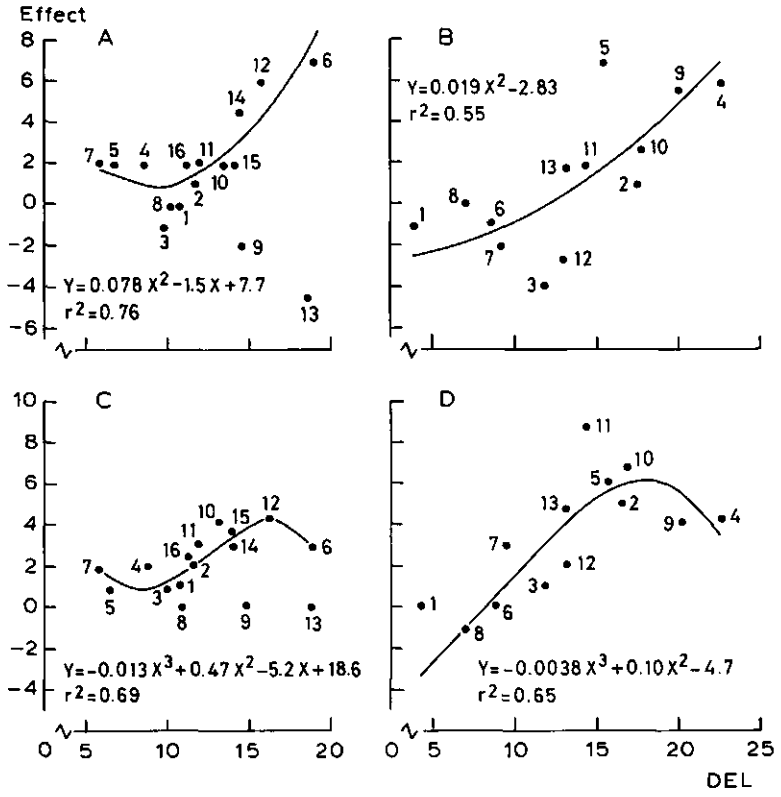

Figure 1
Relationship between the difference (DEL) in the number of leaves at the time GA_{4+7} was applied and the final number of leaves of control plants and the effect (difference between untreated and treated in days) of GA_{4+7} on the time that 10 % (A,B) or 50 % (C,D) of the curds had been harvested. Cv Delira (A,C) and cv Elgon (B,D). Numbers attached to the points in the Figure are crop numbers (Table 1). Best fitting significant regression equations are given.

The experiments which were carried out in 1986 could be analysed on significance of the effects and the results are presented in Table 2. In all crops of 1986 H50 was advanced by a GA_{4+7} treatment and in 4 out of 5 crops this difference was significant ($P<0.05$) for both cultivars. The effect on H10 was only significant in 3 out of 5 crops (both cultivars). There was no significant effect of time of application on H50 of cv Delira and only in two crops there was a significant effect on H10. Cv Elgon showed a different picture there was a significant effect of time of application on H50 in 4 out of 5 crops and in 2 out of 5 crops this was true for H10. Time of maturity was less advanced, when GA_{4+7} was applied later (Table 2).

Table 2
Effect of cultivar, GA_{4+7} treatment, GA_{4+7} application time (for codes see materials and methods) and concentration (mg l^{-1}) on time (days after transplanting) that 10 % (H10) and 50 % (H50) of the curds had been harvested, on length of the harvest period (HP) and on mean final number of leaves of crops grown in 1986. ANOVA was carried out for each crop and cultivar separately, comparisons were made between treated and untreated and within treated between application times and between concentrations. Values followed by the same letter do not differ significantly ($P<0.05$). (Exp. 3, 1986)

'Delira'

Crop number	Treatment		Application time		
	-	+	T1	T2	T3
H10					
12	70.7a	65.7a	64.7a	65.3a	67.0a
13	68.3a	72.7a	73.3a	72.7a	72.0a
14	75.7a	71.7b	71.3a	70.7a	71.3a
15	69.3a	67.0b	66.3a	66.7a	68.0b
16	68.0a	67.0b	67.0ab	66.3a	67.7b
H50					
12	82.3a	77.9b	78.0a	77.3a	78.3a
13	83.3a	82.1a	81.3a	83.3a	81.7a
14	78.3a	74.9b	75.7a	74.7a	74.3a
15	73.3a	70.1b	69.7a	70.0a	70.7a
16	71.7a	69.8b	69.3a	69.3a	70.7a
HP					
12	19.3a	24.1a	26.3a	24.0a	22.0a
13	20.0a	15.3a	14.0a	15.3a	16.7a
14	9.0a	8.1a	8.3a	8.3a	7.7a
15	12.3a	9.6a	10.7a	8.0a	10.0a
16	10.3a	8.8a	8.7a	9.0a	8.7a
Final number of leaves					
12	35.1a	30.6b	29.7a	31.0a	31.2a
13	36.6a	33.8b	33.4a	35.2a	32.7a
14	34.5a	31.5b	31.6a	31.4a	31.4a
15	31.7a	27.4b	28.0a	26.7a	27.5a
16	29.9a	27.9b	26.4a	27.4a	30.0b

Table 2 continued.

'Elgon'

Crop number	Treatment		Application time			Concentration		
	-	+	T1	T2	T3	80	120	160
H10								
9	84.3a	80.6b	80.0a	80.0a	81.7a	81.8a	80.1a	79.8a
10	78.0a	76.2b	75.4a	75.8a	77.2b	76.1a	76.2a	76.1a
11	76.0a	75.1a	74.1a	75.8a	75.4a	75.2a	74.7a	75.4a
12	75.0a	79.1b	78.2a	77.7a	81.4b	79.0a	78.6a	79.8a
13	79.0a	78.2a	77.7a	78.4a	78.4a	78.3a	78.4a	77.8a
H50								
9	89.7a	86.0b	86.6a	86.3a	85.1a	87.2a	85.2b	85.6b
10	86.0a	80.2b	79.6a	79.2a	81.8b	80.7a	80.4a	79.4a
11	86.7a	81.9b	78.1a	80.8a	86.8b	82.0a	82.0a	81.7a
12	86.0a	85.2a	84.4a	84.9a	86.3b	85.0a	84.9a	85.8a
13	85.7a	83.7a	81.6a	84.6b	85.0b	84.0a	83.6a	83.6a
HP								
9	14.7a	14.7a	17.3a	16.4a	10.4b	14.8a	12.8a	16.7a
10	21.3a	12.7b	14.0a	10.9b	13.3ab	13.4a	13.7a	11.1a
11	20.7a	16.1b	14.6a	15.9a	17.8a	16.3a	17.2a	14.7a
12	19.3a	11.8b	11.4a	11.6a	12.3a	11.6a	12.4a	11.3a
13	20.0a	12.6b	12.2a	13.4a	12.1a	12.1a	11.8a	13.9a

GA_{4+7} concentration had only a significant effect in 1 crop of cv Elgon and in none of the crops there was a significant interaction between application time and concentration.

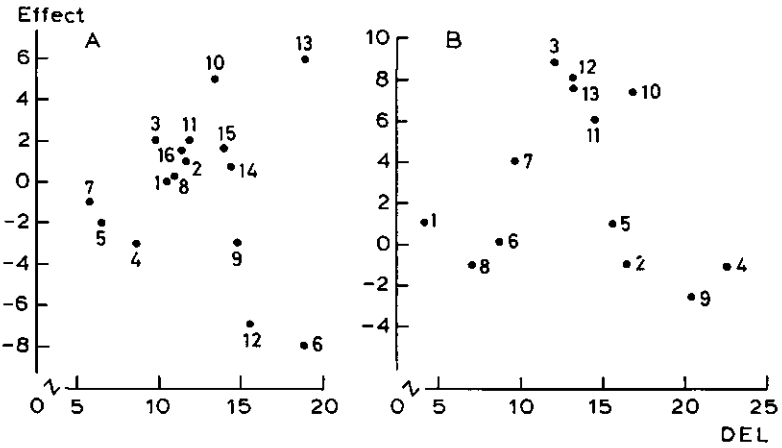

Figure 2
elationship between the difference (DEL) in the number of leaves at the time GA_{4+7} was applied and the final number of leaves of control plants and the effect (difference between untreated and treated in days) of GA_{4+7} on length of the harvest period of cv Delira (A) and cv Elgon (B). Numbers attached to the points in the Figure are crop numbers (Table 1).

The estimates for the coefficients of the polynomials for respectively H10 and H50 (Fig. 1) indicate an effect of GA_{4+7} application on length of the harvest period. A GA_{4+7} application reduced HP in many crops (Fig. 2), in particular of cv Elgon. From the experiment in 1986, it can be concluded that a GA_{4+7} treatment reduced HP significantly ($P<0.05$) in 4 out of 5 crops of cv Elgon and in 2 crops a significant effect of time of application was found (Table 2). GA_{4+7} concentration did not have a significant effect on HP. Although a GA_{4+7} application reduced HP in all crops of cv Delira in 1986, there was no significant effect in any crop.

Final number of leaves

The final number of leaves of treated plants of cv Delira was only determined in 1986. A GA_{4+7} application reduced the final number of leaves significantly ($P<0.05$) in all crops (Table 2). Only in 1 out of 5 crops the time of GA_{4+7} application had a significant effect on the final number of leaves.

Size grade and quality

Harvested curds were graded according to diameter and curds harvested with the largest diameter were of Grade 6. The proportion of curds of this size class varied for the different crops and its percentage was plotted against the mean final number of leaves of the corresponding control plants. In general the proportion of Grade 6

increased at increasing final number of leaves, with the exception of a number of crops grown in 1984 which had a very low percentage of Grade 6 (< 10 %) (Fig. 3). The proportion of curds of Grade 6 was hardly influenced by a GA_{4+7} treatment when GA_{4+7} was applied to crops of cv Elgon. GA_{4+7} reduced curd size when applied to cv Delira crops with a lower final number of leaves (Fig. 3).

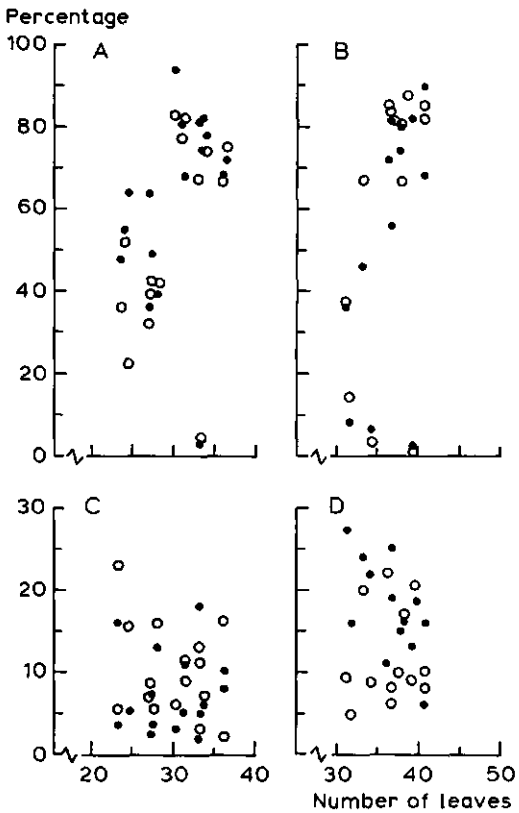

Figure 3
Relationship between the final number of leaves of the control plants and curd size (percentage of curds Grade 6) (A,B) and curd quality (proportion of curds in class II) (C,D) of cv Delira (A,C) and cv Elgon (B,D) for untreated (●) and treated (○) plants.

Curd quality (expressed as the proportion of curds of quality Grade II) was in particular affected negatively, if GA_{4+7} was applied to crops of cv Delira with a low final number of leaves. Quality in the crops with a low final number of leaves was mainly reduced by green tips of a few low order bracts growing through the surface of the curd. A GA_{4+7} application improved curd quality of cv Elgon in many crops, as it suppressed bracting.

Discussion

Variation in length of the growing period from crop-to-crop is mainly the result of a variation in the time of curd initiation (Booij, 1987; Grevsen, in press). Time of curd initiation depends on the end of the juvenile phase (i.e. when a certain number of leaves is initiated (Hand & Atherton, 1987)) and the temperature during the subsequent induction period (Booij, in press). With increasing temperature length of the induction period increases, curd initiation is retarded and the final number of leaves increases. As the final number of leaves is fixed at the time of curd initiation, the mean final number of leaves of a crop can be regarded as a measure for the temperature conditions during curd induction and for the delay of curd initiation of the considered crop. As GA_{4+7} can accelerate curd induction (Booij, 1989), the advancement of maturity after a timely GA_{4+7} application is supposed to be more on crops which should have initiated a high final number of leaves without a GA_{4+7} application. The difference between the final number of leaves of untreated plants and the number of leaves initiated at the time of application is a measure for the advancement towards

curd initiation of the crop at that time. In the present experiments GA_{4+7} affected the number of days between transplanting and maturity more, when the advancement towards curd initiation was less (difference in number of leaves high) at the time of application (Fig. 1). In this context the end of juvenility needs to be regarded, as an application of GA_{4+7} before the end of juvenility is expected to be less or not at all effective. The end of juvenility was determined to be for cv Delira at about 17 leaves initiated and for cv Elgon at about 19 leaves initiated (Booij, in press). From Table 1 can be concluded that the first GA_{4+7} application was in most crops after or just before the end of juvenility. At higher differences in the number of leaves (Fig. 1C,D) the effect of GA_{4+7} on length of the growing period was less again, so probably GA_{4+7} could not subsitute completely the temperature requirement for induction, especially when temperatures were highest. Despite the significant correlation between the difference in the number of leaves and the effect of GA_{4+7} on length of the growing period, there was still a considerable residual variation (Fig. 1).

Although the length of the growing period could be significantly reduced there was still a considerable variation in length of the growing period of the separate crops (Table 2) and in the final number of leaves in treated crops (Table 2). Especially the last indicates that a constant length of the curd induction period could not be obtained by a GA_{4+7} application.

However, a constant length of the growing period could not be achieved, because crops varied in time on which juvenility ends (Table 1) and a GA_{4+7} application did not result in a constant length of the induction period (Table 2). So it does not seem sensible to apply GA_{4+7} to all crops as a kind of common practice. As the time of maturity is related to the time of curd initiation, the harvest pattern during the season can be predicted from the pattern of curd initiation. A decision about applying GA_{4+7} to a certain crop can be based on the pattern of curd initiation until that moment and the expected number of curds to be initiated during the next days, using information about the developmental stage and the temperature during the preceding period and the expected temperature during the next period.

The relation between curd size and final number of leaves (Fig. 3) is in agreement with the results of Wurr et al. (1988). There was only an effect of GA_{4+7} on curd size in crops of cv Delira that had initiated curds at a low number of leaves (Fig. 3A); the reduction in size is likely due to a further reduction in final number of leaves by GA_{4+7}. A reduction in final number of leaves, as a result of an earlier curd initiation, will have a larger impact on curd size at a low final leaf number, when the risk of buttoning is more obvious.

Quality was reduced, when GA_{4+7} was applied to crops of cv Delira with a low final number of leaves (Fig. 3), mainly because of the appearance of a few large green bracts at the bottom of the curd. This is problably not caused by a stimulation of bract growth, but due to the reduction of the final number of leaves. Rate of increase in length of a leaf primordium decreases at increasing leaf number (Booij & Struik, in press), therefore the relation between the bract and the secondary primordium in its axil will depend on the total number of leaves initiated at the time the first secondary primordia are initiated. When the final number of leaves is reduced, due to GA_{4+7}, on crops with a low final number of leaves, the appearance of large bracts at the bottom of the curd is more likely.

It seems that GA_{4+7} can reduce bracting as it has occurred in a number of crops of cv Elgon (Fig. 3). Cv Elgon is susceptible to bracting which can be induced by high temperature (Fujime, 1983) or ethephon (Chapter 8). It should be interesting to study these interrelations and the prospects of using GA_{4+7} as a tool in preventing bracting more in depth.

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Chapter 8

Induction of bracting in cauliflower with 2-chloro-ethylphosphonic acid (ethephon)

In press: Euphytica.

Induction of bracting in cauliflower with 2-chloro-ethylphosphonic acid (ethephon)

Summary

Bracting (i.e. bracts of the inflorescence growing through the surface of the curd) is a serious problem in commercial growing of cauliflower. Ethephon enhanced bracting; an application was most effective when nearly all the plants in the crop had initiated a curd. When ethephon was applied 7 to 10 days later the effect diminished again and it was also small when applied when only a few curds had been initiated. Bracting increased continuously over the applied range (0 to 960 mg l^{-1}) of concentrations. There was an interaction with temperature during the early curd growth. Higher temperatures increased the effectiveness of ethephon.

After an ethephon application significant differences between cultivars were observed in the extent of bracting. For screening cultivar differences in resistance against bracting, an ethephon application (240 mg l^{-1}) when nearly all plants had initiated a curd, appeared to be best.

Introduction

The first visible indication of cauliflower curd initiation is the formation of secondary primordia in the axils of the uppermost leaf primordia. These secondary primordia will become the main branches of the curd. Later, third- and higher order branches are initiated from their respective shoot apices. This process of repetitive branching results in an enormous number of shoot apices covering the surface of the curd (Sadik, 1962).

During the early development of the inflorescence the branches are initiated in the axils of leaf primordia, however, these leaf primordia will now develop into bracts rather than foliages leaves. In the younger parts of the curd the bracts are only rudimentary. Under suitable conditions these bract initials can develop further and when this happens on a large scale the curd will get a hairy appearance and will be declassified. Bracts of lower order branches of the infloresence can expand to such an extent that their tips grow through the outskirts of the curd and will even turn green. The visibility of bracts at the surface of the curd is referred to as bracting.

Bracting is promoted by high temperatures (Nieuwhof, 1969; Fujime, 1983) and can also be induced by ethephon (Booij, 1989). There are genotypical differences regarding the bracting disorder (Crisp et al., 1975), and breeding for low sensitivity to bracting is possible. However, selection in the field is complicated by the influence of the environment on the expression of bracting. The aim of the present study was to determine the effect of concentration and time of application of ethephon on bracting; as Booij (1989) only noticed the effect of ethephon. The effect of ethephon application was studied with four different cultivars, to study genotypical differences in resistance against ethephon induced bracting.

Materials and methods

The trials were carried out in 1984, 1986 and 1987 at the Research Station for Arable Farming and Field Production of Vegetables (PAGV) in Lelystad, the Netherlands, on a fertile marine clay soil. Transplants were grown in cold frames in 1984 and in an unheated glasshouse in 1986 and 1987. Five to six week old bare rooted transplants were transplanted by hand in the field at a plant density of 3.03 m^{-2}. Transplanting dates were 1984-07-04, 1986-07-04 and 1987-06-19 respectively. The crops were treated as in commercial practise. Samples (18 plants) were taken from untreated plots at regular intervals, to determine the time of curd initiation. In all experiments the following cauliflower cultivars were included: Delira (Rijk Zwaan, De Lier, NL); Fortuna (Rijk Zwaan, De Lier, NL); Elgon (Royal Sluis, Enkhuizen, NL) and Andes (Royal Sluis, Enkhuizen, NL).

In 1984, a preliminary experiment (experiment 1) was carried out, in which an unreplicated split-split-plot design was used. The main plot (cultivar) was split into 5 subplots (time of application and control) and each treated subplot was split into 4 sub-subplots (concentration). Each sub-subplot consisted of 8 plants. Time of application depended on the development of the crop and was determined for each cultivar separately. The first application was given when 80 to 100 % of the plants had initiated a curd (T2), the following respectively 10 to 12 (T3), 21 to 24 (T4) or 28 to 31 (T5) days later. Ethephon was applied at a concentration of 120, 240, 480 or 960 mg l^{-1}.

In 1986 (experiment 2) and 1987 (experiment 3), a 3 replicate split-plot design was used in which cultivar was the main plot. The main plot was split into a control plot and all combinations of application time and concentration. Each subplot consisted of 8 plants. The first ethephon application was when 10 to 20 % of the plants had initiated a curd (early curd initiation) (T1); the second when 80 to 100 % of the plants had initiated a curd (late curd initation) (T2) and the third 7 to 10 days after late curd initiation (T3). Ethephon concentrations were 120, 240, 480 or 960 mg l^{-1}.

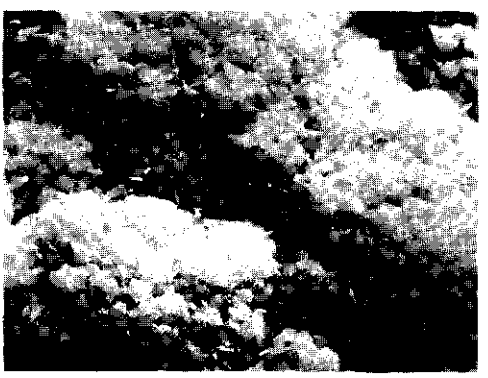

Figure 1
Curd surface with severe bracting (score 5).

Ethephon was dissolved in water and wetting agens (Cytowet) was added to a concentration of 0.25 mg l^{-1}. Each plant of a plot was treated separately with a propane-driven sprayer at a constant overpressure of 0.1 MPa. The dose per plant was 15 to 18 ml of the solution. Plants were scored for bracting when their curds were at a marketable stage using a scale of 0 (bract free) to 5 (severe bracting) (Figure 1). The mean scores of 8 plants per plot were subjected to an analysis of variance (ANOVA) using GENSTAT (Lane et al., 1987).

Results

Experiment 1

Variability due to growing conditions in this experiment, confines the possibilities to draw conclusions. The time on which about 90 % of the plants had initiated a curd was reached for cv Fortuna 38 days, for cv Delira 41 days and for the cvs Andes and Elgon 44 days after transplanting. Therefore application times were different for the cultivars.

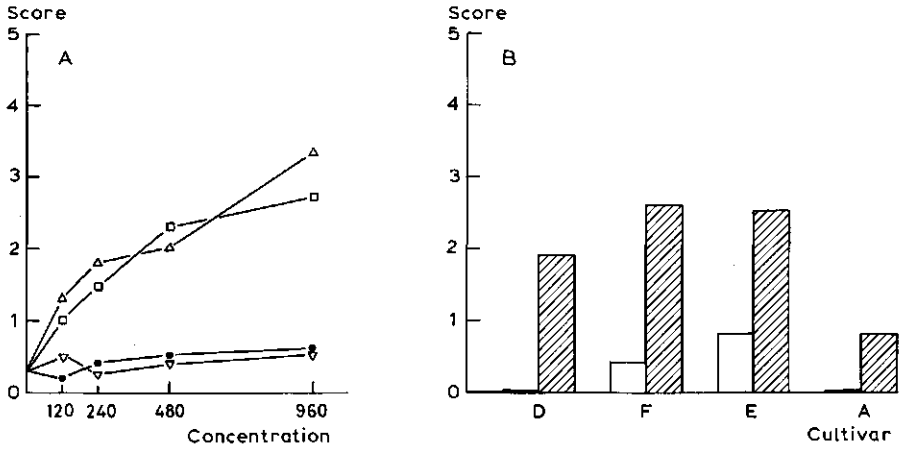

Figure 2

A. Effect of ethephon concentration (mg l^{-1}) on mean bracting score in relation to time of application (△T2; □ T3; ● T4; ▽ T5). Each point represents the mean of the four cultivars used. Application time T2: late curd initiation; T3: 10-12 days after T2; T4: 21- 24 days after T2; T5: 28-31 days after T2. (Experiment 1)

B. Effect of cultivar (D: Delira; F: Fortuna; E: Elgon; A: Andes) on mean bracting score for treated (hatched) and untreated plants. The bracting score was averaged over the four ethephon concentrations of the first two application times for treated plants. (Experiment 1)

In Figure 2A the effect of time of application and concentration is presented averaged over the 4 cultivars. Ethephon application enhanced bracting considerably when applied at late curd initiation or 10 days later, but there was hardly any effect when applied 23 or 30 days after late curd initiation (Fig. 2A). At the first two times of application, bracting increased at increasing concentration (Fig. 2A). No bracting was observed in the control plots of the cvs Andes and Delira, but when ethephon was applied bracting was obvious (Fig. 2B). Bracting was highest for the cvs Elgon and Fortuna, as well for the treated as for the untreated (Fig. 2B).

The mean daily temperatures were very high during the first period of curd growth and dropped to a lower level during the later part of the curd growing period (Table 1).

Table 1.
Mean temperature (°C) during the first 3 week period after late curd initiation (I) and the following 3 week period (II) during the experiments of 1984, 1986 and 1987.

Year	Experiment	Period	
		I	II
1984	1	17.7	13.6
1986	2	15.1	11.3
1987	3	14.5	16.7

Table 2.
Time of ethephon application (days after transplanting, (DAT)) and percentage (%) of plants having initiated a curd and mean curd diameter (mm) at the time of application and final number of leaves. (Experiment 2 and 3)

Cultivar	Application time [a]									Final leaf number
	T1			T2			T3			
	DAT	%	Diam.	DAT	%	Diam.	DAT	%	Diam.±SE	
Experiment 2										
Andes	25	16	0.63	32	88	1.13	42	100	8.4±3.33	31.4
Delira	27	21	0.63	34	53	2.01	42	100	4.7±3.79	31.2
Fortuna	25	23	0.65	32	85	1.21	42	100	8.8±4.50	33.4
Elgon	25	21	0.65	32	91	1.05	42	100	5.3±3.19	37.2
Experiment 3										
Andes	28	12	0.65	39	100	1.91	46	100	5.3±2.37	37.4
Delira	35	41	0.68	42	100	1.34	49	100	4.9±1.94	32.2
Fortuna	35	24	0.57	42	100	1.34	49	100	4.1±1.29	35.5
Elgon	35	22	0.92	42	93	0.89	49	100	2.3±1.08	40.0

[a] T1: early curd initiation; T2: late curd initiaton;
T3: 8 to 10 days after late curd initiation.

Experiments 2 and 3

The differences in developmental rate between cultivars were relatively small in both experiments (Table 2), so that the differences in application times were small. From an analysis of variance of bracting score per concentration, the residual variances appeared to be not homogeneous. Therefore a weighted analysis of variance was carried out for the complete experiment, in which units were weighted per concentration proportional to the reciprocal of the expected residual variance. In both experiments significant effects ($P \leq 0.001$) of cultivar, ethephon application time, ethephon concentration and interactions between these three variates were apparent (Table 3).

Table 3.
Results of an analysis of variance of bracting score for experiment 2 (1986) and experiment 3 (1987). (d.f: degrees of freedom; m.s.: mean square; v.r.: variance ratio).

Source of variation	d.f.	Experiment			
		2		3	
		m.s.	v.r.	m.s.	v.r.
Replicates	2	0.75		0.84	
Cultivar	3	30.55	21.03 ***	204.76	242.31 ***
Residual	6	1.45		0.85	
Treated vs untreated	1	63.63	47.31 ***	67.54	81.03 ***
Within treated:					
cultivar	3	7.46	5.55 ***	16.31	19.56 ***
time	2	14.47	10.76 ***	31.96	38.34 ***
concentration	3	48.47	36.03 ***	58.96	70.73 ***
time*concentration	6	38.09	6.35 ***	11.08	13.29 ***
cultivar*time	6	5.89	4.38 ***	5.36	6.43 ***
cultivar*concentration	9	2.94	2.19 *	3.54	4.24 ***
cultivar*time*concentration	18	3.70	2.75 ***	1.05	1.26
Residual	95	1.35		0.83	
Total	154				

* $0.01 < P \leq 0.05$
** $0.001 < P \leq 0.01$
*** $P \leq 0.001$

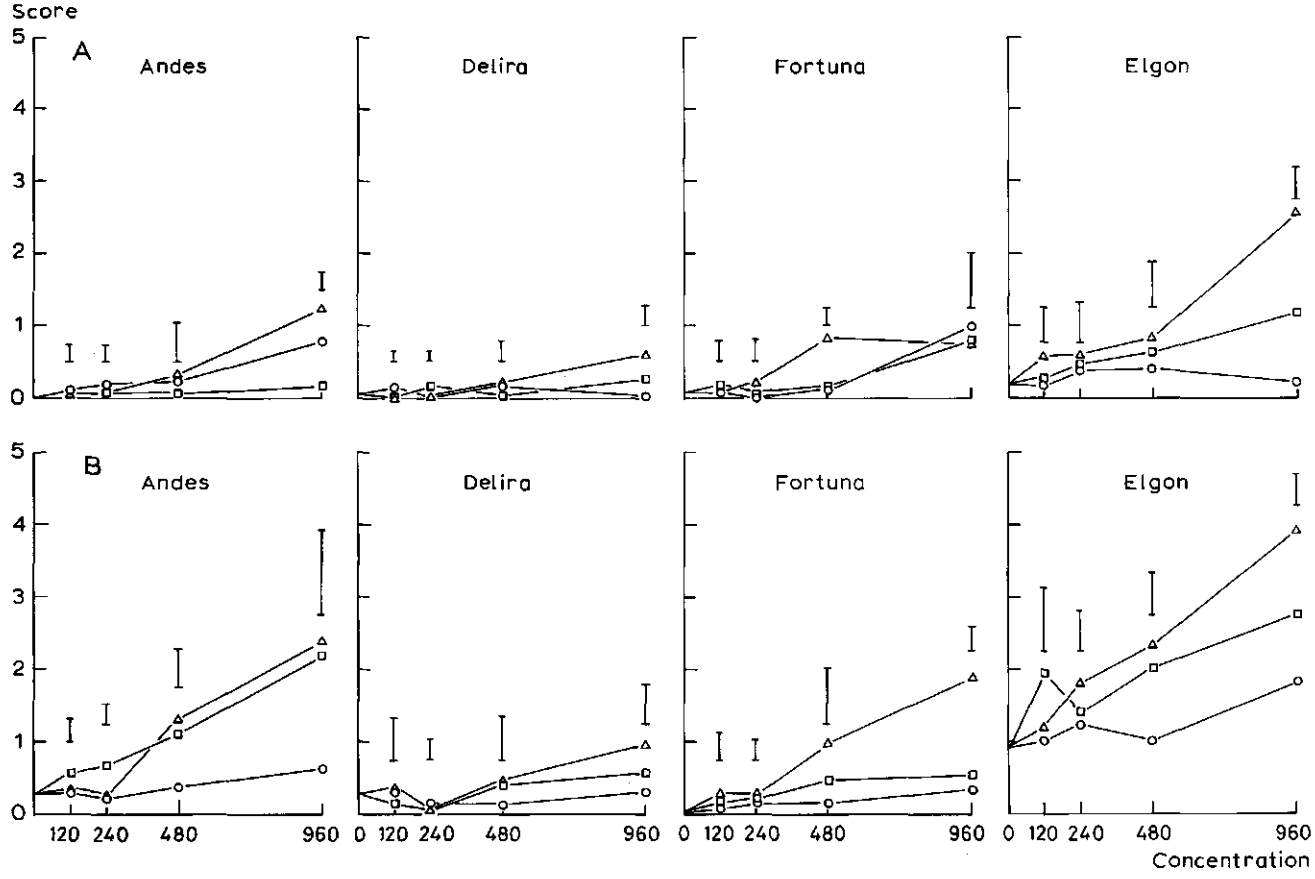
Score
A
Andes
Delira
Fortuna
Elgon
B
Andes
Delira
Fortuna
Elgon
0
1
2
3
4
5
120 240 480 960
0 120 240 480 960
Concentration

Figure 3
Effect of ethephon concentration (mg l^{-1}) on bracting score in relation to time of application (○T1;△T2;□T3) and cultivar for experiment 2 (A) and 3 (B). Vertical bars indicate LSD.05. Application time T1: early curd initiation; T2: late curd initiaton; T3: 8-10 days after late curd initiation.

In Figure 3 the effects of cultivar, application time and concentration are shown for both experiments. The overall score for bracting was considerably lower in experiment 2 than in experiment 3. In both experiments cv Elgon responded most strongly to the ethephon application and cv Delira least. The bracting score increased with ethephon concentration, but this increase differed depending on the application time. The effect of ethephon was lowest when applied at early curd initiation and highest when applied at late curd initiation. An application 7 to 10 days after late curd initiation resulted again in less bracting. In the control plants some bracting occurred, most intensively with cv Elgon (Fig. 3)

The screening ability of an ethephon application for genotypic differences regarding sensitivity for bracting was determined by calculating the heritability ($h^2 = \sigma_g^2/(\sigma_g^2 + \sigma_e^2)$) for each treatment. In summary, the highest heritability was obtained when ethephon was applied at late curd initiation or at a concentration of 240 mg l^{-1} (Table 4).

Table 4.
Effects of ethephon treatments (concentration and application time) on the heritability (h^2) of bracting, for the combination of experiments 2 and 3.

Application time [a]	Concentration (mg l^{-1})				
	120	240	480	960	Mean
T1	0.37	0.79	0.62	0.27	0.51
T2	0.79	0.77	0.64	0.94	0.79
T3	0.62	0.73	0.70	0.64	0.67
Mean	0.59	0.76	0.65	0.62	

[a] T1: early curd initiation; T2: late curd initiaton; T3: 8 to 10 days after late curd initiation.

During curd growth (after 90 % of the plants had initiated a curd (T2)), the mean day temperatures were higher in experiment 3 (Table 1), in particular in the second part.

Discussion

Induction of the cauliflower inflorescence is promoted by low temperatures, while high temperatures can retard or even prevent curd initiation (Aamlid, 1952; Wiebe, 1972; Atherton et al., 1987; Booij, 1987). Plants growing at temperatures just below the maximum temperature for curd induction, form curds with vegetative structures (large bracts) or even vegetative growth can again predominate and vegetative shoots are

formed on the inflorescence (Nieuwhof, 1969). Higher temperatures can induce bracting especially when occurring during the early period of curd growth (Fujime, 1983; Wiebe, 1973a,b). Also ethephon could induce bracting, especially when applied shortly after curd initiation (Fig. 2, Fig. 3). Just as higher temperatures, ethephon applications can delay curd initiation under certain conditions (Booij, unpublished). There seems to be a similarity between the effect of ethephon and of higher temperatures. Bracting can be considered to a minor extent as a partial reversion from the generative to the vegetative stage.

The extent of bracting due to an application of ethephon was different for the three experiments, possibly the result of temperature differences during curd growth. Especially during experiment 2 (1986) temperatures were low (Table 1) and the overall score for bracting was low too. In experiment 1 (1984) daily mean temperatures during the early curd growth were high (Table 1) and the mean bracting score due to an ethephon application at late curd initiation was highest in this experiment. So it is likely to assume an interaction between the prevailing temperatures during curd growth and the effect of ethephon. However, more research is needed to clarify this relation.

Gibberellins are able to induce curd initiation when the the initiation is retarded due to higher temperatures (Booij, 1989). It would therefore be interesting to study the effect of gibberellins on bracting, as antagonistic effects of gibberellins and ethylene are known (Bruinsma, 1983).

The presence or absence of bracts strongly depends on the environment (site, season) (Crisp et al., 1975), which can interfere with the selection against this disorder. In the present experiments differences between cultivars were recorded, also when no ethephon was applied (Fig. 2B, Fig. 3A,B), and the differences depended on the experiment. Cultivars can be better discriminated in the field regarding sensitivity for bracting by an ethephon application, although there is still an interaction with temperature, as is shown in the present study. The significance of the ethephon test can be assessed by comparing the cultivars under a range of environments or by using the tissue culture method developed by Crisp & Gray (1979). The optimal time of ethephon application, namely shortly after curd initiation, can complicate the use for selection purposes, as cauliflower lines (c.q. cultivars) often differ in earliness, due to differences in time of curd initiation. So when a range of lines is to be screened it is necessary to determine the curd initiation time of the single lines. A similar problem can be the variability in time of curd initiation within a population, therefore it is questionable whether the test can be used for selection of individual plants. To what extent this can be avoided by applying ethephon more than once needs to be examined.

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Chapter 9

Final remarks

Final remarks

Some relations between the environment, plant growth, plant development and cultivation are given in Figure 1. The increase in biomass (growth) and development of the plant are regarded, within certain limits, as two fairly independent processes. The time at which the different phase transitions occur, will affect the time of curd maturity. Variation in time of transition within a population of plants (crop) will influence the period during which plants within a crop mature, while the time at which single populations reach maturity during the season influences the total production per unit of time of an individual farm.

Temperature plays a predominant role in controlling developmental rate. The influence of temperature, however, is different for the various developmental steps involved. The main switch in plant development is the initiation of the curd. The process preceding curd initiation, namely induction of the curd is the most temperature sensitive part during development and negatively related to temperature. Developmental rate will determine mainly time at which the curd should be harvested, while growth rate and the time plants are allowed to grow (until harvest) determine the amount of product to be harvested.

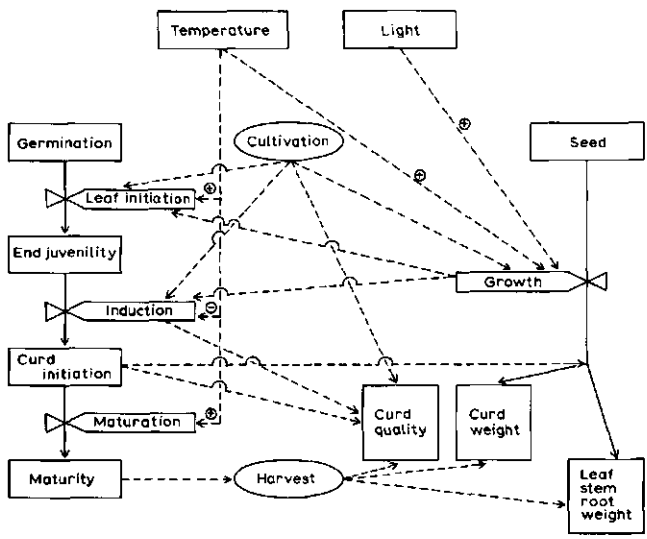

Figure 1
Relations between the plant environment, growth, development and cultivation.

In the following part the mutual relation between development and cultivation is discussed regarding *i*) length of the growing period of a crop, *ii*) length of the period

during which plants mature within a crop (harvest period) and *iii*) curd size and quality at harvest.

Length of the growing period

Variation in length of the growing period from crop-to-crop is mainly due to variation in time of curd initiation (Chapter 2). Therefore the crop-to-crop variation in length of the growing period can be reduced by controlling time of curd initiation of the individual crop. Time at which juvenility ends and temperature in the succeeding period determine time of curd initiation (Chapter 2).

The end of juvenility is characterized by the number of initiated leaves (Chapters 3 and 4), so leaf initiation rate affects time at which the juvenile phase is completed. Leaf initiation rate can be relatively low directly after transplanting, due to a slow resumption of growth. This check will depend upon the change in growing conditions from nursery conditions to the field. Although growing conditions after transplanting will have a large impact on leaf initiation rate, the variation in time at which juvenility ends, can be reduced by using transplants of the same physiological age (number of initiated leaves) for each crop and by applying a transplant raising system, wich reduces the risk of a transplant check.

Another approach could be to look for a method to manipulate the length of the juvenile phase, so that the plant can be forced to become sensitive to the inductive stimulus at a set time. To make the plant sensitive to the inductive stimulus at a younger physiological age (number of initiated leaves) is not desirable, because of the risk of buttoning (Chapter 5).

Length of the developmental phase after the end of juvenility, during which the induction of the curd occurs, is very variable due to variation in environmental conditions experienced by the separate crops. The rate of induction decreases with increasing temperatures (Chapters 2, 3 & 4).

A low temperature treatment to satisfy the cold requirement before transplanting is only possible, when applied after the end of juvenility. This would require plants with a high number of initiated leaves (especially for late cultivars) and sufficient biomass (Chapter 5). Such plants are difficult to handle at transplanting and are likely to suffer more from the transplant shock. Therefore curd induction should be controlled **after** transplanting.

Curd induction is affected by GA_{4+7} applications (Chapters 6 & 7). Although GA_{4+7} can accelerate curd induction, they can problably not substitute completely the temperature requirement. It is also unlikely that they will result in the curd induction period to be independent of temperature. An additional option is to retard curd induction; applying ethephon is a possibility, but research in this direction was cancelled because of the risk of bracting (Chapter 8).

GA_{4+7} can be used to adjust timing of harvest to some extent, in case curd initiation is delayed due to high temperatures. For decisions concerning the adjustment it is necessary to have information about the developmental stage at the present time and about the expected situation in the near future. As the curd growing period is fairly constant during the summer season (Chapter 2), information about curd initiation is sufficient. The number of initiated curds can be estimated from the preceding temperature and leaf initiation rate (Chapters 2 & 3). The expected number of curds to be initiated during the following days can be based on temperature predictions in the

succeeding period. Data about leaf initiation are primarily necessary to estimate the end of juvenility.

As the curd maturation rate is fairly constant (Chapter 2), an early prediction of maturity time of a crop is possible, when time of curd initiation is known. Curd initiation in a crop can be determined by dissecting plants or estimated by using the relations given in de Chapters 2 and 3. A prediction of the supply at the market can be made by using the information about curd initiation obtained at a limited number of farms, because of the similarities in supply (Chapter 1).

Some remarks about the method used to establish the relation between development and environmental factors (Chapters 2 & 3) should be made. The results of the regression analysis, used to establish these relations, depend upon the range of conditions that occurred in the studied period and results are better applicable, when the range has been wider. Their use for predictive purposes will be restricted to the conditions for which the results were obtained.

Another problem is the mutual correlations between climatic factors, e.g. radiation and temperature. This caused some differences in the results of Chapters 2 & 3 regarding the explanation of length of the curd growing period. Irradiance could explain variability best (Chapter 2), but when two extra experimental years were included (Chapter 3) temperature was better. This discrepancy was due to the different relation between irradiance and temperature during one of the included experimental years. This means that correlation between irradiance and length of the curd growing period, as is described in Chapter 2, is a result of the correlation between temperature and length of the considered period.

Length of the harvest period

Many studies were undertaken to synchronize the development of the individual plants within a crop, with the once-over harvest as the ultimate goal. To obtain a synchronization of maturity of plants within a crop, all plants should initiate a curd at the same time. Juvenility of all plants should end at the same time and there should be no differences between plants in cold requirement, so that the duration of the induction period is similar for all plants. Within a population genetic differences may exist in end of juvenility, cold requirement and curd maturation rate. Cultivars, differing in earliness, vary in end of juvenility and/or cold requirement, but not in curd maturation rate (Chapter 2). However, genetic differences between plants of modern cultivars regarding cold requirement and juvenility are unlikely, also because the annual types usually inbreed. Variation within a crop regarding end of juvenility can be due to variation in growing conditions within a field, resulting in differences in time at which a certain number of leaves is initiated (Chapters 3 & 4). Minor differences in growth during juvenility can be magnified into large differences in curd initiation time due to variable weather conditions, because not all plants become responsive to inductive conditions at the same time (Chapter 3).

The complex influence of the environmental factors on harvest time of cauliflower make it difficult to control time of maturity. Due to these effects it is not likely that the use of hybrids will improve enormously the uniformity in time of maturity, although the prospects will be more promising under less variable conditions.

Salter and co-workers at the Institute of Horticultural Research Wellesbourne studied comprehensively the effect of a low temperature treatment of plants before

transplanting to satisfy the cold requirement for curd induction, so that induction should be independent of conditions in the field. In many crops they found a reduction in length of the harvest period due to the treatment, but the variation was still considerable. Although juvenility was not mentioned, it is most likely that plants were treated before the end of juvenility and the results were problably due to the chosen experimental set-up. Cold treated and untreated plants were sown and transplanted at the same time, but while plants were cold treated the untreated remained on the seedbed. As was shown in Chapter 5 continued growth on the seedbed resulted in a higher plant-to-plant variability and a longer period during which individual plants mature within a crop.

Prediction of the plant-to-plant variation in time at which phase transitions occur within a crop will be difficult because these will be mainly due to natural variation in growth conditions within a field. However, if information about the variability in end of juvenility within a crop is available, the variation in curd initiation can be estimated (Chapter 3). A fairly accurate estimate of the end of juvenility can be made by counting the number of visible leaves of a sample, because the number of visible leaves provides a good prediction of the total number of initiated leaves (Chapters 3 & 4).

Curd size and quality

Two quality defects under investigation can be related to development, namely bracting and buttoning.

Bracting can be induced by high temperatures or ethephon (Chapter 8). The risk of bracting can be reduced by growing less sensitive cultivars, as genetic differences are obvious (Chapter 8). Another option can be an application of GA_{4+7}, in case bracting is likely to occur due to suitable conditions for its induction (Chapter 7).

Buttoning can be related to time of curd initiation and the biomass of the plant at that time (Chapter 5). This disorder can be avoided by transplant plants that have initiated a small number of leaves and by using cultivars with a long growing period. However, the grower wants often the earliest possible harvest at the start of the season. As differences in length of the growing period of cultivars are due to differences in time of curd initiation (Chapter 2), it might be impossible to breed cultivars that can be harvested early (short growing period) and which have a small risk of buttoning.

Growth conditions after curd initiation can also influence curd weight; in this case the effect of cultivation will be substantial. Factors like plant density, nitrogen fertilization and soil tillage will have large effects, because maturation rate will be hardly influenced by these factors (Chapters 1 & 5).

In conclusion, the combination of variation of environmental conditions in time and the distinghuised developmental phases the plant has to go through before curd maturity is reached, make it difficult to control timing of harvest and quality of the produce. However, knowledge about the critial steps involved make it possible to take cultural measures reckoning with the effects of environmental conditions and the developmental stages.

Summary

The number of cauliflower heads, which are supplied at the market varies enormously from day-to-day during the season. The relative deviation from the mean is much higher for cauliflower than for other products. Also on the individual farms a strong variation in daily production is observed. The variation in daily production is due to a crop-to-crop variation in length of the growing period and in length of the period during which plants mature within a crop.

The edible part (curd) of the cauliflower plant is an inflorescence and therefore the plant should pass the transition from the vegetative to the generative phase. Development of the plant plays an important role in time of maturity of the curd and three distinct phases can be recognized between transplanting and harvest, being the juvenile phase, the curd induction phase and the curd growing phase. The aim of the present study is to describe the effect of the environment (mainly temperature) on plant development in the field and how developmental rate affects time of curd maturity, curd yield and quality. Moreover the possibilities to manipulate the development of the crop by means of growth regulators are indicated.

Results, gathered during several years from a number of crops, showed that the variation in time between transplanting and curd initiation was higher than in time between curd initiation and maturity. As the cauliflower plant has a determinate inflorescence the number of leaves is fixed at the time of curd initiation and this so called final number of leaves was regarded as the physiological age (number of plastochrons) at which the curd was initiated. The end of juvenility was characterized by the number of initiated leaves.

Time between transplanting and curd initiation could be split into two periods, namely *i*, between transplanting and the time on which juvenility ended and *ii*, the succeeding period until curd initiation. The mean temperature during the last period could explain the variation in length of this period and in mean final number of leaves of a crop. Both increased at increasing temperature. The final number of leaves could be explained best by the temperature after the end of juvenility, when the end of juvenility of the studied cultivars was set on 17-19 initiated leaves. The end of juvenility was also established by transferring plants from weak to strong curd inducing temperature conditions in dependence on the number of initiated leaves at the time of the transfer. The final number of leaves was hardly affected when the plants were transferred before the end of juvenility; when transferred after the end of juvenility the final number of leaves increased at increasing number of initiated leaves at the time of the transfer. The value for the number of initiated leaves characterizing the end of juvenility was in close agreement with the value found by the regression method using field data.

Especially crops grown during the summer season showed little variation in length of the period between curd initiation and curd maturity; for crops grown later in the season the length of the period increased when the curds were initiated later.

Within a crop not all plants initiated curds at the same time. This resulted in a variation in diameter of young curds within a crop. From single plants within a crop, time of curd initiation and time of end of juvenility was estimated. The variation in time of curd initiation within a crop correlated weakly with the variation in time on which plants

reached the end of juvenility. In most crops the variation in time of curd initiation was larger, but in a number of crops the variation was smaller than the variation in end of juvenility.

Because not all plants within a crop reached the end of juvenility at the same time and temperature conditions changed rapidly, not all plants within a crop experienced the same temperature after juvenility, so that variation increased or decreased. The length of the period during which plants within a crop matured, correlated positively with the length of the period during which plants had initiated curds. As not all plants within a crop initiated curds at the same time and temperature fluctuated, not all plants within a crop experienced the same temperature during curd growth, which resulted in differences in length of the growing period of plants within a crop.

Curd size and time of curd maturity could be regarded as two independent variables as the time between initiation and maturity was the same for curds of buttoning plants and of normal plants. Especially plants with a high number of initiated leaves produced small curds, when cold treated at the seed bed. Curd and leaf weight at the time of maturity depended on plant weight at the time of curd initiation. When plants with a low number of initiated leaves were cold treated, curd initiation was not affected because plants were still juvenile at that time.

To synchronize curd maturity within a crop or to control length of the growing period of crops, time of curd initiation should be controlled. A number of growth regulators was applied to study the effect on length of the period between transplanting and maturity. GA_{4+7} reduced the length of the growing period, if applied after the juvenile phase has passed and curd initiation was delayed due to high temperatures. It was most effective when applied twice at a concentration of 80 mg l^{-1}. That curd induction was influenced by GA_{4+7} applications was shown by the reduction in final number of leaves of treated crops.

Harvest was more advanced when G_{4+7} was applied on crops with a high final number of leaves, but the effect decreased when the difference between the number of initiated leaves at the time of application and the final number of leaves of a crop decreased. Although GA_{4+7} could reduce length of the growing period, a constant length of the growing period of all crops was not obtained. First, because the juvenile phase did not end at the same time for all crops and second, because GA_{4+7} was not able to equalize the length of the induction period of all crops.

Ethephon could induce severe bracting when it was applied just after all curds in a crop had been initiated. The phenomenon can also be induced by high temperatures. Genetic differences in sensitivity for bracting, induced by ethephon, were obvious.

Synchronizing maturity of plants within a crop is discussed in relation to rapidly changing environmental conditions and cultural measures. Prospects of controlling the length of the growing period when GA_{4+7} is used and its possible role in timing of harvest are analysed.

Samenvatting

Het aantal bloemkolen dat op de veilingen wordt aangevoerd wisselt gedurende het seizoen sterk van dag tot dag. De relatieve afwijkingen ten opzichte van het gemiddelde zijn groter voor bloemkool dan voor andere produkten. Ook per bedrijf wordt een sterke variatie in het aantal geoogste kolen waargenomen. De variatie in het aantal te oogsten kolen per dag is een gevolg van verschillen in groeiduur en lengte van de oogstperiode van de afzonderlijke teelten.

Het eetbare deel van de bloemkool plant is een bloemgestel en daarom is de overgang van de vegetatieve naar de generatieve fase noodzakelijk. De ontwikkeling van de plant speelt een belangrijke rol ten aanzien van het moment van oogstrijpheid van de kool. Tussen het tijdstip van het planten en van oogstrijpheid kunnen drie stadia worden waargenomen: de jeugdfase, de koolinductiefase en de koolgroeifase. Het doel van dit proefschrift is aan te geven hoe de ontwikkeling van de plant in het veld beïnvloed wordt door omgevingsfactoren en hoe de ontwikkelingssnelheid van invloed is op het tijdstip van oogstrijpheid van de kool, de koolopbrengst en de koolkwaliteit. Daarnaast wordt aangegeven in hoeverre de ontwikkeling met behulp van groeiregulatoren te sturen is.

Resultaten van verschillende teelten gedurende enkele jaren, lieten zien dat de variatie in duur van de periode vanaf het tijdstip van planten tot koolaanleg groter was dan de variatie in duur van de periode tussen koolaanleg en oogstrijpheid van de kool. Daar de bloemkoolplant een eindstandig bloemgestel heeft, is het totaal aantal bladeren vastgelegd op het moment dat de kool wordt aangelegd. Dit totaal aantal afgesplitste bladeren werd beschouwd als de fysiologische leeftijd (aantal plastochrons) waarop de kool was aangelegd. Het einde van de jeugdfase van een plant werd gekarakteriseerd door het aantal afgesplitste bladeren.

De periode tussen het planten en de koolaanleg kon worden verdeeld in twee delen, namelijk (1) tussen planten en het moment waarop de jeugdfase werd beëindigd en (2) de hierop volgende periode tot koolaanleg. De gemiddelde temperatuur gedurende het tweede deel kon de variatie in lengte van de betreffende periode en in het totaal aantal bladeren van de betreffende teelt in belangrijke mate verklaren. Beide namen toe bij toenemende temperatuur. Het totaal aantal bladeren kon het best worden verklaard door de temperatuur na het einde van de jeugdfase, als het einde van de jeugdfase van de bestudeerde rassen op 17-19 afgesplitste bladeren werd gesteld. Het einde van de jeugdfase werd ook bepaald door planten van zwak naar sterk kool inducerende omstandigheden over te brengen bij verschillend aantal afgesplitste bladeren. Het totaal aantal bladeren werd nauwelijks beïnvloed als de planten werden overgeplaatst voordat de jeugdfase was afgelopen; indien de overplaatsing daarna plaats vond nam het totaal aantal bladeren toe bij toenemend aantal bladeren op het moment van de overplaatsing. De gevonden waarde voor het aantal afgesplitste bladeren dat het einde van de jeugdfase karakteriseerde, was overeenkomstig de waarde verkregen uit veldgegevens.

Gewassen welke werden geteeld in de zomer vertoonden weinig variatie in lengte van de periode tussen koolaanleg en oogstrijpheid; later in het seizoen geteelde gewassen gaven een toename in duur van de periode te zien en wel meer naarmate de koolaanleg in het gewas later plaatsvond.

In een gewas legden niet alle planten op hetzelfde tijdstip de kool aan, hetgeen een variatie binnen het gewas in diameter van zich ontwikkelende kolen tot gevolg had. Het tijdstip van koolaanleg en het tijdstip waarop de jeugdfase van de afzonderlijke planten werd beëindigd kon worden geschat. De variatie in het tijdstip waarop koolaanleg plaats vond was zwak gecorreleerd met de variatie in het tijdstip waarop de planten in een gewas de jeugdfase beëindigden. In de meeste gewassen was de variatie in het tijdstip van koolaanleg groter dan de variatie in het tijdstip waarop de jeugdfase werd beëindigd, maar in een aantal gewassen was deze kleiner.

Omdat niet alle planten op hetzelfde moment het einde van de jeugdfase bereikten en de temperatuuromstandigheden wisselden, werden niet alle planten na het einde van de jeugdfase aan dezelfde temperatuur bloot gesteld, waardoor de variatie zowel kon toenemen als afnemen. De duur van de periode waarin binnen een gewas de kolen het oogstrijpe stadium bereikten was positief gecorreleerd aan de lengte van de periode waarin de kolen werden aangelegd. Daar niet alle planten binnen een gewas op hetzelfde moment tot koolaanleg overgingen en er temperatuur fluctuaties optraden, ontstonden er verschillen tussen planten aangaande de gemiddelde temperatuur gedurende de koolgroei, wat resulteerde in verschillen in lengte van de koolgroeiperiode.

Koolgrootte en het tijdstip van oogstrijpheid waren te beschouwen als twee onafhankelijke variabelen daar de lengte van de periode tussen koolaanleg en oogstrijpheid gelijk was voor boorders en normale planten. In het bijzonder gaven planten welke een groot aantal afgesplitste bladeren hadden een kleine kool, als deze een koude behandeling hadden gehad tijdens de opkweek. Kool- en bladgewicht bij oogstrijpheid was afhankelijk van het plantgewicht op het moment van koolaanleg. Als aan planten met een gering aantal afgesplitste bladeren een koude behandeling werd gegeven, dan werd het tijdstip van koolaanleg hierdoor niet beïnvloed, omdat deze planten zich op dat moment nog in de jeugdfase bevonden.

Om te komen tot een gelijktijdige oogstrijpheid binnen een gewas of tot beheersing van de lengte van de groeiduur van een gewas, is het noodzakelijk de koolaanleg te sturen. Een aantal groeiregulatoren werden getest, om het effect op de lengte van de periode tussen planten en oogstrijpheid te bestuderen. GA_{4+7} verkortte de groeiduur als deze werd toegediend na het einde van de jeugdfase en aan een gewas waarvan de koolaanleg werd vertraagd ten gevolge van hoge temperaturen. Het effect van GA_{4+7} was het grootst als het twee keer werd toegediend in een concentratie van 80 mg l^{-1}. Een kleiner totaal aantal bladeren tengevolge van de behandeling gaf aan dat het middel de koolinductie beïnvloedde. GA_{4+7} werd tevens getoetst op een aantal gewassen welke groeiden onder verschillende omstandigheden. De vervroeging van de oogstrijpheid, als gevolg van de GA_{4+7} toediening, was groter naarmate het totaal aantal afgesplitste bladeren van het betreffende gewas groter was. Het effect nam af bij een kleiner verschil in het totaal aantal bladeren en het aantal afgesplitste bladeren op het moment van toediening. De groeiduur van alle met GA_{4+7} behandelde gewassen werd niet constant, omdat de jeugdfase van de gewassen niet op hetzelfde moment

eindigde en GA_{4+7} niet in staat was de inductie periode zodanig te beïnvloeden dat de lengte hiervan constant werd.

Door toediening van ethephon kon doorwas worden geïnduceerd, als het werd toegediend juist nadat alle planten in een gewas een kool had aangelegd. Het verschijnsel kan ook door hoge temperaturen worden geïnduceerd. Er werden genetische verschillen aangetoond in gevoeligheid voor doorwas, geïnduceerd door ethephon.

Synchronisatie van oogstrijpheid binnen een gewas wordt besproken in relatie tot snel wisselende weersomstandigheden en tot teeltmaatregelen. Vooruitzichten ten aanzien van sturing van de groeiduur middels een GA_{4+7} toepassing en de rol van GA_{4+7} in de oogstplanning van bloemkool worden aangegeven.